Absolute seasonal temperature estimates from clumped isotopes in bivalve shells suggest warm and variable greenhouse climate

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Seasonal variability in sea surface temperatures plays a fundamental role in climate dynamics and species distribution. Seasonal bias can also severely compromise the accuracy of mean annual temperature reconstructions. It is therefore essential to better understand seasonal variability in climates of the past. Many reconstructions of climate in deep time neglect this issue and rely on controversial assumptions, such as estimates of sea water oxygen isotope composition. Here we present absolute seasonal temperature reconstructions based on clumped isotope measurements in bivalve shells which, critically, do not rely on these assumptions. We reconstruct highly precise monthly sea surface temperatures at around 50 °N latitude from individual oyster and rudist shells of the Campanian greenhouse period about 78 million years ago, when the seasonal range at 50 °N comprised 15 to 27 °C. In agreement with fully coupled climate model simulations, we find that greenhouse climates outside the tropics were warmer and more seasonal than previously thought. We conclude that seasonal bias and assumptions about seawater composition can distort temperature reconstructions and our understanding of past greenhouse climates.
Seasonal extremes were of vital importance for the evolution and distribution of life over geological history. The effects of greenhouse warming on seasonal variability in temperature and the hydrological cycle are still poorly constrained, while being of considerable interest for projecting future climate and its impact on the ongoing biodiversity crisis. Reconstructions of deep time (pre-Quaternary) greenhouse periods yield valuable insights into the dynamics of warm climates and the ecological response to forcing mechanisms such as rising atmospheric CO₂ levels. Accurate reconstructions are imperative to evaluate climate model predictions under dissimilar climate states. Particularly seasonal range is poorly constrained with little quantitative evidence. The warm, ice free Late Cretaceous period presents a valuable reference period to assess with little quantitative evidence. The warm, ice free Late Cretaceous climate exhibits limited temperature seasonality but is in fact biased to a particular annual mean condition but is in fact biased to a particular season. Since fossil species producing the material that constitutes SST archives may not have a close modern relative for proxy calibration, uncertainties about their growth seasons may unpredictably bias reconstructions. Seawater oxygen isotope composition (δ¹⁸Osw) is an important input parameter into the widely used carbonate δ¹⁸Oc temperature proxy, but it is highly variable across ocean basins and remains poorly constrained across geological timescales. Biases in assumed δ¹⁸Osw composition thus undermine SST reconstructions, especially those from highly variable epi-continental seas.

The advent of carbonate clumped isotope (Δ⁴⁷) SST reconstructions on a seasonal scale promises to eliminate these two biases. The clumped isotope thermometer yields accurate SST reconstructions independent of δ¹⁸Osw assumptions. It also allows the reconstruction of δ¹⁸Osw, yielding information about the local hydrological cycle, an important aspect of climate rarely constrained in deep time, rectifying biases in the popular carbonate δ¹⁸Oc temperature proxy. Recent advances in clumped isotope instrumentation and standardization have reconciled previous inter-lab disagreements and shown that many carbonate paleoarchives (e.g. foraminifera, bivalves, and eggshells) conform to the theoretical Δ⁴⁷ temperature calibration with negligible influence of isotope disequilibrium (see Supplementary Discussion). The large sample sizes required for individual Δ⁴⁷-based temperature estimates (>2 mg) have complicated paleoseasonality reconstructions using this accurate method, but a recently developed statistical approach enables its use for seasonality reconstructions.

Here we use clumped isotope analyses on microsampled (~100 µg) profiles through fossil bivalve shells to obtain, for the first time, absolute SST and δ¹⁸Osw seasonality reconstructions of a greenhouse climate. We apply this new method on well-preserved oyster (Rastellum diluvianum and Acutostrea incurva) and rudist (Biradiolites suecicus) shells from Campanian (78.1 ± 0.3 Ma) coastal localities of the Kristianstad Basin in southern Sweden (46 ± 3°N paleolatitude; see Fig. 1) and “Methods”). We compare these reconstructions with fully coupled climate model simulations of the Campanian greenhouse (see “Methods”) to explore their implications for Late Cretaceous greenhouse climate.

**Results**

All specimens showed clear seasonal δ¹⁸Oc fluctuations of −1.9°–0.0% in R. diluvianum, −2.0°–0.0% in A. incurva, and −2.7° to −1.0% in B. suecicus on which shell chronologies were based (see “Methods”). The assumption that periodic δ¹⁸Oc fluctuations reflect seasonality is demonstrated to be a valid basis for constructing in-shell chronologies in nearly all modern environments. Seasonal δ¹⁸O patterns show that the specimens record 3 (A. incurva and B. suecicus) to 6 (R. diluvianum) full years of growth. Clumped isotope analyses on small aliquots yielded Δ⁴⁷ ranges between 0.62–0.73% for R. diluvianum, 0.64–0.76% for A. incurva, and 0.63–0.75% for B. suecicus. Summaries of measurement results are displayed in Table 1.

Detailed step-by-step results of the data processing routine are shown in Fig. 2, in Supplementary Methods and Supplementary Figs. 2–3. Figure 2 and Table 1 show monthly Δ⁴⁷, SST and δ¹⁸Osw reconstructions for each specimen. Uncertainties at the 95% confidence level on monthly SST vary between 1.8 and 4.2°C owing to variable monthly sampling density related to in-shelf growth rate variability (Fig. 2). While variations in growth rate (Fig. 2A) caused differences in the sample size between monthly time bins, combining data from the same month in multiple growth years allowed reliable SST and δ¹⁸Osw reconstructions for all monthly time bins in each specimen. Calculations of mean annual temperature (MAT) and seasonality from these monthly averages eliminate seasonal bias due to growth rate variability. Statistically significant (p < 0.01) SST seasonality was observed in all specimens. Summer and winter temperatures, defined as mean temperatures of the warmest and coldest month, in A. incurva (13 ± 2–26 ± 4°C) and B. suecicus (14 ± 4–25 ± 3°C) are statistically indistinguishable (p > 0.2), while SST from R. diluvianum are significantly higher (20 ± 2–29 ± 2°C; p < 0.05). Significant δ¹⁸Osw seasonality was found in R. diluvianum (0.0 ± 0.3–1.1 ± 0.3‰ VSMOW; p < 0.01) and B. suecicus (< 1.8 ± 0.8–0.6 ± 0.5‰ VSMOW; p < 0.01), but not in A. incurva (< 0.9 ± 2.0 to −0.4 ± 0.9‰ VSMOW; p = 0.07; Fig. 2; Table 1). R. diluvianum records significantly higher δ¹⁸Osw values (p < 0.01) than the other specimens. In all specimens, monthly δ¹⁸Osw positively correlates with monthly SST (see Fig. 2).

We compare reconstructed SST from this and previous studies with local and global Campanian SSTs modeled using the HadCM3BL-M2.1aE model. Our model has been improved from being highly utilized in IPCC intercomparison assessment reports and compares well with CMIP5-generation model for many variables, including surface temperature. Importantly for this work, it is sufficiently computationally efficient to allow the long simulations required to reach close to equilibrium for palaeoclimates (see “Methods”). We present global Campanian latitudinal gradients in summer, winter, and MAT (Fig. 3A) as well as monthly SST in the Boreal Chalk Sea (Fig. 3B) for both 2× and 4× preindustrial atmospheric pCO₂ simulations (see “Methods”). Model results are summarized in Supplementary Data 5. The modeled Campanian latitudinal SST gradient (difference between tropics and high-latitude MAT; 26°C in both simulations) resembles the modern (25°C gradient). Modeled global mean Campanian SST seasonality (difference between warmest and coldest month) is lower (6.6°C) than that of the modern ocean (8.6°C) under 2× preindustrial pCO₂ conditions and resembles the present (8.2°C) in the 4× preindustrial pCO₂ simulation, corroborating recent studies arguing against the hypothesis of reduced seasonality during greenhouse
conditions\textsuperscript{16,37}. Campanian modeled MAT is \(-18^\circ\mathrm{C}\) and \(-22^\circ\mathrm{C}\) under 2\times and 4\times preindustrial atmospheric pCO\textsubscript{2}, respectively, compared to \(-14^\circ\mathrm{C}\) in the modern ocean\textsuperscript{38}, yielding an equilibrium climate sensitivity, or global warming per doubling of atmospheric pCO\textsubscript{2} concentration, of \(\sim 4^\circ\mathrm{C}\)\textsuperscript{19}. Specifically, simulated seasonal SST ranges in the Campanian Kristianstad Basin of \(7 \pm 3 - 20 \pm 2^\circ\mathrm{C}\) for 2\times and \(12 \pm 2 - 26 \pm 2^\circ\mathrm{C}\) for 4\times preindustrial atmospheric pCO\textsubscript{2} forcing are significantly warmer than present day (3 \(\pm 0.8\) - 17 \(\pm 0.4^\circ\mathrm{C}\))\textsuperscript{38} and modeled pre-industrial local SST seasonality (\(-1.6\) to \(+11.2^\circ\mathrm{C}\))\textsuperscript{19}.

**Discussion**

**Comparison between specimens.** Our novel \(\Delta_{\text{ST}}\)-based monthly SST and \(\delta^{18}\text{O}_{\text{sw}}\) reconstructions from A. incurva and B. suecicus are statistically indistinguishable from 4\times preindustrial pCO\textsubscript{2} simulations (\(p > 0.05\)) and significantly warmer than the 2\times pre-industrial pCO\textsubscript{2} simulations (\(> 4^\circ\mathrm{C}\) higher MAT, \(p < 0.05\)) of local SST seasonality (Fig. 3). Higher (\(p < 0.05\)) SST (\(+4 - 5^\circ\mathrm{C}\)) and \(\delta^{18}\text{O}_{\text{sw}}\) (+1.0 - 1.5‰) in R. diluvianum are likely caused by local differences in its shallower, inter-tidal (\(< 5\mathrm{m}\)) environment\textsuperscript{35}. Temporary areal exposure during low tides could have elevated temperatures and \(\delta^{18}\text{O}_{\text{sw}}\) recorded in R. diluvianum year-round by direct sunlight and evaporation, as in modern inter-tidal oyster species\textsuperscript{39}. By comparison, the deeper (5 - 15 m) subtidal environments of A. incurva and B. suecicus were unaffected by these processes and may have received more water with an open marine \(\delta^{18}\text{O}_{\text{sw}}\) signature (closer to the \(-1\%\text{VSMOW} assumed for ice-free oceans\textsuperscript{40}), especially in winter. Such local environmental differences are not resolved in the climate model simulations but show the unprecedented detail of local SST and \(\delta^{18}\text{O}_{\text{sw}}\) reconstructions from clumped isotope analyses in bivalve shells (see Supplementary Discussion). The \(\sim 1\%\) \(\delta^{18}\text{O}_{\text{sw}}\) seasonality shows that summers in the Campanian Kristianstad Basin either experienced excess evaporation, which increases \(\delta^{18}\text{O}_{\text{sw}}\) by preferentially removing isotopically light seawater, or reduced precipitation, which supplies isotopically light meteoric water, reducing \(\delta^{18}\text{O}_{\text{sw}}\). Both processes lead to comparatively dry summers and wet winters.

**Bias due to \(\delta^{18}\text{O}_{\text{sw}}\) assumptions.** Strong seasonal fluctuations in \(\delta^{18}\text{O}_{\text{sw}}\) (up to 1.3‰ in B. suecicus) and regular deviations from the commonly assumed \(-1\%\text{VSMOW} \delta^{18}\text{O}_{\text{sw}}\) value lead to large differences (up to 8.9 °C in R. diluvianum) between SST estimates based on \(\Delta_{\text{ST}}\) and \(\delta^{18}\text{O}_{\text{sw}}\) (Fig. 2). The risk of assuming constant \(\delta^{18}\text{O}_{\text{sw}}\) is even more clearly illustrated by significantly (+3.5 - 6.0 °C) higher \(\delta^{18}\text{O}_{\text{sw}}\)-based seasonal temperature reconstructions for B. suecicus compared to A. incurva, while both specimens grew under similar SST seasonality conditions (Fig. 2B). Similarly, \(\delta^{18}\text{O}_{\text{sw}}\)-based temperature reconstructions of A. incurva and R. diluvianum are indistinguishable, while the paleoenvironment of R. diluvianum was \(4 - 5^\circ\mathrm{C}\) warmer year-round (Fig. 2B). This illustrates that the constant \(\delta^{18}\text{O}_{\text{sw}}\) assumption is only valid in settings with negligible \(\delta^{18}\text{O}_{\text{sw}}\) seasonality and where \(\delta^{18}\text{O}_{\text{sw}}\) is known. Low-latitude Tethyan SST seasonality reconstructions based on rudist \(\delta^{18}\text{O}\text{c}\)\textsuperscript{15} agree with model simulations, which may indicate that \(\delta^{18}\text{O}_{\text{sw}}\) seasonality is less important in open marine settings. However, data–model agreement is by no means solid evidence for correct \(\delta^{18}\text{O}_{\text{sw}}\) assumptions, which should always be
Seasonal bias. Seasonal variability in growth rates in all specimens (Fig. 2A) illustrates how bulk sampling of bio-archives can lead to significant biases in MAT reconstructions compared to our more accurate estimates of MAT as an average of $\Delta_{47}$-based monthly SST. In this case, considerable differences in growth rate and $\delta^{18}O_{sw}$ seasonality between specimens would cause an unpredictable bias in MAT between $-7.8^\circ$C and $+1.4^\circ$C (Fig. 2A; Supplementary Data 3). Indeed, our Campanian mid-latitude SST ranges ($-15^\circ$–$27^\circ$C, MAT of $20^\circ$C) are significantly higher than previous SST reconstructions of the same paleolatitude based on fish tooth $\delta^{18}O$ ($15^\circ$–$20^\circ$C), bulk mollusk $\Delta_{47}$ ($15^\circ$–$12^\circ$C), $\delta^{18}O$ annual mollusk ($12^\circ$–$15^\circ$C), and sub-annual mollusk $\delta^{18}O$ ($15^\circ$–$22^\circ$C; Fig. 3A). On average, these previous studies yield lower MAT ($-15^\circ$C) than our seasonally controlled reconstructions and model (see Supplementary Discussion and Supplementary Fig. S4), but they highlight considerable variability between localities, even within the same study (Supplementary Discussion). The proxies used in these studies are affected differently by either seasonal or $\delta^{18}O_{sw}$ bias, or both. An additional source of cold bias affecting carbonate microfossil (most notably chalk) records is mixing of biogenic carbonate with carbonate cements precipitated under cooler sea floor conditions during early diagenesis.

Given the increase in frequency and duration of growth stops in modern mussels with increasing latitude, seasonal biases are likely more common in higher latitude environments. Since shallow marine bio-archives can record local climate conditions at higher spatial and temporal resolution than conventional (open ocean) archives, our monthly resolved $\Delta_{47}$ records present a tool for eliminating widespread biases related to seasonal variability and $\delta^{18}O_{sw}$ assumptions on SST reconstructions across time and space by combining long-term MAT reconstructions with snapshots of climate on the seasonal scale. The average seasonal range reconstructed from our three specimens ($15^\circ$–$27^\circ$C range, MAT of $20^\circ$C) likely represents the most accurate SST seasonality reconstructions for the Campanian Boreal Chalk Sea to date. The reconstructions are supported by the remarkable agreement between $\Delta_{47}$-based SST ranges and climate model simulations. Late Cretaceous reconstructions from the same latitude yield similar terrestrial MATs with higher seasonality, analogous to modern terrestrial-marine contrast (see Supplementary Discussion), and corroborate our findings of warmer, highly seasonal Late Cretaceous climate.

Data-model comparison. Robust agreement between our reconstructions and the 4x preindustrial pCO$_2$ model simulation down to the monthly scale provides strong evidence for considerably (up to $8^\circ$C) warmer higher latitudes during the Late Cretaceous greenhouse compared to the present day. Significant disagreement between summer, winter, and annual SST reconstructions from every specimen in this study and the 2x preindustrial pCO$_2$ simulation strongly favor higher (4x preindustrial pCO$_2$) radiative forcing (see Supplementary Data 4). Point-by-point data-model comparisons show that most previous Late Cretaceous SST reconstructions from the same latitudes yield lower temperatures with lesser data-model agreement.
Fig. 2 Paleoseasonality reconstructions. A From bottom to top: relative monthly sampling frequencies reflecting growth rate variability (bar chart), monthly average clumped isotope value (Δ47), sea surface temperature (SST) and seawater oxygen isotope value (δ18Osw) reconstructions from *R. diluvianum* (orange), *A. incurva* (purple) and *B. suecicus* (green). Shaded envelopes indicate 95% confidence levels. Red and blue dots respectively indicate warmest and coldest months. B SST and δ18Osw reconstructions of warmest month (red symbols), coldest month (blue symbols) and annual average (symbols in color of specimen). Thin crosses indicate 95% confidence level uncertainties. Vertical bars on the right indicate summer, winter, and mean annual temperature (MAT) estimates from carbonate oxygen isotope values (δ18Oc; assuming constant δ18Osw of −1‰VSMOW40). Cross-sections through specimens are drawn with horizontal 10 mm scale bars.

Fig. 3 Comparison between model and reconstructions. A Campanian latitudinal sea surface temperature (SST) gradient with vertical orange, purple and green bars showing seasonality reconstructions from this study and dashed black lines indicating modeled mean annual temperatures (560 ppmV = 2× preindustrial and 1120 ppmV = 4× preindustrial CO2 pressure) with gray envelopes representing seasonality. Black symbols and bars show previous SST reconstructions11–13,15,25,42,68,69. The large range in bulk mollusk clumped isotope (Δ47)-based SST estimates is discussed in Supplementary Discussion. The shaded yellow envelope indicates modern seasonal SST range (NOAA, 2021). Horizontal dashed lines mark modern and Campanian global mean annual temperature (MAT). B Monthly SST reconstructions (in orange, purple and green) and local model outputs (in gray) in the Boreal Chalk Sea. Diamonds indicate monthly SST means, with red and blue diamonds showing monthly summer and winter extremes, respectively. Shaded envelopes show 95% confidence levels and color coding follows Fig. 2.
(Supplementary Discussion). Bio-archives from mid to high latitudes are likely much more sensitive to δ18Osw and seasonality bias than low-latitude records21,23, contributing to the flawed paradigm of shallow latitudinal temperature gradients during greenhouse climates. Our results concur with the recent trend of converging data and model reconstructions yielding modern-scale Late Cretaceous latitudinal temperature gradients6,42, thereby challenging the hypothesis of “equable climate” during greenhouse periods14 (see Supplementary Discussion). Moreover, our unique absolute monthly SST reconstructions and model simulations corroborate growing evidence against the hypothesis of reduced temperature seasonality in greenhouse climates37. Future work should aim to further test these hypotheses by applying the clumped isotope seasonality method on bio-archives from a range of latitudes in greenhouse climate periods. Results from B. suecicus represent the first Δ47-based SST reconstructions from rudist bivalves, introducing an abundant archive and method with which to explore latitudinal seasonality gradients throughout the Mesozoic and across different ocean basins31.

Conclusions
Our new absolute temperature seasonality reconstructions merit critical evaluation of classical paleoclimate records that risk bias, such as those based on δ18O (assuming constant δ18Osw11,13), bulk analyses of fossil material with growth seasonality (e.g. mollusks and brachiopods25,27) or a fixed growth season (e.g. planktic foraminifera46) and organic proxies that may be sea-converging data and model reconstructions yielding modern-paradigm of shallow latitudinal temperature gradients during greenhouse periods. Results from B. suecicus and organic proxies that may be sea-converging data and model reconstructions yielding modern-paradigm of shallow latitudinal temperature gradients during greenhouse periods. Results from B. suecicus from a range of latitudes in greenhouse climate periods. Results from B. suecicus from a range of latitudes in greenhouse climate periods. Future work should aim to further test these hypotheses by applying the clumped isotope seasonality method on bio-archives from a range of latitudes in greenhouse climate periods. Results from B. suecicus represent the first Δ47-based SST reconstructions from rudist bivalves, introducing an abundant archive and method with which to explore latitudinal seasonality gradients throughout the Mesozoic and across different ocean basins31. Our new absolute temperature seasonality reconstructions merit critical evaluation of classical paleoclimate records that risk bias, such as those based on δ18O (assuming constant δ18Osw11,13), bulk analyses of fossil material with growth seasonality (e.g. mollusks and brachiopods25,27) or a fixed growth season (e.g. planktic foraminifera46) and organic proxies that may be sea-converging data and model reconstructions yielding modern-paradigm of shallow latitudinal temperature gradients during greenhouse periods. Results from B. suecicus represent the first Δ47-based SST reconstructions from rudist bivalves, introducing an abundant archive and method with which to explore latitudinal seasonality gradients throughout the Mesozoic and across different ocean basins31.

Methods
Geological setting. The bivalve specimens used in this study were obtained from the Ivö Klack (R. diluvianum), Åsen (A. incurva) and Maltesholm (R. suecicus) localities in the Kristianstad Basin35,46 in southern Sweden (56°2'N, 14°9'E; 46 ±3°N paleolatitude based on paleorotation by47 see Fig. 1 and Supplementary Methods). The three distinct localities contain a rich (>200 species), well-preserved Campanian rocky shore fauna45,46 and were all deposited at the peak of transgression of the latest early Campanian, as supported by the restriction of these deposits to the Baleniallochaenomamillatitosa belemnite biozone and Sr-isotope chem stratigraphy35,46,48. The tectonic quiescence of the region since the Late Cretaceous limited burial and promoted excellent shell preservation34,35. Burial of loosely compacted sediments of the studied localities was limited to a maximum of 40 m51. We can therefore conclude that burial temperatures never exceeded 80 °C and that solid-state reordering did not affect clumped isotope results from these specimens45,49 (see Supplementary Methods). The Kristianstad Basin represents the highest latitude location for the occurrence of rudist bivalves known to date46.

Materials. Fossil R. diluvianum oysters were found in situ clunging to the sides of large boulders at a paleodepth of 4 m46, while the B. suecicus rudist and A. incurva oysters were found in life position in a deeper setting (5–15 m) among skeletal fragments on the paleo-seafloor51 (see Supplementary Methods). The preservation of multiple specimens from this site (including the ones used here) was demonstrated through electron and visible light microscopy, trace element (e.g. Sr/Ca and Mn/Ca) analyses and ultrastructure preservation, results of which are reported in detail in34 and summarized in Supplementary Methods and Supplementary Fig. S1.

Sampling. Powdered samples (~300 µg) were drilled in growth direction from polished cross sections through the shell’s axis of maximum growth using a Dre- lader inability drill (Robert Bosch Ltd., Uxbridge, UK) and deposited in the open-source R code repository CRAN61. The number of localities in the Kristianstad Basin35,46 in southern Sweden (56°2'N, 14°9'E; 46 ±3°N paleolatitude based on paleorotation by47 see Fig. 1 and Supplementary Methods). The three distinct localities contain a rich (>200 species), well-preserved Campanian rocky shore fauna45,46 and were all deposited at the peak of transgression of the latest early Campanian, as supported by the restriction of these deposits to the Baleniallochaenomamillatitosa belemnite biozone and Sr-isotope chem stratigraphy35,46,48. The tectonic quiescence of the region since the Late Cretaceous limited burial and promoted excellent shell preservation34,35. Burial of loosely compacted sediments of the studied localities was limited to a maximum of 40 m51. We can therefore conclude that burial temperatures never exceeded 80 °C and that solid-state reordering did not affect clumped isotope results from these specimens45,49 (see Supplementary Methods). The Kristianstad Basin represents the highest latitude location for the occurrence of rudist bivalves known to date46.

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same as in Ref. 19. We evaluate model simulations with radiative forcing (pCO₂) set to 560 ppmV (2× preindustrial concentration) and 1120 ppmV (4× preindustrial concentration), within the range of pCO₂ reconstructions for the Campanian as compiled by ref. 65, and a modern astronomical configuration with dynamic vegetation. HadCM3 is, to our knowledge, the only model to run Campanian-specific boundary conditions with a range of pCO₂ forcing out to full equilibrium. This is critical as it was shown that the deep ocean and hence ocean circulation can take at least 5000 model years to fully equilibrate to the applied boundary conditions19, casting doubt on the validity of alternative model simulations that did not attain equilibrium. The model also compares well with CMIP5-generation model for many variables, including surface temperature66. Details on the HadCM3 model are provided in Supplementary Methods and in ref. 39. Local seasonal SSTs are calculated for the paleorotated Kristianstad Basin47 (42.5–50°N, 7.5–15°E; Supplementary Data 5) from averages of the upper ocean grid boxes in the model simulation. The model has a spatial resolution of 3.75° × 2.5° and uses 20 layers in ocean depth, of which the upper ocean box averages the top 10 m of the ocean. Hence the average SST of the Kristianstad Basin is biased against the shallowest coastal regions of the basin, such as the locality of R. diluvium67. For comparison, modern SST data come from the National Oceanic and Atmospheric Administration58 (Supplementary Data 6 and Supplementary Methods).

Data availability
Extended methods, data and scripts belonging to this study are available in the open-access database Zenodo (https://doi.org/10.5281/zenodo.3865428). This online database contains the following Supplementary Data files:
Supplementary Data 1: Raw results of growth modelling
Supplementary Data 2: Raw clumped isotope results
Supplementary Data 3: Results of statistical sample grouping protocol
Supplementary Data 4: Overview statistical test results
Supplementary Data 5: Modelled sea surface temperature data
Supplementary Data 6: Modern sea surface temperature data
Supplementary Data 7: Paleolatitude evolution of the Kristianstad Basin
Supplementary Data 8: Results of reproducibility tests for clumped isotope analyses
Supplementary Data 9: Matlab age modelling script
Supplementary Data 10: R script for statistical sample grouping

Code availability
Matlab scripts used to produce shell age models are provided in Supplementary Data 9. R scripts used to calculate monthly SST and δ¹⁸O,ω values from Δot and δ¹⁸O,ω data provided in Supplementary Data 7 are available in the data repository CRAN onseasonalclumped package uploaded to the open-course R package repository CRAN61.

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Author contributions
The initial design of the study was conceived by N.J.W., N.T., C.V.U., and M.Z. N.J.W., N.T., C.V.U. and M.Z. together were responsible for clumped isotope data acquisition. N.T. and C.V.U. provided samples used in this study. D.I.L. and A.F. ran the climate model and provided in-depth input on model-data integration. N.J.W. and P.C. were responsible for acquiring the funding needed for this study. N.J.W. wrote the first draft of the manuscript and revision. All authors then contributed to the writing process.

Competing interests
The authors declare no competing interests.

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