

# First absolute seasonal temperature estimates for greenhouse climate from clumped isotopes in bivalve shells

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## Article

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1 First absolute seasonal temperature estimates for greenhouse  
2 climate from clumped isotopes in bivalve shells

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13

14 **ABSTRACT**

15 Seasonal variability in sea surface temperatures plays a fundamental role in climate dynamics and  
16 species distribution. As such, it is essential to better understand seasonal variability in climates of  
17 the past. Previous reconstructions of seasonality in deep time are poorly constrained, relying on  
18 controversial assumptions such as estimates of seawater composition and neglect seasonal bias.  
19 This work presents the first absolute seasonal temperature reconstructions based on clumped  
20 isotope measurements in bivalve shells which, critically, do not rely on these assumptions. Our  
21 new approach reconstructs highly precise higher mid-latitude (~50°N) monthly temperatures from  
22 individual oyster and rudist shells of the Campanian (78 million years ago) greenhouse period  
23 (15–27 °C seasonal range). Our analysis demonstrates that seasonal bias and previous  
24 assumptions about sea water oxygen isotope composition can lead to highly inaccurate temperature  
25 reconstructions, distorting our understanding of the behavior of greenhouse climates and our

26 ability to model them. Our results agree with fully coupled climate model simulations showing  
27 greenhouse climates outside the tropics were warmer and more seasonal than previously thought.

28

29 **MAIN**

### 30 **Introduction**

31 Seasonal extremes were of vital importance for the evolution and distribution of life over  
32 geological history<sup>1</sup>. The effects of greenhouse warming on seasonal variability in temperature and  
33 the hydrological cycle are still poorly constrained, while being of considerable interest for  
34 projecting future climate and its impact on the ongoing biodiversity crisis<sup>2,3</sup>. Reconstructions of  
35 deep time (pre-Quaternary) greenhouse periods yield valuable insights into the dynamics of warm  
36 climates and the ecological response to forcing mechanisms such as rising atmospheric CO<sub>2</sub>  
37 levels<sup>4,5</sup>. Accurate reconstructions are imperative to evaluate climate model predictions under  
38 dissimilar climate states<sup>6</sup>, in particular seasonal range for which there is little quantitative evidence  
39 to constrain climate model behavior. The warm, ice free Late Cretaceous period presents a valuable  
40 reference to assess seasonal variability under greenhouse conditions<sup>7,8</sup>.

41 Reconstructions based on stable oxygen isotope ratios ( $\delta^{18}\text{O}_c$ ) in marine carbonates and  
42 organic paleothermometry (e.g. TEX<sub>86</sub>) indicate that Late Cretaceous global mean sea surface  
43 temperatures (SST) were ~5-6°C warmer than today with a reduced latitudinal temperature  
44 gradient (an “equable climate”<sup>9</sup>), while exhibiting limited temperature seasonality<sup>7,10,11,12</sup>.  
45 However, the reliability of past seasonal reconstructions is undermined by poorly constrained  
46 assumptions. This hampers our understanding of past warm climates and hinders accurate  
47 evaluation of climate models<sup>13,14</sup>. Two potentially significant biases resulting from assumptions

48 underlying SST reconstructions are seasonal bias and bias resulting from assumed seawater  
49 composition ( $\delta^{18}\text{O}_{\text{sw}}$  bias).

50 Seasonal bias occurs if a proxy is interpreted as representing annual mean conditions but is  
51 in fact biased to a particular season. Since fossil species producing the material that constitutes  
52 SST archives may not have a close modern relative for proxy calibration<sup>16</sup>, uncertainties about  
53 their growth seasons may unpredictably bias reconstructions. This bias limits our understanding  
54 of the behavior of greenhouse climates, which further leads to misinterpretation of model-data  
55 comparisons of past warm climates<sup>15</sup> and hinders the use of paleoclimate data for informing future  
56 climate predictions. Seawater oxygen isotope composition ( $\delta^{18}\text{O}_{\text{sw}}$ ) forms an important input  
57 parameter into the widely used carbonate  $\delta^{18}\text{O}_{\text{c}}$  temperature proxy<sup>17</sup>, but remains poorly  
58 constrained across geological timescales<sup>18,19</sup>. Biases in assumed  $\delta^{18}\text{O}_{\text{sw}}$  composition thus  
59 undermine SST reconstructions.

60 The advent of carbonate clumped isotope ( $\Delta_{47}$ ) SST reconstructions on a seasonal scale  
61 promises to eliminate these two biases<sup>20</sup>. The clumped isotope thermometer yields accurate SST  
62 reconstructions independent of  $\delta^{18}\text{O}_{\text{sw}}$  assumptions<sup>21,22</sup>. This technique also allows the  
63 reconstruction of  $\delta^{18}\text{O}_{\text{sw}}$ , yielding information about the (local) hydrological cycle, an important  
64 aspect of climate rarely constrained in deep time, and rectifying bias in the popular carbonate  $\delta^{18}\text{O}_{\text{c}}$   
65 temperature proxy. Recent advances in clumped isotope instrumentation and standardization have  
66 reconciled previous inter-lab disagreements and shown that many carbonate paleoarchives (e.g.  
67 foraminifera, bivalves and eggshells) conform to the theoretical  $\Delta_{47}$  temperature calibration<sup>23,24</sup>  
68 (see **Supplementary Methods and Discussion**). The large sample sizes required for individual  
69  $\Delta_{47}$ -based temperature estimates (>2 mg) have complicated paleoseasonality reconstructions using

70 this accurate method<sup>25</sup>, but a recently developed statistical approach enables its use for seasonality  
71 reconstructions<sup>20</sup>.

72 Here we use clumped isotope analyses on microsampled (~100 µg) profiles through fossil  
73 bivalve shells to obtain, for the first time, absolute SST and  $\delta^{18}\text{O}_{\text{sw}}$  seasonality reconstructions of  
74 a greenhouse climate. We apply this new method on well-preserved oyster (*Rastellum diluvianum*  
75 and *Acutostrea incurva*) and rudist (*Biradiolites suecicus*) shells from Campanian ( $78.1 \pm 0.3 \text{ Ma}$ <sup>26</sup>)  
76 coastal localities of the Kristianstad Basin in southern Sweden ( $46 \pm 3^\circ\text{N}$  paleolatitude<sup>27</sup>; see **Fig. 1**  
77 and **METHODS**). We further supplement these reconstructions with fully coupled climate model  
78 simulations of the Campanian greenhouse (see **METHODS**) to explore their implications for the  
79 “equable climate” hypothesis.

80

## 81 **Results**

82 All specimens showed clear seasonal  $\delta^{18}\text{O}_c$  fluctuations of  $-2.0$ – $0.0\text{‰}$  in *R. diluvianum*, -  
83  $2.0$ – $0.0\text{‰}$  in *A. incurva* and  $-2.7\text{‰}$ – $1.0\text{‰}$  in *B. suecicus* on which shell chronologies were based  
84 (see **Methods**). The assumption that periodic  $\delta^{18}\text{O}_c$  fluctuations reflect seasonality is demonstrated  
85 to be a valid basis for constructing intra-shell chronologies in nearly all modern environments<sup>20</sup>.  
86 Seasonal  $\delta^{18}\text{O}_c$  patterns show that the specimens record 3 (*A. incurva* and *B. suecicus*) to 6 (*R.*  
87 *diluvianum*) full years of growth. Clumped isotope analyses on small aliquots yielded  $\Delta_{47}$  ranges  
88 between  $0.62$ – $0.73\text{‰}$  for *R. diluvianum*,  $0.64$ – $0.76\text{‰}$  for *A. incurva* and  $0.63$ – $0.75\text{‰}$  for *B.*  
89 *suecicus*. Summaries of measurement results are displayed in **Table 1**.

90 Detailed step-by-step results of the data processing routine are shown in **Supplementary**  
91 **Methods** and<sup>20</sup>. **Fig. 2** and **Table 1** show monthly  $\Delta_{47}$ , SST and  $\delta^{18}\text{O}_{\text{sw}}$  reconstructions for each  
92 specimen. Uncertainties at the 95% confidence level on monthly SST vary between  $1.8$  and  $4.2^\circ\text{C}$

93 owing to variable monthly sampling density related to intra-shell growth rate variability (**Fig. 2**).  
94 While growth rate varied through the year (**Fig. 2A**), all monthly time bins in each specimen  
95 contained enough datapoints to allow separate monthly SST and  $\delta^{18}\text{O}_{\text{sw}}$  reconstructions.  
96 Calculations of mean annual temperature (MAT) and seasonality from these monthly averages  
97 eliminates seasonal bias due to growth rate variability. Statistically significant ( $p < 0.01$ ) SST  
98 seasonality was observed in all specimens. Summer and winter temperatures, defined as mean  
99 temperatures of the warmest and coldest month, in *A. incurva* ( $13 \pm 2$ – $26 \pm 4^\circ\text{C}$ ) and *B. suecicus*  
100 ( $14 \pm 4$ – $25 \pm 3^\circ\text{C}$ ) are statistically indistinguishable ( $p > 0.2$ ), while SST from *R. diluvianum* are  
101 significantly higher ( $20 \pm 2$ – $29 \pm 2^\circ\text{C}$ ;  $p < 0.05$ ). Significant  $\delta^{18}\text{O}_{\text{sw}}$  seasonality was found in *R.*  
102 *diluvianum* ( $0.0 \pm 0.3$ – $1.1 \pm 0.3\text{‰VSMOW}$ ;  $p < 0.01$ ) and *B. suecicus* ( $-1.8 \pm 0.8$ – $0.6 \pm 0.5\text{‰VSMOW}$ ;  
103  $p < 0.01$ ), but not in *A. incurva* ( $-0.9 \pm 0.2$ – $-0.4 \pm 0.9\text{‰VSMOW}$ ;  $p = 0.07$ ; **Fig. 2; Table 1**). *R.*  
104 *diluvianum* records significantly higher  $\delta^{18}\text{O}_{\text{sw}}$  values ( $p < 0.01$ ) than the other specimens. In all  
105 specimens, monthly  $\delta^{18}\text{O}_{\text{sw}}$  positively correlates with monthly SST (see **Fig. 2**).

106 We compare our reconstructed SST with local and global Campanian SSTs modelled using  
107 the HadCM3L model, one of the most developed paleoclimate models to date and part of the IPCC  
108 intercomparison assessment reports<sup>6,14</sup>. We present global Campanian latitudinal gradients in  
109 summer, winter and MAT (**Fig. 3A**) as well as monthly SST in the Boreal Chalk Sea (**Fig. 3B**) for  
110 both 2× and 4× preindustrial atmospheric  $\text{pCO}_2$  simulations (see **Methods**). Model results are  
111 summarized in **Supplementary Data 5**. The modelled Campanian latitudinal SST gradient  
112 (difference between tropics and high-latitude MAT;  $26^\circ\text{C}$  in both simulations) resembles the  
113 modern ( $25^\circ\text{C}$  gradient). Modelled global mean Campanian SST seasonality (difference between  
114 warmest and coldest month) is lower ( $6.6^\circ\text{C}$ ) than that of the modern ocean ( $8.6^\circ\text{C}$ ) under 2×  
115 preindustrial  $\text{pCO}_2$  conditions and similar to the present ( $8.2^\circ\text{C}$ ) in the 4× preindustrial  $\text{pCO}_2$

116 simulation, in disagreement with the hypothesis of reduced seasonality during greenhouse  
117 conditions. Campanian modelled MAT is  $\sim 18^{\circ}\text{C}$  and  $\sim 22^{\circ}\text{C}$  under  $2\times$  and  $4\times$  preindustrial  
118 atmospheric  $\text{pCO}_2$ , respectively, compared to  $\sim 14^{\circ}\text{C}$  in the modern ocean (NOAA, 2020), yielding  
119 an equilibrium climate sensitivity, or global warming per doubling of atmospheric  $\text{CO}_2$   
120 concentration, of  $\sim 4^{\circ}\text{C}^{15}$ . Specifically, simulated seasonal SST ranges in the Campanian  
121 Kristianstad Basin of  $7\pm 3$ – $20\pm 2^{\circ}\text{C}$  and  $12\pm 2$ – $26\pm 2^{\circ}\text{C}$  for  $2\times$  and  $4\times$  preindustrial atmospheric  
122  $\text{pCO}_2$  forcing, respectively, are significantly warmer than in present day southern Sweden ( $3\pm 0.8$ –  
123  $17\pm 0.4^{\circ}\text{C}^{28}$ ).

124

## 125 Discussion

126 Our novel  $\Delta_{47}$ -based monthly SST and  $\delta^{18}\text{O}_{\text{sw}}$  reconstructions from *A. incurva* and *B.*  
127 *suecicus* are statistically indistinguishable from  $4\times$  preindustrial  $\text{pCO}_2$  simulations ( $p>0.05$ ) and  
128 significantly warmer than the  $2\times$  preindustrial  $\text{pCO}_2$  simulations ( $>4^{\circ}\text{C}$  higher MAT,  $p<0.05$ ) of  
129 local SST seasonality ( $p>0.05$ ; **Fig. 3**). Higher ( $p<0.05$ ) SST ( $+4$ – $5^{\circ}\text{C}$ ) and  $\delta^{18}\text{O}_{\text{sw}}$  ( $+1.0$ – $1.5\%$ ) in  
130 *R. diluvianum* are likely caused by local differences in its shallower, inter-tidal ( $< 5$  m)  
131 environment<sup>27</sup>. Temporary areal exposure during low tides could have elevated temperatures and  
132  $\delta^{18}\text{O}_{\text{sw}}$  recorded in *R. diluvianum* year-round by direct sunlight and evaporation, as in modern  
133 inter-tidal oyster species<sup>29</sup>. By comparison, the deeper (5–15m) subtidal environments of *A.*  
134 *incurva* and *B. suecicus* were unaffected by these processes and may have received more water  
135 with an open marine  $\delta^{18}\text{O}_{\text{sw}}$  signature (closer to the  $-1\%$  VSMOW assumed for the ice-free  
136 Cretaceous<sup>30</sup>), especially in winter. These local environmental differences are not resolved in the  
137 climate model simulations but show the unprecedented detail of local SST and  $\delta^{18}\text{O}_{\text{sw}}$   
138 reconstructions from clumped isotope analyses on bivalve shells (see **Supplementary**

139 **Discussion**). The  $\sim 1\%$   $\delta^{18}\text{O}_{\text{sw}}$  seasonality shows that summers in the Campanian Kristianstad  
140 Basin either experienced excess evaporation, which increases  $\delta^{18}\text{O}_{\text{sw}}$  by preferentially removing  
141 isotopically light seawater, or reduced precipitation, which supplies isotopically light meteoric  
142 water, reducing  $\delta^{18}\text{O}_{\text{sw}}$ . Both processes lead to comparatively dry summers and wet winters.

143 Strong seasonal fluctuations in  $\delta^{18}\text{O}_{\text{sw}}$  (up to 1.3‰ in *B. suecicus*) and regular deviations  
144 from the commonly assumed -1‰ VSMOW  $\delta^{18}\text{O}_{\text{sw}}$  value<sup>26</sup> lead to large differences (up to 8.9°C  
145 in *R. diluvianum*) between SST estimates based on  $\Delta_{47}$  and the widely used  $\delta^{18}\text{O}_{\text{c}}$  proxy (**Fig. 2**).  
146 The risk of assuming constant  $\delta^{18}\text{O}_{\text{sw}}$  is even more clearly illustrated by significantly (+3.5–6.0°C)  
147 higher  $\delta^{18}\text{O}_{\text{c}}$ -based seasonal temperature reconstructions for *B. suecicus* compared to *A. incurva*,  
148 while both specimens grew under similar SST seasonality conditions (**Fig. 2B**). Similarly,  $\delta^{18}\text{O}_{\text{c}}$ -  
149 based temperature reconstructions of *A. incurva* and *R. diluvianum* are indistinguishable, while the  
150 paleoenvironment of *R. diluvianum* was 4–5°C warmer year-round (**Fig. 2B**), illustrating that the  
151 constant  $\delta^{18}\text{O}_{\text{sw}}$  assumption is only valid in settings with negligible  $\delta^{18}\text{O}_{\text{sw}}$  seasonality and where  
152  $\delta^{18}\text{O}_{\text{sw}}$  is known. Low-latitude Tethyan SST seasonality reconstructions based on rudist  $\delta^{18}\text{O}_{\text{c}}$ <sup>10</sup>  
153 agree with model simulations, which may indicate that  $\delta^{18}\text{O}_{\text{sw}}$  seasonality is less important in open  
154 marine settings, although data–model agreement is by no means solid evidence for correct  $\delta^{18}\text{O}_{\text{sw}}$   
155 assumptions, which should always be independently verified (**Fig. 3A**). Our findings corroborate  
156 previous  $\Delta_{47}$ -based and proxy comparison studies which also report a significant cold bias ( $\sim -8^\circ\text{C}$ )  
157 in  $\delta^{18}\text{O}_{\text{c}}$ -based SST reconstructions due to inaccurate  $\delta^{18}\text{O}_{\text{sw}}$  assumptions<sup>8,31</sup>. However, these  
158 studies did not account for seasonal biases.

159 Seasonal variability in growth rates in all specimens (**Fig 2A**) illustrates how bulk sampling  
160 of bio-archives can lead to significant biases in MAT reconstructions compared to our more  
161 accurate estimates of MAT as an average of  $\Delta_{47}$ -based monthly SST. In this case, slower summer

162 and autumn growth (months 4-7 in **Fig. 2A**), especially in *A. incurva* and *B. suecicus*, would cause  
163 bulk analysis of shell material to underestimate MAT. Indeed, our Campanian mid-latitude SST  
164 ranges (~15-27°C, MAT of 20°C) are significantly higher than previous reconstructions of the  
165 same paleolatitude based on fish tooth  $\delta^{18}\text{O}_c$  (15–20°C<sup>11</sup>), chalk  $\delta^{18}\text{O}_c$  (12–15°C<sup>12</sup>), bulk mollusk  
166  $\Delta_{47}$  (5–12°C<sup>32</sup>),  $\text{TEX}_{86}$  (15–20°C<sup>8</sup>) and sub-annual mollusk  $\delta^{18}\text{O}_c$  (15–22°C<sup>10,26</sup>; **Fig. 3A**). All  
167 these reconstructions are potentially affected by either seasonal or  $\delta^{18}\text{O}_{\text{sw}}$  bias, or both. Our more  
168 accurate reconstructions of  $\delta^{18}\text{O}_{\text{sw}}$  and SST on a seasonal scale aid in evaluating these biases and  
169 correct for them by combining long-term MAT reconstructions with snapshots of climate on the  
170 seasonal scale.

171         Given the increase in frequency and duration of growth stops in modern mollusks with  
172 increasing latitude<sup>33</sup>, seasonal biases are likely more common in higher latitude environments. The  
173 accuracy of our new method for SST reconstruction and the remarkable agreement between  $\Delta_{47}$ -  
174 based SST ranges and our climate model strongly suggest that the average seasonal range  
175 reconstructed from our three specimens (15-27°C range, MAT of 20°C) represents the most  
176 accurate SST seasonality reconstructions for the Campanian Boreal Chalk Sea to date. Since  
177 shallow marine bio-archives can record local climate conditions at higher spatial and temporal  
178 resolution than conventional (open ocean) archives, our monthly resolved  $\Delta_{47}$  records showcase a  
179 tool for eliminating widespread biases related to seasonal variability and  $\delta^{18}\text{O}_{\text{sw}}$  assumptions on  
180 SST reconstructions across time and space.

181         Robust agreement between our reconstructions and the 4× preindustrial  $\text{pCO}_2$  model  
182 simulation down to the monthly scale provides strong evidence for considerably warmer (~8°C)  
183 higher latitudes during the Late Cretaceous greenhouse compared to the present day. Significant  
184 disagreement of summer, winter and annual SST reconstructions from every specimen in this study

185 with the 2× preindustrial pCO<sub>2</sub> simulation strongly favor warmer (4× preindustrial pCO<sub>2</sub>) climate  
186 conditions (see **Supplementary Data 4**). Bio-archives from mid to high latitudes are likely much  
187 more sensitive to δ<sup>18</sup>O<sub>sw</sub> and seasonality bias than low-latitude records, contributing to the flawed  
188 paradigm of shallow latitudinal temperature gradients during greenhouse climates. Instead, our  
189 results concur with the recent trend of converging data and model reconstructions yielding modern-  
190 scale Late Cretaceous latitudinal temperature gradients<sup>13</sup>, thereby challenging the hypothesis of  
191 “equable climate” during greenhouse periods<sup>9</sup>. Moreover, our unique absolute monthly SST  
192 reconstructions and model simulations corroborate growing evidence against the hypothesis of  
193 reduced temperature seasonality in greenhouse climates<sup>30</sup>. Future work should aim to further test  
194 these hypotheses by applying the clumped isotope seasonality method on bio-archives from a range  
195 of latitudes in greenhouse climate periods. Results from *B. suecicus* represent the first Δ<sub>47</sub>-based  
196 SST reconstructions from rudist bivalves, introducing an abundant archive for accurate Mesozoic  
197 SST seasonality reconstructions with which these new insights can be evaluated.

198

## 199 **Conclusions**

200 Our new absolute temperature seasonality reconstructions merit critical evaluation of  
201 classical paleoclimate records that risk bias, such as those based on δ<sup>18</sup>O<sub>c</sub> (assuming constant  
202 δ<sup>18</sup>O<sub>sw</sub><sup>7,10</sup>), bulk analyses of fossil material with growth seasonality (e.g. mollusks and  
203 brachiopods<sup>31</sup>) or a fixed growth season (e.g. planktic foraminifera<sup>36</sup>) and organic proxies that may  
204 be seasonally biased (e.g. TEX<sub>86</sub> and U<sup>k</sup><sub>37</sub><sup>5,37</sup>). In addition, our monthly δ<sup>18</sup>O<sub>sw</sub> reconstructions  
205 for the first time allow evaluation of local seasonality in the hydrological cycle from accretionary  
206 bio-archives, revealing dry summers and wet winters in the Campanian Kristianstad Basin. This  
207 unique advantage of Δ<sub>47</sub>-based seasonality reconstructions enables the reconstruction of previously

208 unknown high-resolution variability in salinity, local rainfall and evaporation in past climates.  
209 Combined with longer-term, global-scale paleoclimate records and models, our new method for  
210 absolute monthly SST and  $\delta^{18}\text{O}_{\text{sw}}$  reconstructions has the potential to resolve critical  
211 disagreements between SST proxies, reduce biases of deep-time paleoclimate reconstructions,  
212 shed light on new aspects of past climate seasonality and reconcile proxy reconstructions and  
213 model simulations of greenhouse climate.

214

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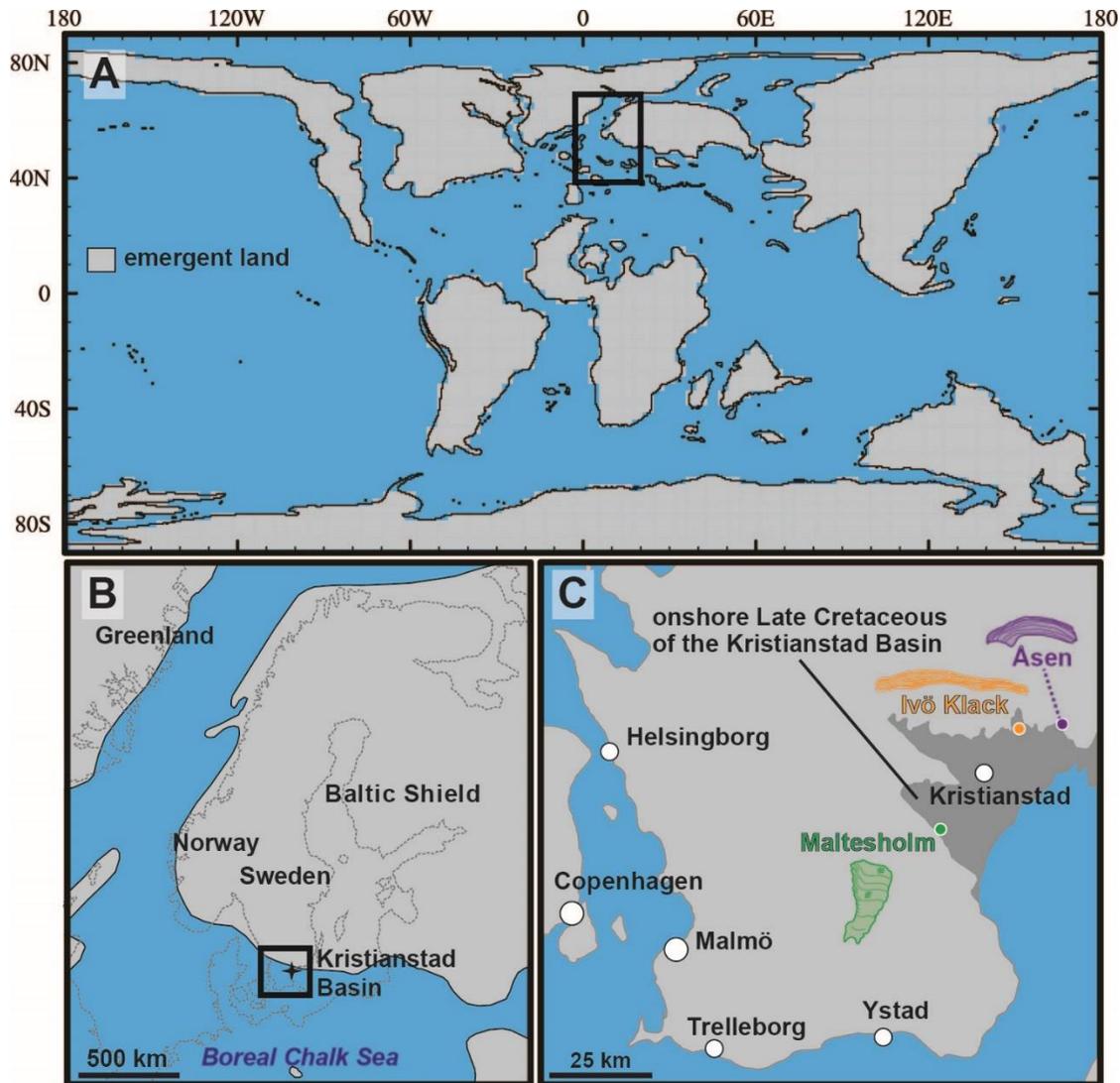
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316 **Table 1: Overview of analytical results ( $\delta^{18}\text{O}_c$  and  $\Delta_{47}$ ) and reconstructions**

Species (locality)	age [yr]	Measurement results									Monthly reconstructions					
		$\delta^{18}\text{O}_c$			$\Delta_{47}$			$\delta^{18}\text{O}_{sw}$			SST					
		$N^b$	[‰VPDB]		$N$	[‰]		[‰VSMOW]			[°C]					
	<i>min.</i>	<i>mean</i>	<i>max</i>		<i>min.</i>	<i>mean</i>	<i>max</i>	<i>CM</i> <sup>c</sup>	<i>MA</i> <sup>d</sup>	<i>WM</i> <sup>e</sup>	<i>CM</i>	<i>MA</i>	<i>WM</i>			
<i>R. diluvianum</i> (Ivö Klack)	6.2	198	<b>-2.08</b>	<b>-1.16</b>	<b>0.18</b>	121	<b>0.605</b>	<b>0.678</b>	<b>0.795</b>	<b>0.00</b>	<b>0.56</b>	<b>1.08</b>	<b>19.6</b>	<b>24.6</b>	<b>29.2</b>	
			$\pm 0.08$	$\pm 0.08$	$\pm 0.08$		$\pm 0.077$	$\pm 0.077$	$\pm 0.077$	$\pm 0.27$	$\pm 0.11$	$\pm 0.36$	$\pm 1.8$	$\pm 0.7$	$\pm 2.3$	
<i>A. incurva</i> (Åsen)	3.3	150	<b>-2.26</b>	<b>-0.71</b>	<b>0.15</b>	115	<b>0.601</b>	<b>0.706</b>	<b>0.831</b>	<b>-0.89</b>	<b>-0.46</b>	<b>-0.36</b>	<b>12.7</b>	<b>16.4</b>	<b>25.7</b>	
			$\pm 0.08$	$\pm 0.08$	$\pm 0.08$		$\pm 0.077$	$\pm 0.077$	$\pm 0.077$	$\pm 0.18$	$\pm 0.09$	$\pm 0.87$	$\pm 2.3$	$\pm 0.7$	$\pm 4.2$	
<i>B. suecicus</i> (Maltesholm)	3	178	<b>-2.93</b>	<b>-1.99</b>	<b>-0.98</b>	102	<b>0.565</b>	<b>0.688</b>	<b>0.779</b>	<b>-1.81</b>	<b>-1.18</b>	<b>-0.55</b>	<b>13.7</b>	<b>19.3</b>	<b>24.8</b>	
			$\pm 0.08$	$\pm 0.08$	$\pm 0.08$		$\pm 0.077$	$\pm 0.077$	$\pm 0.077$	$\pm 0.78$	$\pm 0.17$	$\pm 0.45$	$\pm 3.9$	$\pm 0.9$	$\pm 2.6$	

317 N = Number of measurements and the age is estimated from the age modelling results (**Supplementary Data 1**), CM =

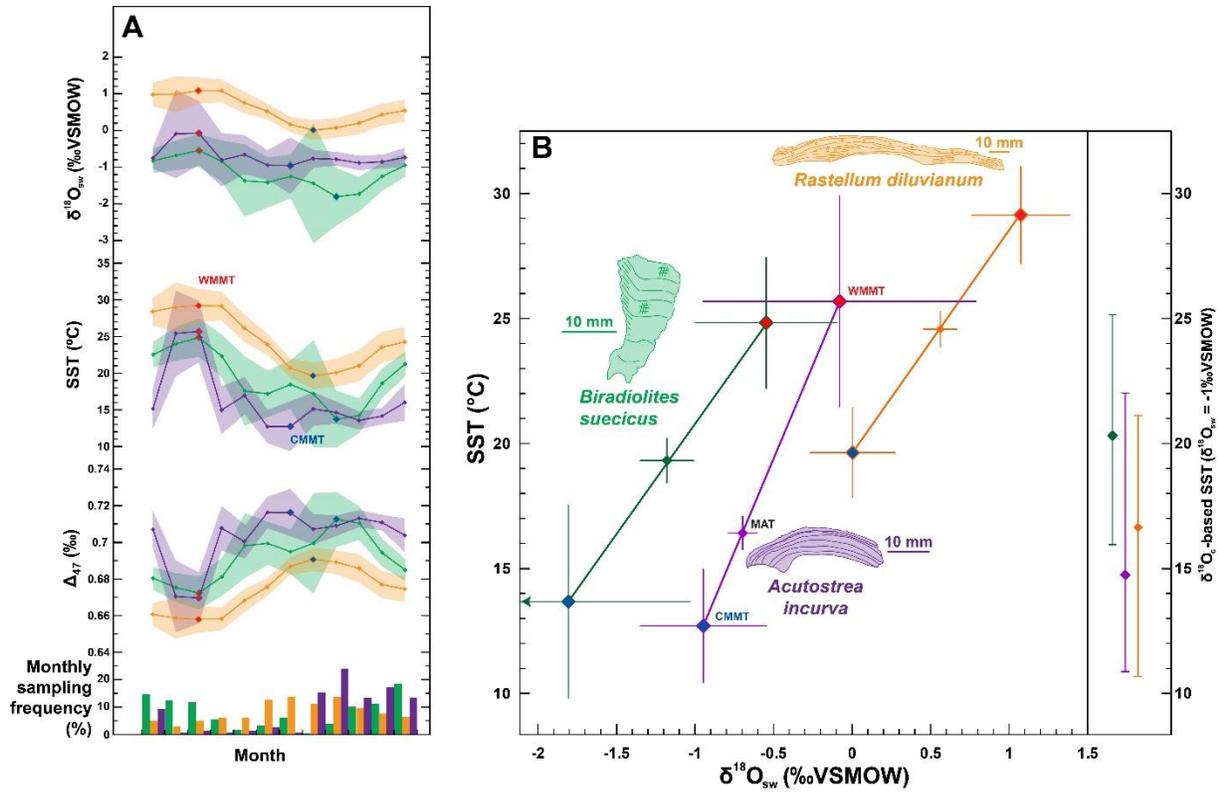
318 Coldest Month, MA = Mean Annual, WM = Warmest Month. All uncertainties are given as 95% confidence levels.



319

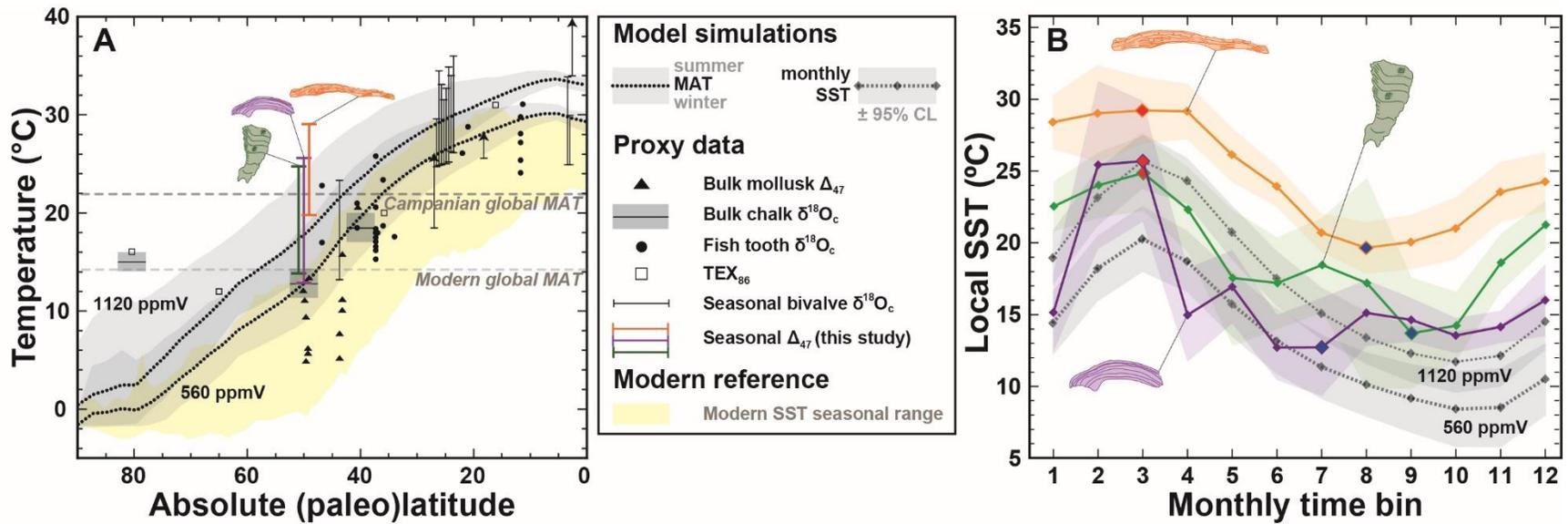
320 **Fig. 1: Campanian (78 Ma) paleogeography and geological setting** A) Global paleogeography  
 321 used in climate model<sup>14</sup> B) Northern Europe, black star indicates the Kristianstad Basin C)  
 322 Southern Sweden with Kristianstad Basin (in dark grey, submerged in the Campanian). Colored  
 323 dots indicate the three sampled localities on the paleoshoreline with schematic representations of  
 324 the species. In all maps, blue color indicates sea surface and light grey indicates emergent land.  
 325 Maps B) and C) are adapted from<sup>38</sup>.

326



327

328 **Fig. 2: Paleoseasonality reconstructions** A) From bottom to top: relative monthly sampling  
 329 frequencies reflecting growth rate variability (bar chart), monthly average  $\Delta_{47}$ , SST and  $\delta^{18}\text{O}_{\text{sw}}$   
 330 reconstructions from *R. diluvianum* (orange), *A. incurva* (purple) and *B. suecicus* (green). Shaded  
 331 envelopes indicate 95% confidence levels. Red and blue dots respectively indicate warmest and  
 332 coldest months. B) SST and  $\delta^{18}\text{O}_{\text{sw}}$  reconstructions of warmest month (red symbols), coldest  
 333 month (blue symbols) and annual average (symbols in color of specimen). Thin crosses indicate  
 334 95% confidence level uncertainties. Vertical bars on the right indicate summer, winter and MAT  
 335 estimates from  $\delta^{18}\text{O}_c$  (assuming constant  $\delta^{18}\text{O}_{\text{sw}}$  of -1‰ VSMOW). Scaled cross-sections through  
 336 specimens are drawn with horizontal 10 mm scale bars.



337

338 **Fig. 3: Comparison between model and reconstructions.** A) Campanian latitudinal SST gradient with vertical orange, purple and  
 339 green bars showing seasonality reconstructions and dashed black lines indicating modeled mean annual temperatures (560 ppmV = 2×  
 340 preindustrial and 1120 ppmV = 4× preindustrial pCO<sub>2</sub>) with grey envelopes representing seasonality. Black symbols and bars show  
 341 previous SST reconstructions<sup>7,8,10,11,12,32,39,40</sup>. The shaded yellow envelope indicates modern seasonal SST range<sup>28</sup>. Horizontal dashed  
 342 lines mark modern and Campanian global MAT. B) Monthly SST reconstructions (in orange, purple and green) and local model outputs  
 343 (in grey) in the Boreal Chalk Sea. Diamonds indicate monthly SST means, with red and blue diamonds showing monthly summer and  
 344 winter extremes, respectively. Shaded envelopes show 95% confidence levels and color coding follows **Fig. 2**.

## 345 METHODS

### 346 Geological setting

347 The bivalve specimens used in this study were obtained from the Ivö Klack (*R. diluvianum*),  
348 Åsen (*A. incurva*) and Maltesholm (*B. suecicus*) localities in the Kristianstad Basin in southern  
349 Sweden (56°2' N, 14° 9' E; 46±3°N paleolatitude<sup>27,41</sup>; see **Fig. 1** and **Supplementary Data 7**).  
350 The three distinct localities contain a rich (> 200 species), well preserved Campanian rocky shore  
351 fauna<sup>27,38</sup> and were all deposited at the peak of transgression of the latest early Campanian, as  
352 supported by the restriction of these deposits to the *Belemnellocamax mammillatus* belemnite  
353 biozone and Sr-isotope chemostratigraphy<sup>26,38,42</sup>. The tectonic quiescence of the region since the  
354 Late Cretaceous limited burial and promoted excellent shell preservation<sup>27</sup>. Burial of loosely  
355 compacted sediments of the studied localities was limited to a maximum of 40 meters<sup>27</sup>. We can  
356 therefore conclude that burial temperatures never exceeded 80°C and that solid-state reordering  
357 did not affect clumped isotope results from these specimens<sup>43,44</sup> (see **Supplementary Methods**).  
358 The Kristianstad Basin represents the highest latitude location for the occurrence of rudist bivalves  
359 known to date<sup>38</sup>.

360

### 361 Materials

362 Fossil *R. diluvianum* oysters were found *in situ* clinging to the sides of large boulders at a  
363 paleodepth of <5 m<sup>27</sup>, while the *B. suecicus* rudist and *A. incurva* oysters were found in life position  
364 in a deeper setting (5–15m) among skeletal fragments on the paleo-seafloor<sup>45</sup> (see **Supplementary**  
365 **Methods**). The preservation of multiple specimens from this site (including the ones used here)  
366 was demonstrated through electron and visible light microscopy, trace element (e.g. Sr/Ca and

367 Mn/Ca) analyses and ultrastructure preservation, results of which are reported in detail in <sup>26</sup> and <sup>45</sup>  
368 and summarized in **Supplementary Methods**.

369

### 370 **Sampling**

371 Powdered samples (~300 µg) were drilled in growth direction from polished cross sections  
372 through the shell's axis of maximum growth using a Dremel<sup>®</sup> 3000 rotary drill (Robert Bosch Ltd.,  
373 Uxbridge, UK) operated at slow rotation equipped with a 300 µm wide tungsten carbide drill bit.  
374 High (~100 µm) uniform sampling resolution was achieved by careful abrasive drilling using the  
375 side of the drill parallel to the growth lines in the shell. In oyster shells, the well-preserved dense  
376 foliated calcite was targeted, while in the rudist the dense outer calcite was sampled, avoiding the  
377 honeycomb structure in the inner part of the outer shell layer which is more susceptible to  
378 diagenetic alteration<sup>46</sup>. A total of 145 samples was obtained, from which 338 aliquots of ~100 µg  
379 were analyzed (see **Table 1**).

380

### 381 **Clumped isotope analyses**

382 Clumped isotope ( $\Delta_{47}$ ) analyses were carried out on Thermo Fisher Scientific MAT253 and  
383 253 Plus mass spectrometers coupled to a Kiel IV carbonate preparation devices. Calcite samples  
384 (individual replicates of ~90 µg for MAT253 Plus and ~150 µg for MAT253) were reacted at 70  
385 °C with nominally anhydrous (103%) phosphoric acid. The resulting CO<sub>2</sub> gas was cleaned from  
386 water and organic compounds with two cryogenic LN<sub>2</sub> traps and a PoraPak Q trap kept at -40 °C.  
387 The purified sample gases were analyzed in micro-volume LIDI mode with 400 s integration time  
388 against a clean CO<sub>2</sub> working gas ( $\delta^{13}\text{C} = -2.82\text{‰}$ ;  $\delta^{18}\text{O} = -4.67\text{‰}$ ), corrected for the pressure  
389 baseline<sup>41,42</sup> and converted into the absolute reference frame by creating an empirical transfer  
390 function from the daily analyzed ETH calcite standards (ETH-1, -2, -3) and their accepted values<sup>49</sup>.

391 All isotope data were calculated using the new IUPAC parameters following <sup>49</sup> and  $\Delta_{47}$  values  
392 were projected to a 25 °C acid reaction temperature with a correction factor of 0.071 ‰<sup>22</sup>. Long-  
393 term  $\Delta_{47}$  reproducibility standard deviation was 0.04‰ (0.039‰ for MAT253 Plus and 0.045‰  
394 for MAT253) based on repeated measurements of ~100 µg aliquots of our check standard IAEA  
395 C2 ( $\Delta_{47}$  of 0.719‰; measured over a 20-month period; see **Supplementary Data 8** for details).  
396 No statistical difference was found between results from both instruments (see **Supplementary**  
397 **Data 8**). For the  $\delta^{18}\text{O}_c$  compositions we applied an acid correction factor of 1.00871<sup>17</sup> and reported  
398 versus VPDB with a typical reproducibility below 0.13‰ (95% confidence level). Results were  
399 combined with  $\delta^{18}\text{O}_c$  data previously measured in the same shells<sup>26,45</sup> (**Supplementary Data 2**) to  
400 improve the confidence of seasonal age models and the temporal resolution of SST and  $\delta^{18}\text{O}_{sw}$   
401 reconstructions.

402

### 403 **Absolute paleoseasonality reconstructions**

404 We reconstructed absolute SST seasonality by aligning  $\Delta_{47}$  data relative to the seasonal cycle  
405 observed in  $\delta^{18}\text{O}_c$  using an age modelling routine<sup>51</sup> (**Supplementary Data 1 and 9**). Note that  
406 while chronologies were based on seasonal oscillations in  $\delta^{18}\text{O}_c$  records, the resulting age model  
407 is not compromised by unconstrained seasonal variability in  $\delta^{18}\text{O}_{sw}$  (see discussion in **[REF20]**  
408 and **Supplementary Methods**). Since only the shape of the seasonally oscillations in  $\delta^{18}\text{O}_c$  is used  
409 for age modelling, age model results are independent on the absolute SST and  $\delta^{18}\text{O}_{sw}$  seasonality  
410 and yield accurate results as long as the shape of the  $\delta^{18}\text{O}_c$  curve exhibits annual cyclicity (see <sup>50</sup>  
411 and <sup>20</sup>; **Supplementary Methods**). We used a statistical approach to combine aliquots for  $\Delta_{47}$ -  
412 based seasonality reconstructions. A step-by-step explanation of our  $\Delta_{47}$ -  $\delta^{18}\text{O}_c$  seasonality routine  
413 as well as a detailed evaluation of its precision and accuracy on a range of  $\Delta_{47}$ -  $\delta^{18}\text{O}_c$  datasets is

414 provided in <sup>20</sup> and in **Supplementary Methods**. The number of 100  $\mu\text{g}$   $\Delta_{47}$  aliquots to combine  
415 into monthly SST estimates is optimized by grouping aliquots from the same month in different  
416 growth years. Analytical uncertainties are propagated through this optimization procedure using  
417 Monte Carlo simulations (details in **Supplementary Methods** and **Supplementary Data 10**).  
418 SST's are calculated from  $\Delta_{47}$  values in monthly time bins (1/12<sup>th</sup> of the seasonal cycle) using the  
419 temperature calibration by <sup>51</sup> recalculated in <sup>23</sup>, and  $\delta^{18}\text{O}_{\text{sw}}$  is reconstructed from  $\Delta_{47}$ -SST and  $\delta^{18}\text{O}_c$   
420 following <sup>17</sup> (**Supplementary Methods** and **Supplementary Data 3**). The accuracy of this  
421 statistical approach for combining  $\Delta_{47}$  aliquots for seasonal SST and  $\delta^{18}\text{O}_{\text{sw}}$  reconstructions is  
422 tested on a diverse group of modern datasets and evaluated in <sup>20</sup>. It is demonstrated that this method  
423 achieves the ideal compromise between eliminating bias and retaining high reproducibility while  
424 keeping SST and  $\delta^{18}\text{O}_{\text{sw}}$  reconstructions independent of the  $\delta^{18}\text{O}_c$  values on which the age model  
425 is based<sup>20</sup> (see also **Supplementary Methods**). The clumped isotope temperature calibration by <sup>23</sup>  
426 is statistically indistinguishable from the temperature relationship based on theoretical principles  
427 within the temperature range discussed in <sup>24</sup> and is the culmination of recent convergence of  
428 measurement results between labs across the world and inter-lab standardization efforts<sup>22,49</sup>.  
429 Seasonality is defined as the difference between the average temperatures in the warmest and  
430 coldest month, while mean annual temperature (MAT) is expressed as the average of all monthly  
431 temperatures, following USGS definitions<sup>52</sup>. Statistical analyses of seasonality, differences  
432 between specimens and differences between data and model are summarized in **Supplementary**  
433 **Data 4**.

434

435 **Climate model**

436 We utilize a fully equilibrated (>11,000 model years) paleoclimate model (HadCM3L)  
437 Campanian (78 Ma) simulation. Model boundary conditions (topography, bathymetry, solar  
438 luminosity) for the Campanian are the same as in <sup>14</sup>. We evaluate model simulations with radiative  
439 forcing ( $p\text{CO}_2$ ) set to 560 ppmV (2× preindustrial concentration) and 1120 ppmV (4× preindustrial  
440 concentration), within the range of  $p\text{CO}_2$  reconstructions for the Campanian as compiled by <sup>53</sup>, and  
441 a modern astronomical configuration with dynamic vegetation. Details on the HadCM3L model  
442 are provided in **Supplementary Methods** and in <sup>14</sup>. Local seasonal SSTs are calculated for the  
443 paleorotated Kristianstad Basin<sup>41</sup> (42.5-50°N, 7.5-15°E; **Supplementary Data 5**) from averages  
444 of the upper ocean grid boxes in the model simulation. The model has a spatial resolution of 3.75°  
445 × 2.5° and uses 20 layers in ocean depth, of which the upper ocean box averages the top 10 meters  
446 of the ocean. Hence the average SST of the Kristianstad Basin is biased against the shallowest  
447 coastal regions of the basin, such as the locality of *R. diluvianum*<sup>54,55</sup>. For comparison, modern  
448 SST data come from the National Oceanic and Atmospheric Administration<sup>25</sup> (**Supplementary**  
449 **Data 6** and **Supplementary Methods**).

450

#### 451 **Data availability**

452 Extended methods, data and scripts belonging to this study are available in the open-access  
453 database Zenodo (<https://doi.org/10.5281/zenodo.3865428>).

454

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500

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510

#### 511 **AUTHOR CONTRIBUTIONS**

512 The initial design of the study was conceived by NJW, NT, CVU and MZ. NJW, IAM, IJK and  
513 MZ together were responsible for clumped isotope data acquisition. NT and CVU provided  
514 samples used in this study. DJL and AF ran the climate model and provided in-depth input on  
515 model-data integration. NJW and PC were responsible for acquiring the funding needed for this  
516 study. NJW wrote the first draft of the manuscript and revision. All authors then contributed to  
517 the writing process.

518

#### 519 **COMPETING INTEREST DECLARATION**

520 The authors have no competing interest to declare.

521

#### 522 **SUPPLEMENTARY INFORMATION**

523 All supplementary material belonging to this manuscript is deposited in the open-source online  
524 database Zenodo (<https://doi.org/10.5281/zenodo.3865428>).

# Figures

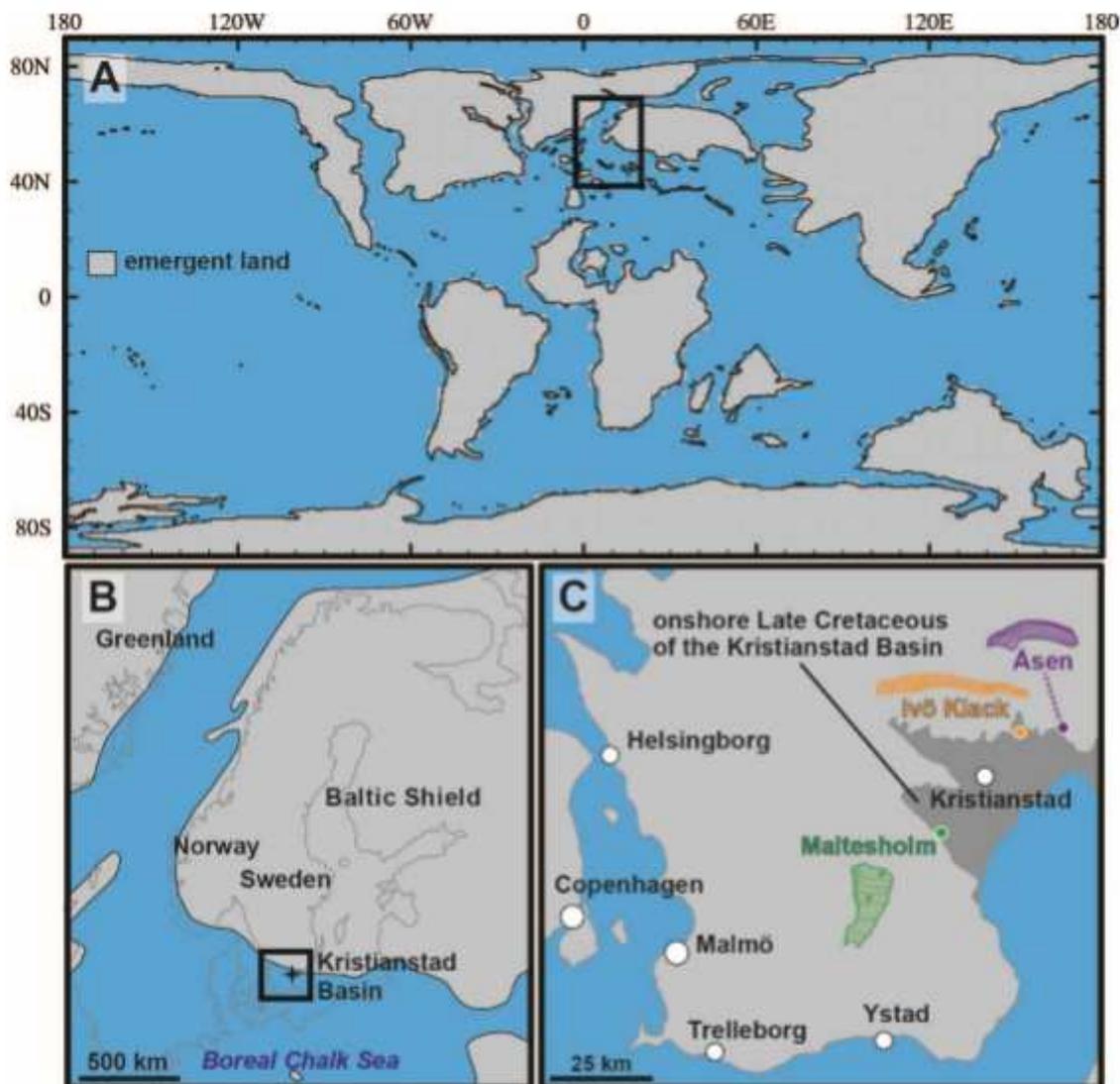


Figure 1

Campanian (78 Ma) paleogeography and geological setting A) Global paleogeography used in climate model14 B) Northern Europe, black star indicates the Kristianstad Basin C) Southern Sweden with Kristianstad Basin (in dark grey, submerged in the Campanian). Colored dots indicate the three sampled localities on the paleoshoreline with schematic representations of the species. In all maps, blue color indicates sea surface and light grey indicates emergent land. Maps B) and C) are adapted from38. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

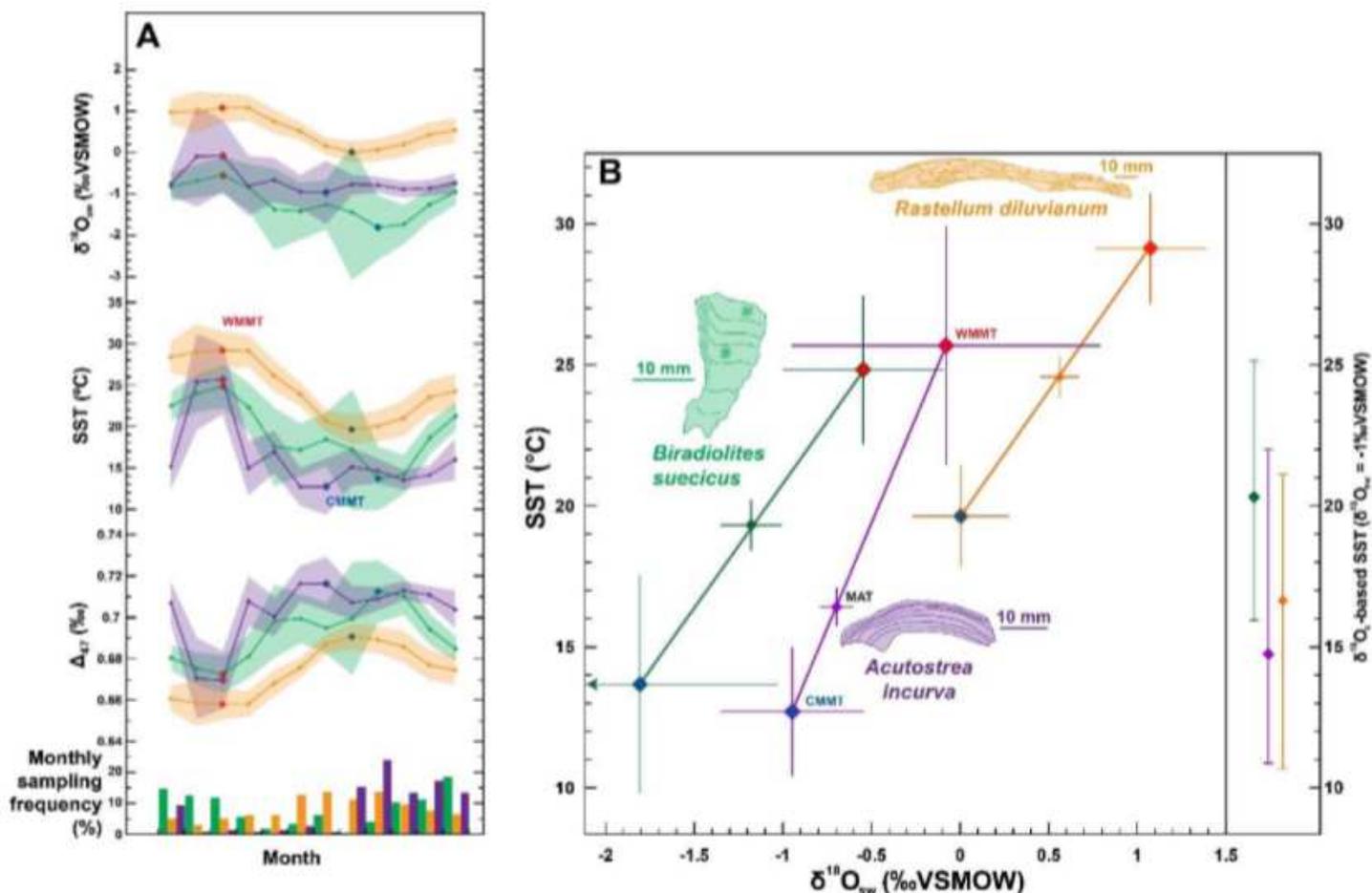
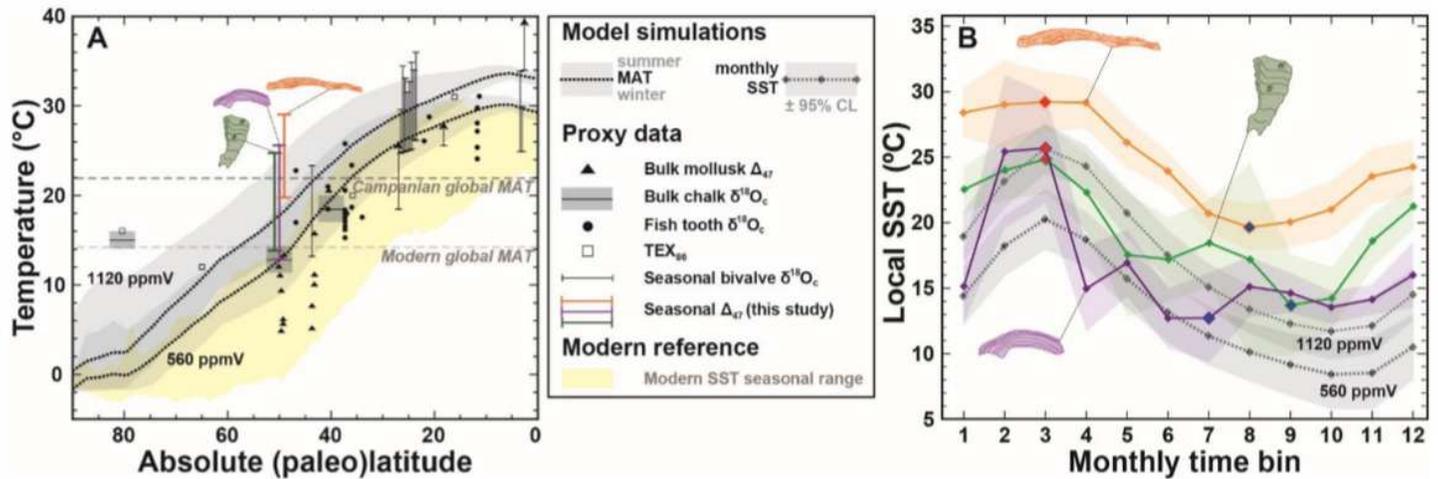


Figure 2

Paleoseasonality reconstructions A) From bottom to top: relative monthly sampling frequencies reflecting growth rate variability (bar chart), monthly average  $\Delta_{47}$ , SST and  $\delta^{18}O_{sw}$  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  $\delta^{18}O_{sw}$  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 MAT estimates from  $\delta^{18}O_c$  (assuming constant  $\delta^{18}O_{sw}$  of -1‰ VSMOW). Scaled cross-sections through specimens are drawn with horizontal 10 mm scale bars.



**Figure 3**

Comparison between model and reconstructions. A) Campanian latitudinal SST gradient with vertical orange, purple and green bars showing seasonality reconstructions and dashed black lines indicating modeled mean annual temperatures (560 ppmV = 2× preindustrial and 1120 ppmV = 4× preindustrial pCO<sub>2</sub>) with grey envelopes representing seasonality. Black symbols and bars show previous SST reconstructions<sup>7,8,10,11,12,32,39,40</sup>. The shaded yellow envelope indicates modern seasonal SST range<sup>28</sup>. Horizontal dashed lines mark modern and Campanian global MAT. B) Monthly SST reconstructions (in orange, purple and green) and local model outputs (in grey) 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 Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryTextNatCommEarthEnv.pdf](#)