



1 **Ultradian rhythms in shell composition of photosymbiotic and non-photosymbiotic**  
2 **mollusks**

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19



20 **Abstract**

21 The chemical composition of mollusk shells is a useful tool in (paleo)climatology since it captures  
22 inter- and intra-annual variability in environmental conditions. Trace element and stable isotope  
23 analyses with improved sampling resolution now enable the use of mollusk shells for  
24 paleoenvironmental reconstructions at a daily to sub-daily resolution. Here, we discuss hourly  
25 resolved Mg/Ca, Mn/Ca, Sr/Ca and Ba/Ca profiles measured by laser ablation ICP-MS through  
26 shells of photosymbiotic giant clams (*Tridacna maxima*, *Tridacna squamosa* and *Tridacna*  
27 *squamosina*) and the non-photosymbiotic scallop *Pecten maximus*. Precise sclerochronological  
28 age models and spectral analysis allowed us to extract daily and tidal rhythms in the trace element  
29 composition of these shells. We find significant expression of these periodicities but conclude that  
30 this cyclicity explains less than 10% of the sub-annual variance in trace element profiles. Tidal  
31 and diurnal rhythms explain variability of at most 0.2 mmol/mol (~10% of mean value) in Mg/Ca  
32 and Sr/Ca, while Mn/Ca and Ba/Ca cyclicity has a median amplitude of less than 2  $\mu\text{mol/mol}$   
33 (~40% and 80% of the mean of Mn/Ca and Ba/Ca, respectively). Daily periodicity in Sr/Ca and  
34 Ba/Ca is stronger in *Tridacna* than in *Pecten*, with *Pecten* showing stronger tidal periodicity. One  
35 *T. squamosa* specimen which grew under a sunshade exhibits some of the strongest diurnal  
36 cyclicity. Daily cycles in trace element composition of giant clams are therefore unlikely to be  
37 driven by variations in direct insolation itself but reflect an inherent biological rhythmic process  
38 affecting element incorporation. Finally, the large amount of trace element variability unexplained  
39 by periodic variability highlights the dominance of aperiodic processes in mollusk physiology  
40 and/or environmental conditions on shell composition at the sub-daily scale. Future studies should  
41 aim to investigate whether part of this aperiodic variability in shell chemistry reliably records  
42 weather patterns or circulation changes in the paleoenvironment.

43

44 **1. Introduction**



45 Patterns in growth increments, microstructure, and chemical composition of accretionary  
46 carbonate bioarchives yield detailed information about the environmental conditions and  
47 biological rhythm of carbonate producing animals (Dunbar and Wellington, 1981; Jones, 1983;  
48 Witbaard et al., 1994; Klein et al., 1996; Surge et al., 2001; Schöne et al., 2005a; Ivany, 2012;  
49 Schöne and Gillikin, 2013; DeCarlo and Cohen, 2017; Killam and Clapham, 2018). These  
50 characteristics have spurred the development of a multitude of techniques for extracting  
51 information about life history (Jones and Quitmyer, 1996; Schöne et al., 2005b; Goodwin et al.,  
52 2009; Mahé et al., 2010; Comboul et al., 2014; DeCarlo and Cohen, 2017; Judd et al., 2018; de  
53 Winter, 2022), carbonate chemistry (Sinclair et al., 1996; Lazareth et al., 2003; Schöne et al.,  
54 2010; de Winter and Claeys, 2017; Warter and Müller, 2017; Huyghe et al., 2021; de Winter et  
55 al., 2021a) and microstructure (Lazier et al., 1999; Checa et al., 2007; Popov, 2014; Gilbert et al.,  
56 2017; Crippa et al., 2020; Höche et al., 2020; 2021; Wichern et al., 2022) from carbonate shells  
57 and skeletons. As a result, (fossil) carbonate skeletons have gained much attention as archives  
58 of past environmental and climate change (e.g., Lough, 2010; Schöne and Gillikin, 2013; Ivany  
59 and Judd, 2022 and references therein).

60 Three characteristics make the shells of marine mollusks especially valuable as climate archives:  
61 (1) Nearly all marine mollusks precipitate their shells in isotopic equilibrium with ambient sea  
62 water, except for juvenile oysters and some mollusks growing near hydrothermal vents (Schöne  
63 et al., 2004; Wisshak et al., 2009; Huyghe et al., 2021; de Winter et al., 2022), (2) mollusk shells  
64 have a high fossilization potential and long geological history, dating back to the beginning of the  
65 Phanerozoic (Al-Aasm and Veizer, 1986a; b; Jablonski et al., 2003; Cochran et al., 2010;  
66 Jablonski et al., 2017; de Winter et al., 2017; 2018; Coimbra et al., 2020), (3) the incremental  
67 growth of mollusk shells allows for internal dating within the shell, yielding chronologies of shell  
68 growth with sub-annual precision (Richardson et al., 1980; Jones, 1983; Schöne et al., 2005c;  
69 Goodwin et al., 2009; Huyghe et al., 2019). These advantages enable mollusk shells to record



70 important information about climate and ambient water chemistry on the seasonal scale. Thereby,  
71 reconstructions from mollusk shells are highly complementary to other, less highly resolved but  
72 longer-term, climate and environmental reconstructions like sedimentary records, tree rings and  
73 ice cores (Black, 2009; Bougeois et al., 2014; Petersen et al., 2016; Tierney et al., 2020; de Winter  
74 et al., 2021b).

75 The resolution of the mollusk shell archive is not limited to seasonal variability. Studies monitoring  
76 the behavior of mollusks during growth experiments show that their activity varies as a function  
77 of environmental conditions (e.g., temperature and food availability) and follows ultradian rhythms  
78 which may contain daily to hourly periodicities, probably linked to diurnal and tidal cycles, or lack  
79 periodic behavior altogether (Rodland et al., 2006; García-March et al., 2008; Tran et al., 2011;  
80 Ballesta-Artero et al., 2017; Xing et al., 2019; Tran et al., 2020). Analyses of growth patterns and,  
81 more recently, composition of shell carbonate deposited at these short time intervals show that  
82 these rhythms can be recorded in mollusk shells (Pannella, 1976; Richardson et al., 1980; Sano  
83 et al., 2012; Warter et al., 2018; de Winter et al., 2020). This raises the question whether mollusk  
84 shells reliably record behavioral changes, high frequency (paleo-) weather or circulation patterns  
85 (e.g., Komagoe et al., 2018; Yan et al., 2020; Poitevin et al., 2020). Alternatively, the presence of  
86 daily cyclicity in shell chemistry may yield information about the paleobiology of extinct mollusks,  
87 such as the presence of photosymbiosis (e.g., Sano et al., 2012; Warter et al., 2018; de Winter et  
88 al., 2020). The latter seems plausible given the effect of photosymbiosis on shell mineralization  
89 in modern tridacnids (Ip and Chew, 2021) and on the trace element composition of aragonite in  
90 modern photosymbiotic scleractinian corals (Cohen et al., 2002; Meibom et al., 2003; Inoue et al.,  
91 2018). If proven true, daily variability in bivalve shells may serve as a proxy for photosymbiosis in  
92 the fossil record (e.g., de Winter et al., 2020). This is of interest because photosymbiosis is a  
93 derived adaptation of some tropical bivalve species (e.g., tridacnids) and its prevalence in the  
94 fossil record has important implications for the ecological niche of fossil mollusks (e.g., Vermeij,



95 2013). In addition, photosymbiosis can affect mollusk shell composition, and understanding it is  
96 therefore critical for the interpretation of chemical proxies in mollusk shells for environmental  
97 reconstructions (Killam et al., 2020). Finally, improving our understanding of photosymbiosis in  
98 tropical ecosystems sheds light on the resilience of photosymbiotic organisms to environmental  
99 change, now and in the geological past. The latter is of special interest in light of the ongoing  
100 climate and biodiversity crises, which are profoundly affecting these sensitive ecosystems  
101 (Pandolfi and Kiessling, 2014).

102 In this study, we investigate shell growth patterns and shell chemistry of the photosymbiotic  
103 bivalves *Tridacna maxima*, *T. squamosa* and *T. squamosina* as well as the non-photosymbiotic  
104 scallop *Pecten maximus*. *P. maximus* was chosen as a non-photosymbiotic counterpart in  
105 comparison with the tridacnids because of its comparatively high growth rate and the presence of  
106 daily striae on the outside of its shell, which make it possible to construct accurate shell  
107 chronologies (Chauvaud et al., 2005). We combine ultra-high-resolution (hourly resolved) Mg/Ca,  
108 Sr/Ca, Mn/Ca and Ba/Ca measurements in the shells with detailed sclerochronology to investigate  
109 the variability in these trace elements over time in all four species. The aim of this study is to  
110 investigate (1) whether the shells record high-frequency variability in shell chemistry that can be  
111 linked to environmental and/or circadian rhythms and (2) whether the presence of photosymbiosis  
112 influences the expression of this variability in the shells' composition.

113



114 **2. Materials and methods**

115 2.1 Preparation of *P. maximus* specimens

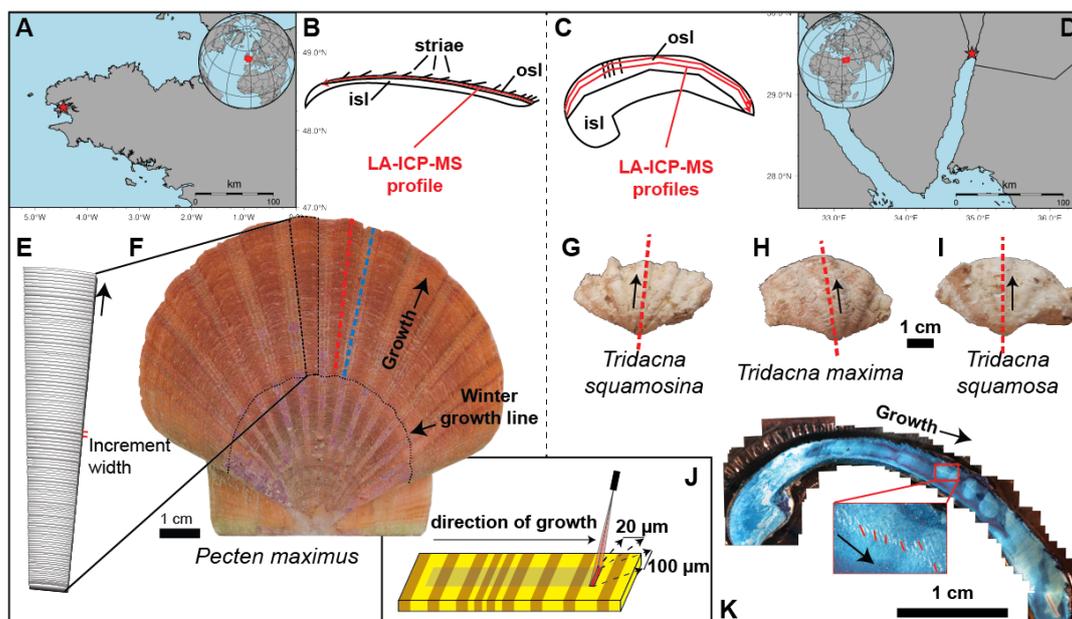
116 Three specimens of the King scallop *P. maximus* (labeled “PM2”, “PM3” and “PM4”) were  
117 collected alive on 15/11/2019 on the southern coast of the Bay of Brest near Lanvéoc, France  
118 (48°17'N 4°30'W) by SCUBA divers at a depth of approximately 8 m (see Fröhlich et al., 2022;  
119 **Figure 1**). Note that water depth in the Bay of Brest varies significantly due to the macrotidal  
120 regime with a mean tidal range of 2.8 – 5.9m with extreme ranges up to 7.2m (Guillaume-Olivier  
121 et al., 2021; Service Hydrographique et Océanographique de la Marine; 2022). Collected  
122 specimens contained at least one full year of growth based on the visibility of one winter growth  
123 line on the outside of the shell (age class 1; see Thébault et al., 2022 ; **Fig 1F** and **S1**). Specimens  
124 were frozen at -20°C immediately after collection. Soft body parts and epibionts were removed  
125 from the shells before further treatment. Shells were superficially cleaned using a plastic brush  
126 and adhering sediment was removed by ultrasonication in deionized water. The flat, left valves  
127 were used for elemental and sclerochronological analysis following previous studies on *P.*  
128 *maximus* (Thébault et al., 2022; Fröhlich et al., 2022).

129 High-resolution color photos were made of the outside of the left valve of the shell using a mirror-  
130 reflex camera (Canon EOS 600 DSLR camera connected to a Wild Heerbrugg binocular  
131 microscope equipped with a Schott VisiLED MC 1000 light source) aimed downward  
132 perpendicular to the working surface. Overlapping images of the shells were stitched together  
133 using Image Composite Editor v2.0.3.0 (Microsoft Research Computational Photography Group,  
134 Redmond, WA, USA). The stitched images were used to count and measure daily striae on the  
135 shell surface (see **Fig. 1** and **S1**). To obtain a fully focused composite of the complete shell,  
136 dynamic focusing was applied to allow all parts of the slightly curved surface of the shell to come  
137 into focus. Dynamic focus images were later stitched together using focus stacking in Helicon  
138 Focus (Helicon Focus 7.7.5; HeliconSoft, Kharkiv, Ukraine; see **S1**).



139 Cross sections were cut through all three *P. maximus* shells perpendicular to the daily growth  
140 lines (striae) from the ventral margin of the shell to the shell hinge (see **Fig. 1B**, **Fig. 1E-F** and  
141 **S1**) along the axis of maximal growth. Shells were fortified with a protective layer of metal epoxy  
142 (Gluetec Wiko Epofix 05) before sectioning using a Buehler Isomet 1000 low-speed precision saw  
143 (Buehler Inc, Lake Bluff, IL, USA) equipped with a diamond-coated wafering thin blade (0.4 mm  
144 thickness; number 15LC 11–4255) at 200 rpm. Parallel cuts were made to allow shell sections to  
145 be glued to glass plates for high-grade polishing (down to F1200 grit SiC powder and 1  $\mu\text{m}$   $\text{Al}_2\text{O}_3$   
146 suspension). Two cross sections were made through specimens **PM2** and **PM3**: One through a  
147 “rib” of the shell (i.e., radial segment that protrudes away from the interior, named **PM2\_1** and  
148 **PM3\_1**) and one through a “valley” (i.e., radial segment between two “ribs” that lies deeper  
149 towards the interior, named **PM2\_2** and **PM3\_2**; see **Fig. 1** and **S1**). The dual sections were cut  
150 to compare shell chemistry between the “ribs” and “valleys” of the shell . Specimen **PM4** was only  
151 sectioned once, through a “valley” in the shell, making a total of five cross sections through the *P.*  
152 *maximus* specimens.

153



154

155 **Figure 1: Overview of sample locations and preparation steps. A)** Location of the Bay of  
 156 Brest, with the red star indicating the sampling location. **B)** Schematic cross section through *P.*  
 157 *maximus* showing how the LA-ICP-MS linescan (red line) was positioned within the outer shell  
 158 layer (OSL). **C)** Schematic cross section through a tridacnid, illustrating the positions of parallel  
 159 LA-ICP-MS line scans (red lines) through these shells within the OSL. **D)** Position of the Gulf of  
 160 Aqaba, with the red star indicating the sample location for tridacnids. **E)** Schematic representation  
 161 of a segment through the shell of *P. maximus* showing the striae which are deposited daily and  
 162 which were counted to establish age models (see also **B**). **F)** Left valve of *P. maximus* (**PM2**)  
 163 used in this study, with dashed lines showing the position of cross sections through ribs (red) and  
 164 valleys (blue) in the shell. Black arrow indicates growth direction away from the shell hinge. The  
 165 black dotted line highlights a winter growth stop. **G-I)** Pictures of (from left to right) *T. squamosa*  
 166 (specimen **TSFRS1**), *T. maxima* (specimen **TM29**) and *T. squamosina* (specimen **SQSA1**) with  
 167 dashed red lines indicating the positions of the cross sections used for LA-ICP-MS analysis (see  
 168 **C**) and black arrows indicating the direction of growth. **J)** Schematic representation of the LA-ICP-



169 MS line scanning setup with the rectangular spot size (100 \* 20  $\mu\text{m}$ ; see **S11**) that was positioned  
170 parallel to the growth layers in the shell. **K)** Example of Mutvei-stained cross section through a *T.*  
171 *maxima* specimen used to visualize and count growth lines, with the insert showing part of the  
172 OSL where growth lines were counted (red lines) to establish age models for the tridacnids. Black  
173 arrows indicate the direction of growth.

174



175 2.2 Preparation of *Tridacna* specimens

176 A total of 5 tridacnid specimens, two *T. maxima* (named **TM29** and **TM84**), two *T. squamosa*  
177 (named **TS85** and **TSFRS1**) and one *T. squamosina* (**SQSA1**) specimen, were collected in the  
178 summer of 2016 from beach death assemblages on the coast of the Gulf of Aqaba with permit  
179 from the Israeli National Parks Authority (**Figure 1**; see details in Killam et al., 2020). One cultured  
180 *Tridacna squamosa* shell (**TSM1**) was obtained from the National Center for Mariculture, Eilat.  
181 Species were determined following shell characteristics of the local population as cited in Roa-  
182 Quiaoit (2005).

183 All shells were sectioned along the axis of maximum growth after removing epibionts using a  
184 metal brush (see **Fig. 1G-I**). Original microstructure and preservation of the original aragonite  
185 mineralogy of all specimens was confirmed using Scanning Electron Microscopy and X-ray  
186 Diffraction Spectroscopy following Gannon et al. (2017) and Kontoyannis and Vagenas (2000;  
187 see details in Killam et al., 2020). Shell segments were partially embedded in Araldite 2020 epoxy  
188 resin (Huntsman Corp., Woodlands, TX, USA) before being sectioned in direction of maximum  
189 growth using a slow-rotating saw equipped with a thin wafered saw blade ( $\varnothing < 1$  mm). Parallel  
190 cross sections produced 5-10 mm thick sections that were polished using progressively finer SiC  
191 polishing disks.

192

193 2.3 Microscopy and photography

194 Polished surfaces of all 11 cross sections (5 *Pecten*, 6 *Tridacna*) were imaged using an Epson®  
195 1850 flatbed scanner (Seiko Epson Corp., Nagano, Japan) at a pixel resolution of 6400 dpi ( $\pm 4$   
196  $\mu$ m pixel size) as well as by stitching micrographs made using a KEYENCE VHX-5000 digital  
197 microscope using x250 magnification together into composite images (see **S1**). Cross sections



198 were imaged both before and after trace element analyses to allow the trace element profiles to  
199 be referenced relative to the cross sections.

200

#### 201 2.4 LA-ICP-MS analyses

202 Elemental ratios were based on measuring ratios of the isotopes  $^{25}\text{Mg}$ ,  $^{87}\text{Sr}$ ,  $^{55}\text{Mn}$  and  $^{137}\text{Ba}$  to  
203  $^{43}\text{Ca}$  along profiles through all shell cross sections using Laser Ablation – Inductively Coupled  
204 Plasma – Mass Spectrometry (LA-ICP-MS). Measurements were carried out on a laser ablation  
205 system (ESI NWR193UC; Elemental Scientific, Omaha, NE, USA) coupled to a quadrupole ICP-  
206 MS (iCap-Q, Thermo Fisher Scientific, Waltham, MA, USA) at the Royal Netherlands Institute for  
207 Sea Research (NIOZ). Operation parameters are provided in **S11**.

208



209

210 Scan lines were programmed on the polished shell cross sections in direction of growth as close  
211 as possible to the outer edge of the shell, with the LA-ICP-MS spot oriented parallel to the growth  
212 lines (with a width of 20  $\mu\text{m}$  in scanning direction, see **Fig. 1J**; **S11**). For the pectinids, care was  
213 taken to target the outer portion of the outermost shell layer (oOSL) and avoid sampling of the  
214 inner portion of the outer shell layer (iOSL) or inner shell layer (ISL), which was demonstrated to  
215 have a different chemical composition (see Freitas et al., 2009). For the tridacnids, profiles were  
216 placed within the OSL close to (within 100  $\mu\text{m}$  of) the outer edge of the shell in a first analytical  
217 session. However, since spikes of high Mg/Ca and Mn/Ca ratios were observed in these results,  
218 parallel transects placed  $\sim$ 100  $\mu\text{m}$  further towards the inside of the shell were measured through  
219 all tridacnid shells to verify whether these spikes in Mg and Mn were reproducible further inward  
220 (see **S2**). All scan lines in pectinids and tridacnids were repeated a second time at the exact same  
221 location using a faster scan rate of 10  $\mu\text{m}\cdot\text{s}^{-1}$  to assess repeatability of the elemental signals (see  
222 **S2**).

223 Data reduction was performed using an adapted version of the data reduction software SILLS  
224 (Signal Integration for Laboratory Laser Systems; Guillong et al., 2008) in Matlab. Raw LA-ICP-  
225 MS data were calibrated using NIST610, (National Institute of Standards and Technologies,  
226 Gaithersburg, MD, USA) using the reference values reported in the GeoReM database (Jochum  
227 et al. 2005, 2011). Quality control materials BAS752 (Bureau of Analyzed Samples,  
228 Middlesbrough, UK), RS3 and one matrix-matched carbonate standard (MACS-3; United States  
229 Geological Survey, Reston, VA, USA; Wilson et al., 2008) were used to monitor the quality of the  
230 measurement. To increase the stability of the ICP-MS signal and to correct for drift,  $^{43}\text{Ca}$  was  
231 used as internal standard. External drift-correction using repeated measurements on the JCp1  
232 standard was applied if the element/Ca drift was  $>5\%$  during the analytical sequence. Drift during  
233 a single transect was found to be negligible.



234

## 235 2.5 Age models

236 Trace element profiles in *P. maximus* shells were internally dated using daily striae visible on the  
237 outer shell surface (**Fig. 1E**). Daily increment widths (perpendicular distances between  
238 successive striae) were counted and measured multiple times, both on the outside of the shell  
239 using the focus-stacked images (see **section 2.3**) and by counting and measuring the distance  
240 between growth layers in cross sections through the “valleys” of the shells (**PM2\_2** and **PM3\_2**;  
241 see **S3**) by different persons. Positions of daily striae on the outside of the shells were plotted  
242 relative to distance along the LA-ICP-MS scan line using manual alignment of striae and the LA-  
243 ICP-MS path on microscope composites of cross sections through the shells, taking into account  
244 the curvature of growth lines with distance away from the outer shell surface (see **S3**). The timing  
245 of shell formation was determined by backdating the daily striae from the ventral margin (last  
246 visible stria mineralized on the date of shell collection, i.e., November 15, 2019), and by linearly  
247 interpolating the timing of measurements located between daily growth lines based on their  
248 distance from daily striae positions (**S5**).

249 Trace element profiles from *Tridacna* shells were also dated using layer counting. However, since  
250 expression of daily and semi-diurnal growth markings was insufficiently clear to count individual  
251 growth lines along the full (multi-year) growth period recorded in all the shells, age models were  
252 constructed based on parts of the shell where daily and tidal layers could be identified with  
253 confidence. Polished cross sections through all tridacnids were imaged using UV luminescence  
254 (see **Fig. 1K** and **S4**) to facilitate this counting. The median widths of daily or semi-diurnal  
255 increments were determined on these cross sections and compared to the width of annual  
256 increments identified based on growth breaks visible on the outer margin of the shell. The  
257 distinction between diurnal (24h) and tidal (~12h) pacing of growth increments was made based  
258 on the width of small-scale increments relative to the width of annual increments in the shell. A



259 von Bertalanffy growth model (Von Bertalanffy, 1957) was constructed for each specimen based  
260 on the annual growth ( $\Delta L$ ) inferred from growth line counting and the maximum shell height ( $L_{inf}$ )  
261 known for these species in the Red Sea from the literature (Roa-Quiaoit, 2005; Mohammad et al.,  
262 2019):

$$263 \quad L_t = L_{inf} * (1 - e^{-kt}), \text{ with } k = -\ln\left(\frac{\Delta L}{L_{inf}}\right)$$

264 In this formula,  $L_t$  is the shell height at time  $t$  and  $k$  is the growth constant (Brody growth coefficient;  
265 Munro, 1984). Since cross sections through the tridacnids were made through the shell hinge (in  
266 direction of the shell height) and literature values for  $L_{inf}$  are reported with reference to shell length  
267 (measured parallel to the shell hinge), allometric data on *T. maxima*, *T. squamosa* and *T.*  
268 *squamosina* from the literature was used to convert  $L_{inf}$  values (which are commonly reported as  
269 shell length) to shell height and make them relevant for the direction in which the trace element  
270 profiles were measured on the cross sections (Roa-Quiaoit, 2005; Richter et al., 2008;  
271 Mohammad et al., 2019). Uncertainties on the annual growth increment widths ( $\Delta L$ ) were  
272 calculated from the standard error of the mean width of daily and semi-diurnal growth increments  
273 on which  $\Delta L$  is based, and uncertainties on the values for  $L_{inf}$  were taken from variability in the  
274 values in the literature. Both sources of uncertainty were propagated through the growth model  
275 using the variance formula (Ku, 1966) to obtain error envelopes on age-distance relationships  
276 (growth curves) of tridacnids (see **S5**). All data processing steps described in this manuscript are  
277 carried out using the open-source computational software package R (R Core Team, 2022), and  
278 scripts detailing these calculations are provided in **S6** and deposited on the open-access software  
279 repository GitHub (<https://zenodo.org/record/6603175>)

280

281 2.6 Spectral analysis



282 Spectral analysis on the LA-ICP-MS data was used to isolate trace element variability at the sub-  
283 annual scale. All trace element profiles were first detrended using a LOESS filter with a span of  
284 0.2 times the length of the record to remove longer term (i.e., seasonal to multi-annual) trends.  
285 The detrended series were linearly resampled in the time domain before applying the Multi-Taper  
286 Method (MTM; Thomson, 1982) to extract dominant frequencies from the data. Spectral analysis  
287 was carried out using the “astrochron” package (Meyers, 2014) in R (R Core Team, 2022; see  
288 script in **S6**). The significance of relevant periodicities was tested using a combination of “red  
289 noise” estimation and a harmonic F-test (see Meyers, 2021). To visualize the evolution of periodic  
290 behavior across the shells, wavelet analysis was applied on all trace element profiles using the  
291 “dplr” package in R (see **S6**).

292

## 293 2.7 Extracting high-resolution variability

294 After detrending and spectral analysis, all trace element profiles were smoothed using a Savitzky-  
295 Golay filter with a width of 21 datapoints (8.4  $\mu\text{m}$ ; equivalent to a timespan of  $\sim 1\text{-}5\text{h}$ ; **S6**) to remove  
296 high-frequency measurement noise. Statistically significant (see **section 2.6**) variability in daily  
297 ( $\sim 22\text{-}36\text{h}$ ; centered on the 24h diurnal cycle) and tidal ( $\sim 8\text{-}14\text{h}$ ; centered on the 12.4h tidal cycle)  
298 frequency bands was extracted from the trace element records using a combination of bandpass  
299 filtering (using the “bandpass” function in the “astrochron” R package) and stacking (see **S6**).  
300 Trace element data was stacked along bandpass filters using the following procedure: Maxima  
301 and minima in the bandpass filter were used as tie points to reference each datapoint of the  
302 smoothed dataset relative to its position within the cycle on a scale from 0 to 1. These relative  
303 positions were then used to divide the data into 10 bins (bin 1 contains positions 0 – 0.1, bin 2  
304 contains data from positions 0.1 – 0.2, etc.), giving the stacked data a resolution of 0.1 times the  
305 length of the cycle under investigation. The full breakdown of variability within and between bins  
306 created in the stacking routine is provided in **S7**. Different sources of variance in the trace element



307 records were isolated by sequentially determining the variance left in the trace element records  
308 after each of the data treatment steps explained above (see example in **S7**). This procedure  
309 allowed us to quantify the amount of variance in each trace element profile explained by either  
310 diurnal or semi-diurnal variability.



311 **3. Results**

312 3.1 Trace element data

313 LA-ICP-MS line scans yielded profiles of Sr/Ca, Mg/Ca, Mn/Ca and Ba/Ca in growth direction on  
314 11 cross sections through shells of *P. maximus*, *T. maxima*, *T. squamosa* and *T. squamosina*.  
315 Trace element profiles of consecutive line scans on the same transect show high repeatability:  
316 sub-millimeter scale patterns in Sr/Ca, Mg/Ca, Mn/Ca, and Ba/Ca are repeated between  
317 consecutive line scans,  $R^2$  values between trace element results of time-equivalent shell samples  
318 typically exceed 0.8, and the mean ratio difference between time equivalent samples in different  
319 line scans is less than 0.05 mmol/mol for the most variable profiles (Mg/Ca, with lower differences  
320 for the lower-concentration Mn/Ca and Ba/Ca records; see **S2**). Remeasured transects further  
321 away from the outer shell surface in tridacnids (see **section 2.4**) differ more from the original  
322 transects than those measured on the exact same locality in the shell:  $R^2$  values between parallel  
323 lines in different localities are 0.3 – 0.5 for Mg/Ca and Sr/Ca and <0.3 for Mn/Ca and Ba/Ca,  
324 reflecting intra-shell variability in trace element composition in the tridacnids (**S2**). Overall, sub-  
325 millimeter scale patterns in trace element composition are reproduced in parallel line scans, and  
326 the mean offset between the lines was always less than 0.2 mmol/mol.

327 Pectinid and tridacnid shells contain similar mean Sr/Ca and Ba/Ca ratios (Sr/Ca of  $1.3 \pm 0.3$  and  
328  $1.5 \pm 0.6$  mmol/mol respectively; Ba/Ca of  $2.8 \pm 2.5$  and  $3.0 \pm 5.1$   $\mu\text{mol/mol}$  respectively;  
329 uncertainty is calculated as  $1\sigma$ ). Mean Mg/Ca and Mn/Ca ratios are higher in *P. maximus* than in  
330 *Tridacna* species (Mg/Ca =  $3.1 \pm 0.9$  and  $0.7 \pm 0.9$  mmol/mol; Mn/Ca =  $7.8 \pm 4.7$  and  $2.7 \pm 7.8$   
331  $\mu\text{mol/mol}$ ;  $1\sigma$ ; **Figure 2**; **S4**). Differences between tridacnid specimens generally exceed the  
332 differences between tridacnids and pectinids ( $1\sigma$  of Ba/Ca among all tridacnid specimens = 2.1  
333  $\mu\text{mol/mol}$ ). Individual records like those in **TM84** and **PM3\_1** show large variability (especially in  
334 Ba/Ca and Mn/Ca) compared to other specimens of the same species. Inter-specimen variability  
335 is higher in tridacnid shells than in pectinids (inter-specimen relative standard deviations as a

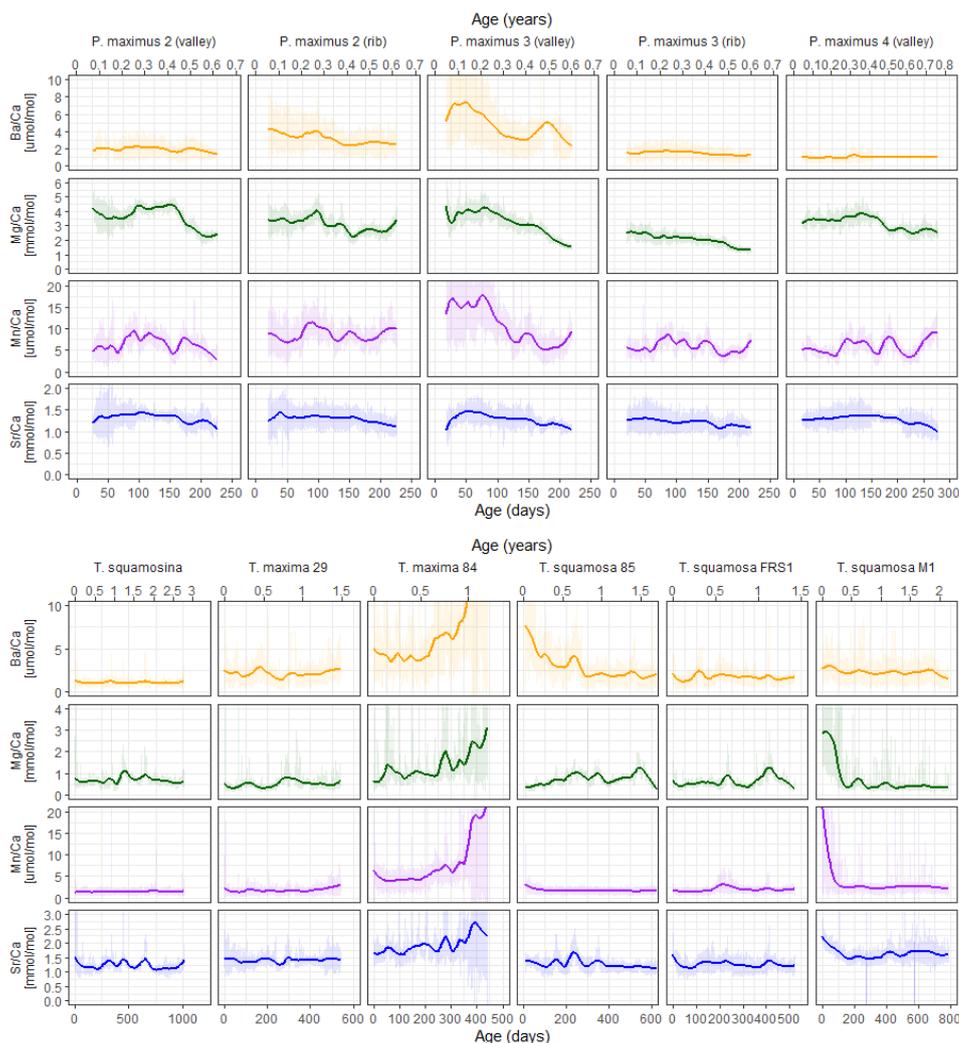


336 fraction of mean ratio for Ba/Ca: 0.74 vs 0.64, Mg/Ca: 0.37 vs 0.20, Sr/Ca: 0.19 vs 0.03 and  
337 Mn/Ca: 0.78 vs 0.33 for tridacnids and pectinids, respectively). **Figure 2** shows that this variability  
338 between tridacnids is not readily explained by differences between species, but mostly reflects  
339 differences in the trends within the records, with some specimens (e.g., **TM84**, **TSM1** and **TS85**)  
340 showing trends in composition towards the end of the record (see also **S8**). Trace element  
341 compositions in tridacnid shells are significantly more skewed towards higher values than in  
342 pectinids (mean skewness per element and per specimen is 9.7 for tridacnids and 0.9 for  
343 pectinids), reflecting the high peaks in trace element composition observed in tridacnid profiles,  
344 especially near the ventral margin (e.g., specimens **TM84**, **TSM1** and **TS85**; see **section 2.4**; **Fig.**  
345 **2**; **S8**). Finally, “rib” and “valley” segments through the same specimen of *P. maximus* show similar  
346 patterns in trace elements, but absolute concentrations (especially of Ba and Mn) can be quite  
347 different, highlighting heterogeneity within the shells of *P. maximus* (**Fig. 2**).

348 Plots of trace element variability reveal dominant high-frequency variability superimposed on  
349 seasonal-scale patterns (**Figure 2**). Trace element profiles in pectinids, reflecting only one  
350 growing season, show a typical seasonal pattern in Sr/Ca and Mg/Ca with maxima in the  
351 elemental ratio in the middle of the profile (corresponding to the summer). Mn/Ca and Ba/Ca in  
352 pectinids are more variable, showing multiple peaks in the same growth year. Peaks in Mn/Ca  
353 and Ba/Ca are synchronous between profiles through the same specimen, but not between  
354 specimens, possibly showing that growth resumed on different days for different specimens after  
355 the winter stop. Like in the pectinid profiles, Mg/Ca, and Sr/Ca ratios in tridacnids show similar  
356 patterns, with one or two distinct cycles per growth year. However, higher frequency variability in  
357 tridacnid ratio profiles is characterized by more extreme peaks, especially in Mg/Ca, skewing the  
358 distribution of trace element values. Mn/Ca and Ba/Ca appear to be less variable in tridacnid  
359 shells than in pectinids, except for specimen **TM84**, which shows a sharp increase in Mn and Ba  
360 towards the end of its lifetime. Mn/Ca and Ba/Ca ratios in tridacnids show more regular annual or



361 biannual variability than pectinids (most notably specimen **SQSA1**). It must be noted, however,  
362 that *P. maximus* shells only recorded one growth season, limiting the interpretation of seasonal  
363 growth patterns.



364

365 **Figure 2:** Overview of LA-ICP-MS results of Sr/Ca (blue), Mg/Ca (green), Mn/Ca (purple) and  
 366 Ba/Ca (orange) in pectinid (upper panel) and tridacnid (lower panel) specimens. Vertical axes are  
 367 equal for plots positioned next to each other (but different for the two groups of tridacnid and  
 368 pectinid plots). Shaded lines show raw LA-ICP-MS data while solid lines indicate 0.2 span LOESS  
 369 fits through the data highlighting monthly-scale variability. A direct comparison of trace elemental  
 370 ratios between specimens is provided in **S8**.



371 3.2 Age models

372 Growth line counting in the *P. maximus* shells was repeated multiple times on both the outer shell  
373 surface and in cross sections through the shell by different persons (**Table 1; S3**). The variability  
374 in counting results shows that the growth lines were not always equally easy to distinguish. In  
375 **PM2** and **PM3**, the most likely number of increments (228 and 220 respectively) was counted in  
376 both cross sections and on the outside of the shell, with other analyses yielding both higher and  
377 lower numbers. In **PM4**, counts on the outside and on the one available cross section were very  
378 close (**Table 1**). In this case, the counting in the cross section (278 increments) was chosen as  
379 reference since the LA-ICP-MS profile was measured on the same cross section and could be  
380 directly linked to the counted increments. The fact that the mean increment width between the *P.*  
381 *maximus* specimens which grew in the same year in the same environment is highly consistent  
382 lends confidence to the layer counting result (**Table 1**). The difference in number of days of growth  
383 between specimens can be caused either by variability in the day on which seasonal growth  
384 commenced (in spring) or the day on which the winter growth stop commenced (in autumn;  
385 Chauvaud et al., 1998). The sampling date (November 15<sup>th</sup>, 2019) does not preclude the onset of  
386 winter growth cessation before the time of sampling. The age-distance relationships (growth  
387 curves) resulting from the sclerochronology are shown in **S5**.

388



389 **Table 1: Growth increments counting in *P. maximus***

<b>Specimen</b>	<b>Increments counted on outer surface</b>	<b>Increments counted in cross sections</b>	<b>Mean increment width [<math>\mu\text{m} \pm 1\sigma</math>]</b>
<b>PM2</b>	226, <b>228</b> , 234, 241	227, <b>228</b> , 233	249 $\pm$ 19
<b>PM3</b>	<b>220</b> , 226, 243	213, <b>220</b> , <b>220</b>	249 $\pm$ 22
<b>PM4</b>	272, 273	<b>278</b>	247 $\pm$ 4

390

391



392 Layer counting in tridacnid shells yielded estimates of semi-diurnal, daily and annual growth  
393 (**Table 2; S4**). Annual growth rates calculated from layer counting are highly consistent between  
394 specimens from the same species from the same environment, lending confidence to the growth  
395 line counting results. The von Bertalanffy growth models based on these growth line countings  
396 are plotted in **S5**. Statistics of the parameters ( $L_{inf}$  and  $k$ ) of these growth models and their  
397 uncertainty are provided in **S4**.

398



399 **Table 2: Growth line counting in *Tridacna* shells.** Column 3 shows the total number of  
 400 increments counted in the specimen, column 4 shows their median width and column 5 shows  
 401 the width of an annual increment in the specimen. Note that increments could not be counted over  
 402 the entire growth period of the shells, so the numbers in column 3 represent representative  
 403 numbers of increments counted in those parts of the shells where they were distinct enough for  
 404 counting (see **section 2.5**) Increment timing (semi-diurnal vs diurnal) was established based on  
 405 the relative difference between small increment width and annual increment width.

Specimen	Species	# counted increments	Median increment width [ $\mu\text{m}$ ]	Annual growth [mm]	Increment timing
TM29	<i>T. maxima</i>	274	26.5	27.9	Semi-diurnal
TM84	<i>T. maxima</i>	109	39.1	26.6	Diurnal
TS85	<i>T. squamosa</i>	310	40.3	20.2	Diurnal
TSFRS1	<i>T. squamosa</i>	225	23.3	20.1	Semi-diurnal
TSM1	<i>T. squamosa</i>	180	33.3	20.6	Diurnal
SQSA1	<i>T. squamosina</i>	153	22.3	14.9	Diurnal

406

407



408 Growth rates are highly similar between specimens of the same species (**Table 1 and Table 2;**  
409 **S3-5**), with *P. maximus* achieving the highest growth rates ( $\sim 220$  growth days \*  $\sim 250$   $\mu\text{m}/\text{d} \approx 55$   
410  $\text{mm}/\text{yr}$ ; **Table 1**), followed by *T. maxima* ( $\sim 27$   $\text{mm}/\text{yr}$ ; **Table 2**), *T. squamosa* ( $\sim 20$   $\text{mm}/\text{yr}$ ; **Table**  
411 **2**) and *T. squamosina* ( $15$   $\text{mm}/\text{yr}$ ; **Table 2**). The age models reveal that the average temporal  
412 resolution of the LA-ICP-MS line scans was 0.04h, 0.24h, 0.44h and 0.27h for *P. maximus*, *T.*  
413 *maxima*, *T. squamosa* and *T. squamosina*, respectively. These estimates were calculated by  
414 dividing the width of the daily increments (e.g.,  $250$   $\mu\text{m}$  for *P. maximus*) by the resolution of the  
415 LAICPMS data ( $0.4$   $\mu\text{m}$ ) to obtain the number of LAICPMS measurements per day (e.g.,  $625$   
416  $\text{pts}/\text{day}$  for *P. maximus*, yielding a mean sampling resolution of 0.04h). Note that the LA-ICP-MS  
417 slit is wider ( $20$   $\mu\text{m}$ ) than the spatial sample resolution, causing some smoothing on the scale of  
418 this very fine temporal resolution. The LA-ICP-MS profiles record trace element variability during  
419 growth periods ranging between 220 days (for **PM3**) and 1041 days (for **SQSA1**).

420

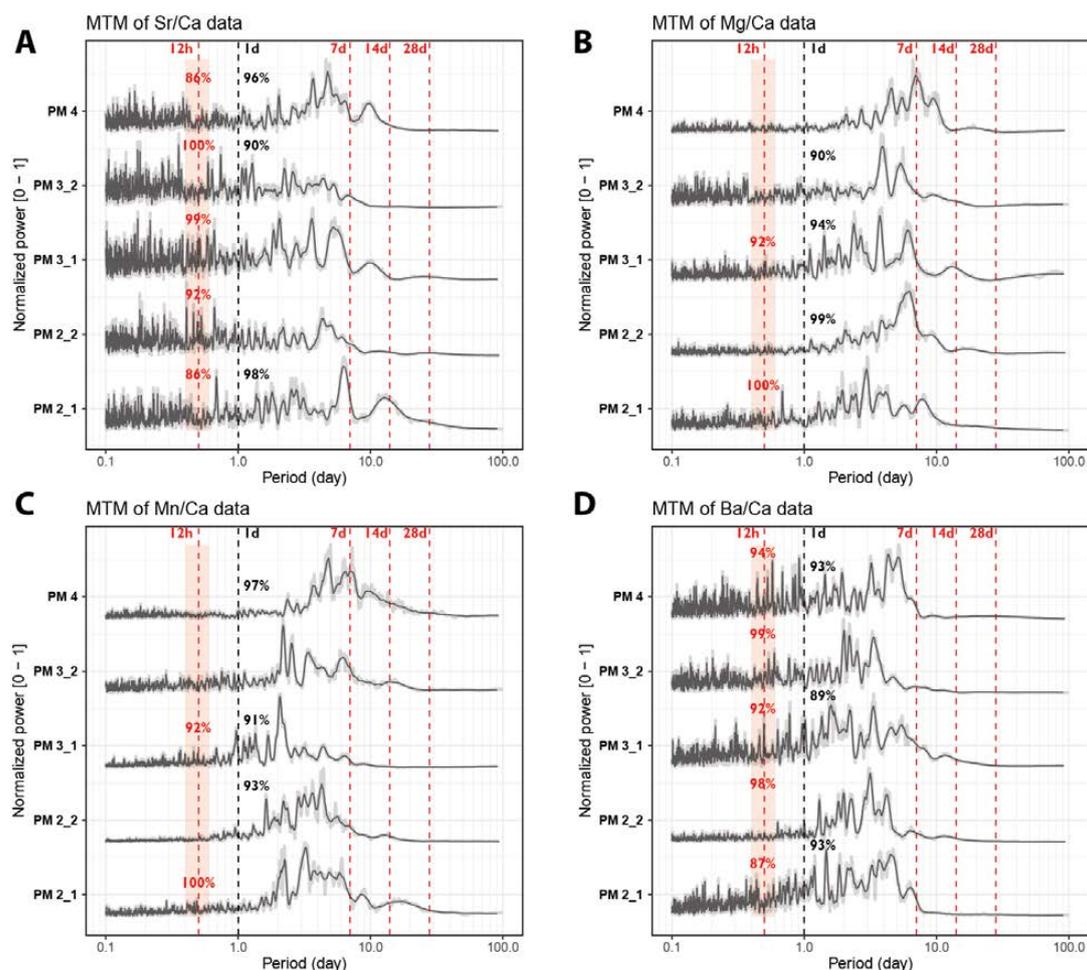
### 421 3.3 Spectral analysis

422 Normalized power spectra and significance level of daily and tidal periodicities in pectinid and  
423 tridacnid records are shown in **Figure 3** and **Figure 4**, respectively. Full spectral analysis results  
424 for all trace element records in all specimens are provided in **S9**. All *P. maximus* power spectra  
425 (**Fig. 3**) reveal semi-diurnal (12h) periodicity in Sr/Ca and Ba/Ca with  $>86\%$  statistical significance.  
426 Only sections through the ribs of the shells (**PM2\_1** and **PM3\_1**) show semi-diurnal periodicity in  
427 Mg/Ca and Mn/Ca ( $>90\%$  significance). Daily periodicity is present in some pectinid profiles, but  
428 there seems to be no consistent pattern in the presence of diurnal variability between specimens,  
429 between sections through ribs or valleys in the shell or between trace element records. Most  
430 power spectra of trace element profiles in pectinids show peaks associated with multi-day tidal  
431 periodicities, the most dominant being a 7-day period, with weaker expression of cyclicity  
432 associated with the fortnightly (14d) cycle or lunar month (28d). The latter is partly suppressed by



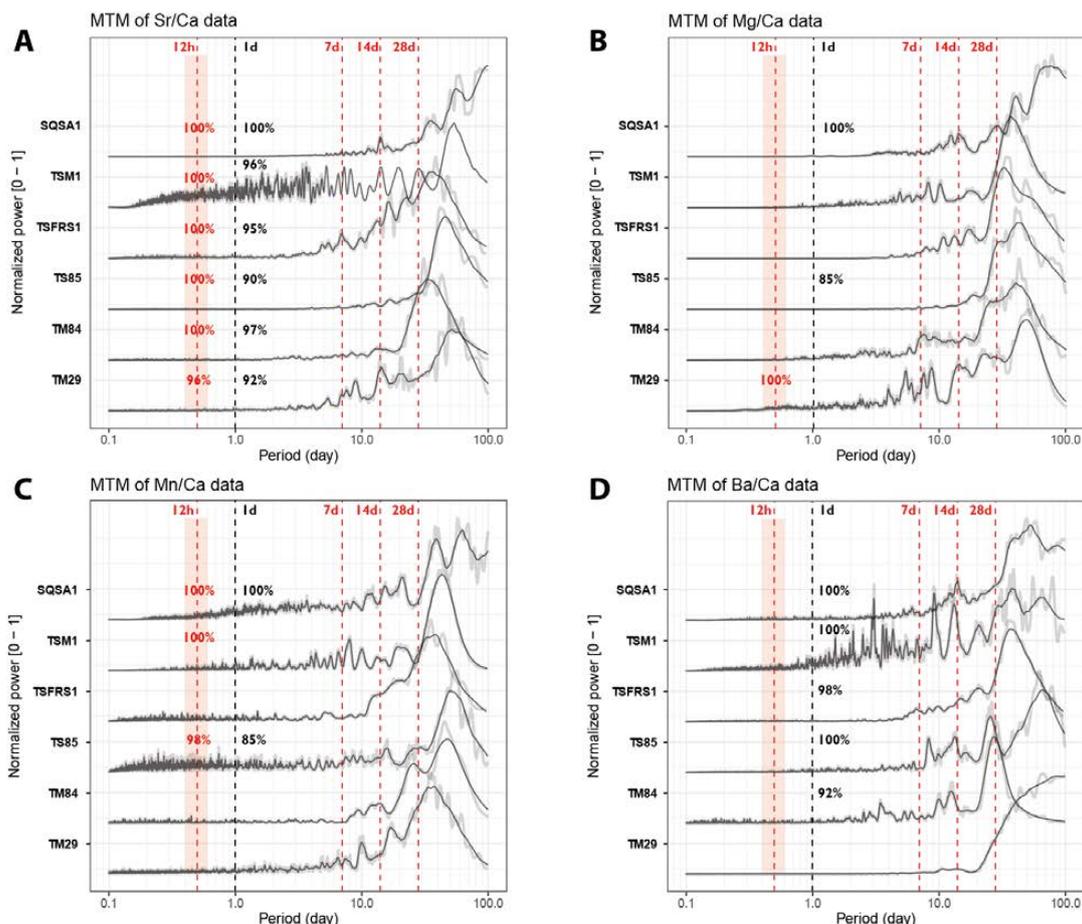
433 the 0.2 span LOESS filter (equivalent to a 44-56 day period depending on the length of the record)  
434 applied on the records to remove the seasonal trend from the records. However, these lower  
435 frequency cycles are clearly visible in the wavelets (see **S9**).

436 A much more consistent expression of diurnal periodicity is found in the tridacnid trace element  
437 profiles compared to those in the pectinids (**Fig. 4**). Especially Sr/Ca and Ba/Ca records through  
438 nearly all tridacnid specimens exhibit strong (>90% confidence level) power in the daily period,  
439 while Mn/Ca and Mg/Ca records exhibit much less periodicity. Sr/Ca records in the tridacnids also  
440 contain a significant (>96%) semi-diurnal component, whose tidal origin seems clear in most  
441 specimens by peaks in power in the longer (7d, 14d and 28d) tidal components.



442

443 **Figure 3:** Multi-taper method spectrograms of Sr/Ca (A), Mg/Ca (B), Mn/Ca (C) and Ba/Ca (D)  
 444 records through the five pectinid cross sections after detrending (see **section 2.6**). All spectra are  
 445 normalized by dividing by the highest power peak and plotted on the same horizontal axis. Grey  
 446 shaded lines show raw data while solid black lines plot 21-point moving average smoothed  
 447 curves. Red vertical dashed lines highlight the expected periods of tidal variability while black  
 448 vertical dashed lines indicate 1-day periodicities. Significance levels of peaks on these periods  
 449 (see **section 2.6** and Meyers, 2012) are rounded to the nearest whole percentage point.



450

451 **Figure 4:** Multi-taper method spectrograms of Sr/Ca (A), Mg/Ca (B), Mn/Ca (C) and Ba/Ca (D)  
 452 records through the six tridacnid cross sections after detrending (see **section 2.6**). All spectra are  
 453 normalized by dividing by the highest power peak and plotted on the same horizontal axis. Grey  
 454 shaded lines show raw data while solid black lines plot 21-point moving average smoothed  
 455 curves. Red vertical dashed lines highlight the expected periods of tidal variability while black  
 456 vertical dashed lines indicate 1-day periodicities. Significance levels of peaks on these periods  
 457 (see **section 2.6** and Meyers, 2012) are rounded to the nearest whole percentage point.

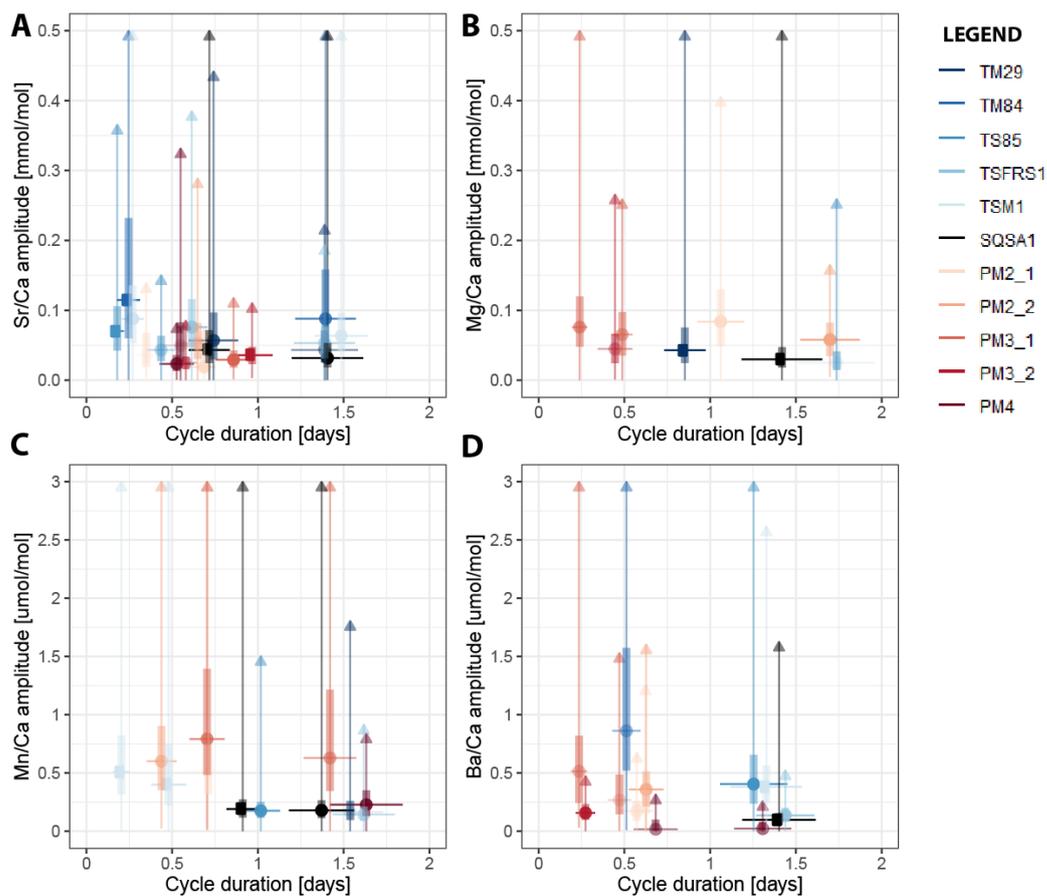
458



459 3.4 Variance decomposition

460 Variability at the daily (24h) and tidal (12h) scale in all trace element records through all specimens  
461 was extracted using bandpass filtering (**section 2.7**; see **S9** and **S10**). The median amplitude of  
462 variability within these stacks was plotted against the median period of the variability per element  
463 and per specimen to highlight dominant periodicities in the trace element data (**Figure 5**). As  
464 noted in the spectral analysis results (**section 3.3**), trace element composition in tridacnid shells  
465 is more strongly controlled by daily variability than in pectinid shells (**Fig. 5**; **S10**). The difference  
466 is especially noticeable in Sr/Ca and Ba/Ca ratios, which show a clear divide between daily  
467 periodicity in tridacnid shells and tidal periodicity in pectinids (see **Fig. 5**). The differences in  
468 Mg/Ca and Mn/Ca ratios are less clear.

469



470

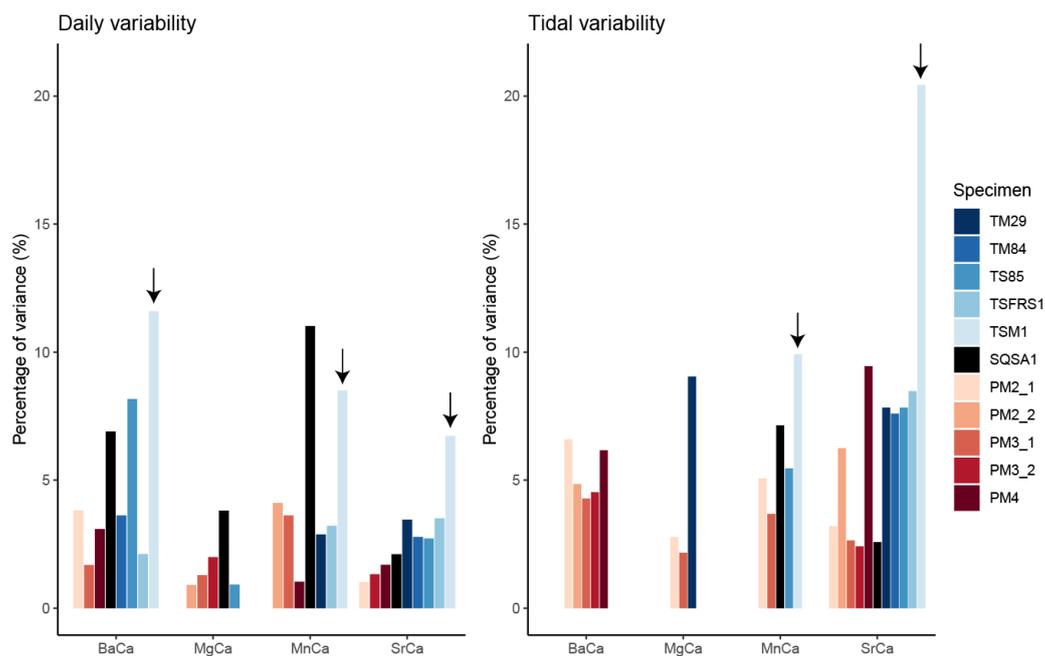
471 **Figure 5:** Cross plot showing the amplitude of variability of dominant spectral periods in Sr/Ca  
472 (A), Mg/Ca (B), Mn/Ca (C) and Ba/Ca (D) against the period (duration) of the cycle. Round  
473 symbols indicate the median amplitude of the cycle, while vertical bars and lines show interquartile  
474 differences and ranges in the amplitude over the record. Horizontal bars indicate the width of the  
475 bandpass filter used to extract periodic variability. Colors highlight different specimens (see  
476 legend).

477



478 An example of the distribution of normalized variability within the trace element records after each  
479 data processing step is shown in **S7**. From this example it is clear that a large fraction of the  
480 variance in the records (73% in this record after trimming outliers) is explained by low-frequency  
481 variability (**S7**). Of the remaining smoothed and detrended dataset, at most 20% of the variance  
482 is explained by daily and tidal (semi-diurnal) periodicity (see **Figure 6** and **Table 3**). A full  
483 decomposition of variance in all trace element records through all specimens is provided in **S7**.  
484 **Figure 5** and **Figure 6A** shows that, overall, the variance explained by daily periodicity is higher  
485 in tridacnids than in pectinids (Wilcoxon signed rank test;  $W = 44$ ;  $p = 0.009$ ). The difference  
486 between species is smaller for tidal variability (**Fig. 6B**). There is no clear difference in relative  
487 dominance of tidal variability between trace element records, but daily variability is more strongly  
488 expressed in Ba/Ca and Mn/Ca records, especially in tridacnid shells. Finally, *T. squamosa*  
489 specimen **TSM1**, which grew under a sunshade, does not exhibit significantly lower daily  
490 periodicity compared to the other tridacnid specimens.

491



492

493 **Figure 6:** Summary of relative variance (in %) of significant daily (left) and tidal (right) variability  
494 extracted from trace element records. Colors highlight different specimens (see legend). Note that  
495 the *T. squamosa* specimen **TSM1** which grew under a sunshade is highlighted with a black arrow.

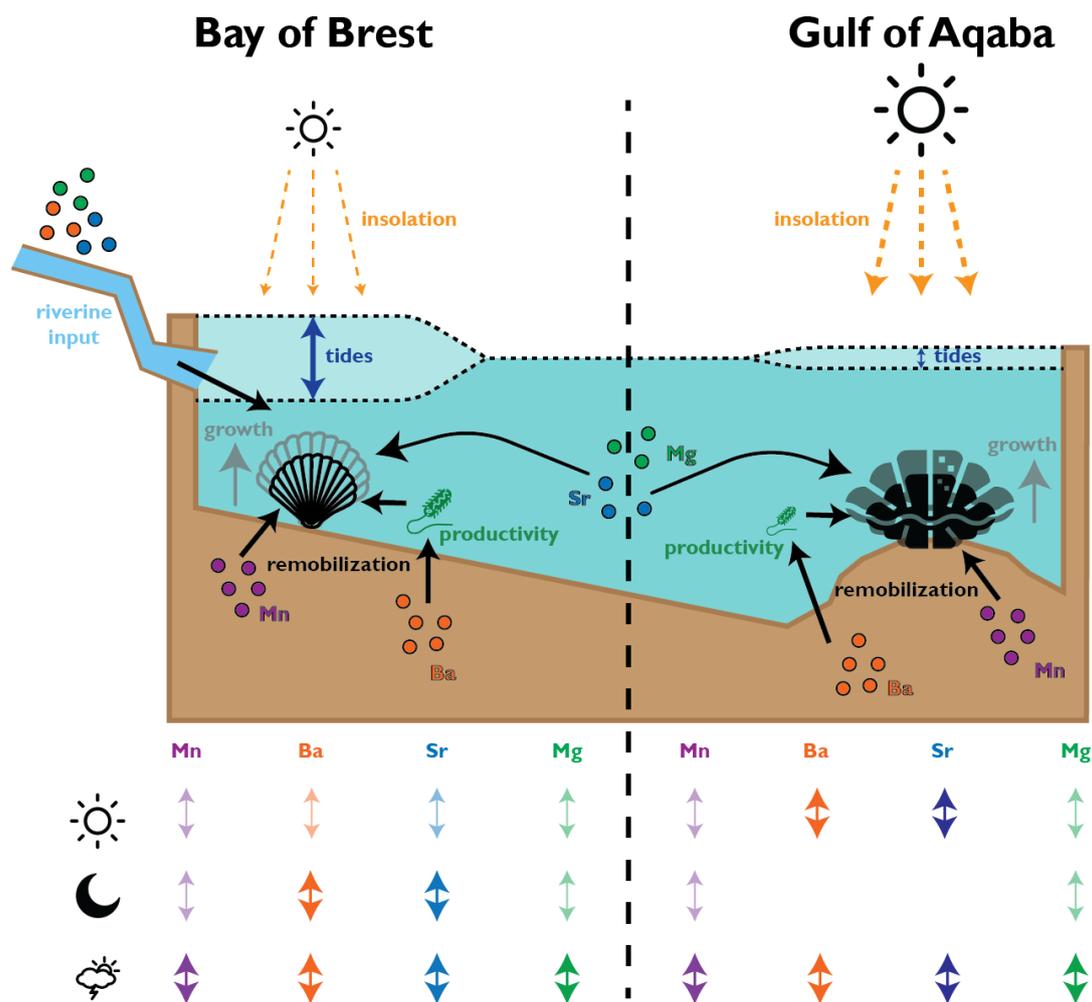
496



497 **Table 3:** Overview of the relative (in %) variance associated with daily and tidal variability in all  
 498 trace element records through all specimens. Empty cells represent records for which no  
 499 significant tidal or daily periodicity was found (see Fig. 3-4).

	Daily variance				Tidal variance			
	[% relative to detrended record]				[% relative to detrended record]			
	Ba/Ca	Mg/Ca	Mn/Ca	Sr/Ca	Ba/Ca	Mg/Ca	Mn/Ca	Sr/Ca
<b>PM2_1</b>	3.8 %			1.0 %	6.6 %	2.8 %	5.1 %	3.2 %
<b>PM2_2</b>		0.9 %	4.1 %		4.9 %			6.3 %
<b>PM3_1</b>	1.7 %	1.3 %	3.6 %		4.3 %	2.2 %	3.7 %	2.7 %
<b>PM3_2</b>		2.0 %		1.3 %	4.5 %			2.4 %
<b>PM4</b>	3.1 %		1.0 %	1.7 %	6.2 %			9.5 %
<b>TM29</b>			2.9 %	3.5 %		9.0 %		7.8 %
<b>TM84</b>	3.6 %			2.8 %				7.6 %
<b>TS85</b>	8.1 %	0.9 %		2.7 %			5.5 %	7.8 %
<b>TSFRS1</b>	2.1 %		3.2 %	3.5 %				8.5 %
<b>TSM1</b>	12 %		8.5 %	6.7 %			10 %	20 %
<b>SQSA1</b>	6.9 %	3.8 %	11 %	2.1 %			7.1 %	2.6 %

500



501

502 **Figure 7:** Schematic overview of environmental parameters interpreted to affect shell growth and  
 503 composition of pectinids in the Bay of Brest and tridacnids in the Gulf of Aqaba. The table at the  
 504 bottom provides a schematic qualitative overview of the amount of variance in the trace element  
 505 records of the taxa is explained by daily (sun symbol), tidal (moon symbol) or aperiodic (cloud  
 506 symbol) variability in the environment.

507



508 **4. Discussion**

509 4.1 Trace element variability in *P. maximus*

510 4.1.1 Comparison with previous studies

511 Trace element concentrations in *P. Maximus* analyzed in this study are in close agreement with  
512 concentrations found in wild (live collected) *pectinid* shells in the literature (Lorrain et al., 2005;  
513 Barats et al., 2008; Poitevin et al., 2020; Fröhlich et al., 2022). In these studies, Sr/Ca shows a  
514 strong link with calcification rate (as measured by the width of daily shell increments; Lorrain et  
515 al., 2005), although previous studies did not assess variability on the (sub-)daily scale. The long-  
516 term trends in our Sr/Ca records seem to confirm this correlation, with higher values being  
517 recorded in the middle of the growing season (day 50-150; **Fig. 2**) when growth rates are highest  
518 (see **S5**). There is some discussion on the dependence of Mg/Ca ratios in pectinid shells to  
519 temperature and/or salinity (Lorrain et al., 2005; Poitevin et al., 2020). This study's individuals that  
520 grew during the same year in the same environment do not show a synchronous Mg/Ca pattern  
521 (**Fig. 2**), arguing against a simple temperature dependence for Mg/Ca in *P. maximus*. In addition,  
522 the lack of strict coherence between profiles of Mg/Ca (and other elements) in parallel transects  
523 through *P. maximus* shells (e.g., **PM2\_1** and **PM2\_2**; **Fig. 2**) hints at compositional heterogeneity  
524 within the shells. Low correlations between profiles through the same shell at the daily scale are  
525 also partly driven by small misalignments of the timing of shell formation between the transects  
526 at the sub-millimeter scale and variations in the height of trace element peaks, especially in Mn/Ca  
527 and Ba/Ca, which are higher further towards the outside of the shell (**S2**). There is evidence  
528 suggesting that Mg content varies in mollusk shells in function of the amount of organic matter in  
529 the biomineral (Dauphin et al., 2003; Richard, 2009; Tanaka et al., 2019). Contrarily, Mn is taken  
530 up in thermodynamic equilibrium in the mineral fraction of bivalve shells (Onuma et al., 1979;  
531 Soldati et al., 2016), and Mn/Ca ratios in *P. maximus* have been shown to faithfully record  
532 fluctuations of dissolved Mn in the coastal environment driven by riverine input and redox



533 conditions (Barats et al., 2008). Similarly, there is strong evidence that Ba/Ca ratios in *P. maximus*  
534 (and other mollusks) record changes in Ba available in the environment linked to primary  
535 productivity (e.g., Gillikin et al., 2008; Thébault et al., 2009; Fröhlich et al., 2022). This relationship  
536 would explain the skewed (skewness > 1; **S8**) character of the Ba/Ca records and the correlation  
537 between Ba/Ca and Mn/Ca in our *P. maximus* specimens, as the reducing conditions following  
538 peaks in primary productivity favor the remobilization of Mn into the water column causing short-  
539 lived simultaneous increases in Ba/Ca and Mn/Ca in the shells (Dehairs et al., 1989; Barats et al.,  
540 2008; 2009).

#### 541 4.1.2 Short-term changes in shell composition in tridacnids

542 In the context of the high-resolution trace element variability central to this study, it seems  
543 plausible that short-term changes in the environment of the Bay of Brest were drivers of Mn/Ca  
544 and Ba/Ca variability in *P. maximus* shells, while Mg/Ca and Sr/Ca composition is mostly driven  
545 by changes in calcification rate. This would suggest that the significant tidal (12h) component in  
546 Ba/Ca and Mn/Ca records through *P. maximus* (**Fig. 3**) is driven directly by redox changes over  
547 the strong tidal cycle in the Bay of Brest (see Polsenaere et al., 2021) and resuspension of Ba  
548 and Mn due to tidal currents (Hily et al., 1992), while tidal rhythms in Mg/Ca and Sr/Ca may be a  
549 consequence of the scallop's calcification response to changes in its environment (e.g.,  
550 temperature, salinity and light availability) through the large (up to 7m range) tidal cycle (**Fig. 7**).  
551 The latter corroborates with previous studies in other calcitic mollusk shells which demonstrated  
552 that Mg incorporation on short timescales is driven by the metabolic response to subtle changes  
553 in the environment (Lazareth et al., 2007). Finally, care must be taken to interpret trace element  
554 variability in *P. maximus* shells, since large intra-shell gradients in Mg/Ca, Sr/Ca and Mn/Ca have  
555 previously been observed in this species, making trace element composition highly dependent on  
556 the location of measurements relative to the outer shell surface or positioning relative to striae on  
557 the shell surface (Freitas et al., 2009). Even though the LA-ICP-MS line scans in this study



558 targeted exclusively the oOSL of *P. maximus* specimens, variability in elemental ratios resulting  
559 from small changes in the distance of the line scan from the outer edge of the shell cannot be fully  
560 excluded (Richard, 2009).

561

## 562 4.2 Trace element variability in tridacnids

### 563 4.2.1 Comparison with previous studies

564 Results for Sr/Ca, Mg/Ca and Ba/Ca in this study's tridacnid specimens broadly corroborate trace  
565 element results in other tridacnid studies (e.g., Elliot et al., 2009; Sano et al., 2012; Yan et al.,  
566 2013; Warter et al., 2018). While data on Mn/Ca in the OSL of tridacnids is scarce, the Mn/Ca  
567 ratios in tridacnids in this study (mean Mn/Ca =  $7.8 \pm 4.7$   $\mu\text{mol/mol}$ ) are similar to LAICPMS Mn/Ca  
568 data available in the literature (Warter et al., 2015, 4-10  $\mu\text{mol/mol}$ ), but significantly lower than  
569 Mn/Ca values measured using total digestion Atomic Absorption Spectrometry (Madkour, 2005,  
570  $\sim 30$   $\mu\text{mol/mol}$ ). The main difference between the techniques is that LA-ICP-MS (both in this study  
571 as in Warter et al., 2015) sampled shell layers where growth lines were visible and did not include  
572 pre-treatment, while the total digestion study (Madkour, 2005) removed organic matter by roasting  
573 the shells at 200°C prior to bulk shell analysis. The difference in results may therefore hint at  
574 differences between shell layers within tridacnids, or differences in Mn concentration between the  
575 organic and mineral fractions in the shells. Bivalve typically contain between 1% and 5% organic  
576 matter (Marin and Luquet, 2004), with tridacnid shells being notable for their low organic matter  
577 content (<1%; Agbaje et al., 2017; Taylor and Layman, 1972). Given that most Mn in bivalve  
578 shells is typically associate with the mineral fraction of the shell (Soldati et al., 2016), it seems  
579 unlikely that such a large fraction of Mn could originate from the organic matrix. Therefore, we  
580 consider a difference in Mn concentration between shell layers in tridacnids more likely. The lack  
581 of consistent trace element offsets between the tridacnid species under study here (*T. maxima*,



582 *T. squamosa* and *T. squamosina*) confirms the chemical similarities of shells tridacnid species  
583 found in previous studies (e.g., *T. gigas*; Elliot et al., 2009; Yan et al., 2013; *T. crocea*; Warter et  
584 al., 2018; *T. derasa*; Sano et al., 2012).

#### 585 4.2.2 Short-term variability in Sr/Ca

586 Sr/Ca in tridacnids is thought to be strongly controlled by light intensity through a circadian rhythm  
587 linked to the day-night cycle (Sano et al., 2012; Warter et al., 2018). This would explain the strong  
588 daily periodicity in Sr/Ca records through all tridacnids in this study. This daily periodicity may be  
589 caused by the ctenidium in tridacnids working on a daily rhythm to keep the acid-base balance in  
590 the hemolymph of the clams to offset the CO<sub>2</sub> depletion by photosymbionts (which is paced to the  
591 day-night cycle of light availability). In the process, Ca<sup>2+</sup>-channels and Na<sup>+</sup>/H<sup>+</sup>-exchangers work  
592 to keep the charge balance in the internal fluid and provide nutrients and ions for shell  
593 mineralization, letting in compatible trace elements such as Sr<sup>2+</sup> (Ip and Chew, 2021). This  
594 mechanism could explain the indirect link between trace element uptake in the shell in tridacnids  
595 and the day-night cycle without a direct causal relationship between trace element concentration  
596 and light availability (as demonstrated by the strong daily cycle in trace elements in the shaded  
597 **TSM1** specimen). It is worth noting that experiments on freshwater bivalves (e.g., *Corbicula*  
598 *fluminea*; Zhao et al., 2017) revealed that a closure of the Ca<sup>2+</sup> channels did not influence Sr  
599 concentrations in the shell, arguing against a kinetic effect on Sr partitioning into the shell.

#### 600 4.2.3 Tidal vs. diurnal variability

601 Our spectral analysis does not allow us to distinguish between the expression of the solar day  
602 (24h) and lunar day (~24.8h) because the width of the bandpass filters used to extract periodicities  
603 encompass both frequencies. While we cannot exclude the possibility that some of the daily (24h  
604 frequency band) periodicity in tridacnid records is an expression of the lunar cycle, it seems  
605 unlikely for most records except Sr/Ca, because the expression of the other lunar cycles (most



606 notably the ~12h cycle) is much weaker in tridacnids compared to the pectinids. Nevertheless, it  
607 remains possible that the diurnal cycle in Sr/Ca in tridacnids, previously interpreted as a response  
608 to the day-night cycle, is in fact caused by a circadian rhythm paced to the lunar day. Additionally,  
609 vertical mixing, a major driver of sea surface temperature changes in the northern Gulf of Aqaba  
610 is shown to be driven by a combination of surface wind intensity (which has strong daily variability)  
611 and the presence of tidal currents (Carlson et al., 2014). It is therefore possible that changes in  
612 local surface water temperature partly control the observed (semi-)diurnal variability.

#### 613 4.2.4 Seasonal variability

614 On longer (seasonal) timescales, Sr/Ca in tridacnids has been suggested as a temperature proxy  
615 similar to the well-known Sr/Ca-Sea Surface Temperature relationship in tropical corals (Lough,  
616 2010; Yan et al., 2013). However, significantly lower Sr/Ca ratios in tridacnids compared to coral  
617 aragonite (1.5 – 2.0 mmol/mol vs. 7.5 – 9.5 mmol/mol in corals; Elliot et al., 2009; **Fig. 2**) suggest  
618 that tridacnids exert a large degree of biological control on the Sr concentration in their shells,  
619 either possibly through the light-sensitive photosymbiosis-calcification relationship outlined above  
620 or otherwise through active Sr removal from the biomineralization site by Sr-binding organic  
621 molecules. Similarly, Mg/Ca ratios in tridacnids were previously thought to primarily record water  
622 temperature (e.g., Batenburg et al., 2011) but detailed investigation shows here large differences  
623 in Mg concentration within tridacnid shells. and a strong anticorrelation of Mg with sulfur  
624 compounds associated with the organic matrix in the shell (see **section 4.1**; Dauphin et al., 2003),  
625 has been put forward as evidence for a strong control of calcification and microstructure on Mg  
626 composition in tridacnid shells (Yoshimura et al., 2014). However, evidence from studies on  
627 foraminifera calcification demonstrate that the sulfur in biocarbonates is not organically bound  
628 and that the covariation with Mg might instead be caused by lattice distortion due to incorporation  
629 of Mg favoring simultaneous S incorporation (van Dijk et al., 2017).

#### 630 4.2.5 Ba/Ca and Mn/Ca in tridacnids



631 As in the pectinids, Ba/Ca ratios in tridacnids likely reflect changes in Ba in the environment, which  
632 can be caused by river input, upwelling of comparatively nutrient-rich waters or blooms of Ba-rich  
633 phytoplankton (Vander Putten et al., 2000; Elliot et al., 2009). Given that Mn is mostly associated  
634 with the mineral fraction of bivalve shells and seems to fractionate into the shell close to  
635 equilibrium with seawater (Onuma et al., 1979; Soldati et al., 2016), Mn/Ca ratios in tridacnids  
636 likely reflect the availability of dissolved Mn in the water column, as in other mollusk taxa (e.g.,  
637 Barats et al., 2008; see **section 4.1**). This assumption is supported by the correlation between  
638 Mn/Ca and Ba/Ca measured in this study (**Fig. 2**), suggesting that both records are influenced on  
639 seasonal timescales by variability in nutrient availability and redox conditions (*sensu* Dehairs et  
640 al., 1989). Part of this correlation between Mn/Ca and Ba/Ca is driven by synchronous increases  
641 in both elements near the start and end of the profiles through tridacnid shells (**Fig. 2**). These  
642 changes may reflect a decrease of control on shell composition during periods of stress, or  
643 alternatively reflect periods of slower growth which cause more primitive microstructures  
644 (characterized by higher concentrations of trace elements) to be formed (Warter et al., 2018).

#### 645 4.2.6 Environmental changes in the Gulf of Aqaba

646 Given that the Gulf of Aqaba is oligotrophic, seasonally stratified, and lacks significant riverine  
647 input (Nassar et al., 2014; Manasrah et al., 2018), the variability in nutrient concentrations and  
648 redox conditions driving Mn/Ca and Ba/Ca variability in tridacnids are likely driven by convective  
649 overturning. The tidal amplitude is much smaller than in the Bay of Brest (<1 m; Manasrah et al.,  
650 2018) and is unlikely to drive significant short-term fluctuations in sea water chemistry. This may  
651 therefore explain the lack of tidal (12h) periodicity in Ba/Ca and Mn/Ca in tridacnids (**Fig. 5** ).  
652 Nevertheless, tidal rhythms have been observed in the behavior and growth of deep-sea bivalves  
653 living far below the direct influence of tides on the environment, proving that such patterns can be  
654 recorded by the animals through their circadian rhythm (Schöne and Giere, 2005; Nedoncelle et  
655 al., 2013; Mat et al., 2020). In this case, the daily cycle seems to have been more important for



656 Ba/Ca in tridacnids, plausibly by driving diurnal changes in primary productivity in the Gulf of  
657 Aqaba. Alternatively, the daily periodicity found in tridacnid shell chemistry may in fact be a  
658 response to the lunar day (~24.8h) cycle, which is imprinted in the shell's chemical composition  
659 through periodic exposure of the clams to extreme heat or air (subaerial exposure) in their shallow  
660 water environment during exceptionally low tides. The stress induced from this exposure could  
661 have affected calcification and incorporation of trace elements (see above).

662 Interestingly, Sr/Ca ratios in tridacnids do exhibit tidal periodicity (**Table 2**), perhaps driven by a  
663 circadian rhythm in calcification linked to the tidal cycle, or by subtle changes in water temperature  
664 driven by tidal currents (Carlson et al., 2014). This 12h periodic behavior is not observed in  
665 previous studies of Sr/Ca ratios in tridacnids (Sano et al., 2012; Warter et al., 2018). A recent  
666 valvometric study on tridacnids found a 12h period in activity, which supports the hypothesis that  
667 a circadian rhythm paced to the tidal cycle could influence shell calcification (Killam et al., 2022).  
668 Significant daily fluctuations in solar radiation (up to 1500 W m<sup>-2</sup>; Manasrah et al., 2018) likely  
669 exerted a dominant control on the calcification of tridacnids, explaining the strong diurnal  
670 periodicity in Sr/Ca and Ba/Ca records in this study (see **Fig. 7** and **Fig. 9**). As in the (non-  
671 symbiotic) pectinid data, it seems likely that the majority of Mn/Ca and Ba/Ca variability in  
672 tridacnids directly reflects changes in the chemistry of the sea water and its constituents (e.g.,  
673 particulate organic matter) while Mg/Ca and Sr/Ca variations are driven by changes in calcification  
674 and microstructure. The latter may be indirectly influenced by light intensity through  
675 photosynthesis by the symbionts, or by circadian rhythms paces to the diurnal or tidal cycle.

676

677 4.3 Role of photosymbiosis on high-frequency chemical variability

678 4.3.1 Effect of symbiosis on calcification



679 While the amplitude of diurnal variability in trace element concentrations does not vary much  
680 between the symbiotic tridacnids and the non-symbiotic pectinids (**Fig. 5**), the amount of variance  
681 in the trace element records explained by daily cyclicity is up to twice as high in tridacnids (**Fig.**  
682 **6; Table 3**). This suggests that the 24h cycle has a much larger relative influence on trace element  
683 composition (especially Sr/Ca and Ba/Ca) in tridacnids than in pectinids. This seems to point  
684 towards a role of the photosymbionts in calcification by tridacnids, such as through symbiont-  
685 mediated diurnal variation in the pH of the extrapallial fluid (Ip et al., 2006), as well as active  
686 transport of  $\text{HCO}_3^-$  for calcification (Chew et al., 2019) and as a C supply to the symbionts from  
687 the host (Boo et al., 2021). Given the differences in absolute ratios between these two groups of  
688 bivalves, comparing variance yields a more robust assessment of the relative importance of tidal  
689 or diurnal variability on shell composition than looking at the absolute size (amplitude) of the  
690 chemical cycle. While the difference in variance is clear, the importance of diurnal cyclicity on the  
691 photosymbiotic tridacnids is not as big as one might expect. Rarely more than 10% of the variance  
692 is explained by day-night variability (**Table 3**). This seems to contradict the large daily Sr/Ca  
693 amplitudes found in Warter et al. (2018) and the trace element fluctuations found in de Winter et  
694 al. (2020), which rival the seasonal cycle in these trace element ratios in terms of amplitude.  
695 However, the percentages in **Table 3** relate to the amount of variation in the complete records  
696 through these individuals and therefore also contain areas of the shell where daily cyclicity is less  
697 pronounced, while values in previous studies often reflect maximum amplitudes recorded in parts  
698 of the shell with exceptionally clear daily increments.

#### 699 4.3.2 Effect of differences in the environment

700 It seems plausible that part of the difference in diurnal variability between pectinids and tridacnids  
701 is explained by a difference in the environment between the Gulf of Aqaba and the Bay of Brest,  
702 rather than the presence of photosymbionts. The diurnal insolation cycle in the Gulf of Aqaba is  
703 larger than in the Bay of Brest (1500 vs 546  $\text{W}\cdot\text{m}^{-2}$  maximum summer irradiance; Roberts et al.,



704 2018; Manasrah et al., 2019). If calcification in pectinids would be equally sensitive to sunlight,  
705 this difference may explain much of the difference between the species. In this scenario, part of  
706 the strong tidal component in the pectinid trace element data may be explained by the influence  
707 of differences in water depth on the penetration of sunlight through the murky waters of the Bay  
708 of Brest (Roberts et al., 2018). In fact, tidal movement can cause strong non-linear amplification  
709 or reduction of the solar irradiance at the sea floor of the Bay of Brest by factors exceeding 10,  
710 especially outside the summer months, which in turn has a significant effect on primary  
711 productivity in the water column (Roberts et al., 2018). This tidal effect is likely to be much weaker  
712 in the Gulf of Aqaba, given its comparatively low tidal amplitude, clear oligotrophic waters, and  
713 much stronger and less seasonal day-night cycle (Manasrah et al., 2019). Indeed, even in non-  
714 photosymbiotic bivalves, light and food availability are demonstrated to be major drivers of the  
715 animal's behavior (e.g., Ballesta-Artero et al., 2017). The combination of the daily and tidal cycles  
716 on solar irradiance at depth and photosynthesis in the Bay of Brest may therefore pose an  
717 alternative pathway for strong tidal cyclicity in the trace element composition of pectinids in this  
718 study and account for part of the twofold increase in daily variability in tridacnids compared to the  
719 pectinids (**Fig. 6-7; Table 3**).

#### 720 4.3.3 Effect of direct insolation

721 Specimen **TSM1** poses an interesting case study for investigating the link between sunlight and  
722 calcification in tridacnids, since it grew under a sunshade and therefore experienced a dampened  
723 diurnal variability in insolation compared to other giant clams in the area. The fact that this  
724 specimen exhibits similar or even higher diurnal variability in shell chemistry (**Fig. 6**) argues  
725 against a direct influence of the rate of photosynthesis itself on calcification. Instead, it seems that  
726 daily chemical variability is mostly an expression of circadian rhythm in tridacnids, which is  
727 strongly (evolutionarily) coupled to the day-night cycle to optimize the symbiosis with primary  
728 producers in its mantle, possibly through respiration rhythms carried out by the ctenidium (see



729 **section 4.2;** Ip and Chew, 2021). Symbionts have been shown to directly aid in calcification in  
730 terms of proton pumping (Armstrong et al., 2018), influencing internal acid-base chemistry (Ip et  
731 al., 2006), and valvometric studies show the clams bask in sunlight in daylight hours and close  
732 partially at night when symbiosis is likely reduced (Schwartzmann et al., 2011). This conclusion  
733 is further supported by the lack of a clear difference in diurnal cyclicity between trace element  
734 records in *T. maxima*, *T. squamosa* and *T. squamosina* (**Fig. 6; Table 3**), even though the degree  
735 of reliance on photosymbiosis is demonstrated to be highly variable between these species  
736 (Killam et al., 2020). Therefore, it seems unlikely that sub-daily resolved trace element records in  
737 tridacnids can be used as quantitative recorders of paleo-insolation, as was originally suggested  
738 by Sano et al. (2012). While the degree of symbiotic activity may not be clearly recorded in the  
739 daily amplitude of trace element oscillations, the greater consistency of daily periodic signal in the  
740 studied giant clams could relate to the direct biological control exerted by the symbionts on the  
741 hosts' rhythms of calcification. Light exposure in giant clams promotes expression of genes coding  
742 for proteins involved  $\text{Ca}^{2+}$ ,  $\text{H}^+$  and  $\text{HCO}_3^-$  transport in the mantles of giant clams (Ip et al., 2017;  
743 Chew et al., 2019), with the expression proposed to be at least partially mediated by photosensing  
744 on the part of the symbionts themselves (Ip et al., 2017). Differences between the daily  
745 consistency (spectral power) of photosymbiotic and non-photosymbiotic trace element profiles  
746 might still allow paleontologists to use the presence of strong daily periodicity as a proxy for  
747 photosymbiosis in the fossil record (as suggested in de Winter et al. 2020). However, the small  
748 differences found between pectinids and tridacnids in this study and the comparatively large  
749 influence of environmental variability show that such records should be interpreted with caution.  
750 Future studies could measure photosynthetic activity of the symbionts in tridacnids and attempt  
751 to relate this to the trace element composition of the shell in an attempt to isolate the direct effect  
752 of photosymbiosis on shell composition.

753



754 4.4 Aperiodic drivers of shell chemistry

755 4.4.1 Circadian and behavioral changes

756 Even after controlling for instrumental noise, most (~90%) of the variance observed in our trace  
757 element records is not directly related to the diurnal or tidal cycle. This suggests that aperiodic  
758 events at the scale of hours to days play an important role in the calcification of pectinids and  
759 tridacnids. Given the large difference in ecological niche (e.g., photosymbiotic versus non-  
760 symbiotic) between these taxa, and the difference between the environment in which they grew,  
761 this observation suggests that calcification of bivalves at the (sub-)daily scale may generally be  
762 dominated by aperiodic variability in calcification or in the environment. Part of this unaccounted  
763 variability may be caused by variability in the animal's behavior, as documented by observations  
764 of siphon and valve gape activity in cultured or monitored specimens of a variety of bivalve taxa  
765 (Rodland et al., 2006; Ballesta-Artero et al., 2017). While these experiments revealed quasi-  
766 periodic (3-7 minute and 60–90 minute periods) behavior unassociated with the tidal or daily cycle,  
767 records of activity of the individuals also reveal less regular patterns on the scale of 2-24h which  
768 may contribute to the aperiodic variance in trace element records (Rodland et al., 2006). Another  
769 example of aperiodic behavior potentially influencing shell chemistry is rapid valve adduction or  
770 “coughing” observed in both pectinids and tridacnids, which serves as a mechanism for expelling  
771 respiratory CO<sub>2</sub> and faeces from the pallial cavity or to evade predation attempts (Robson et al.,  
772 2012; Soo and Todd, 2014). This behavior could resuspend sediment and produce pulses of Mn  
773 and Ba at the sediment-water interface which are recorded as short-term, aperiodic variability in  
774 these elements in the shell. The temporal sampling resolution (>1h) of trace element records after  
775 smoothing out measurement noise does not allow us to resolve periodic variability at the sub-  
776 hourly scale cited in these previous studies, meaning that aperiodic variability in behavior and  
777 aliasing of these ultradian patterns likely contribute to the aperiodic variability in our trace element  
778 records. On longer (sub-)seasonal timescales, activity in bivalves is shown to be highly dependent



779 on food and light availability (Ballesta-Artero et al., 2017), suggesting that aperiodic, short-term  
780 changes in these environmental factors could be a main driver of shell growth and composition  
781 and explain a large part of the variance in the trace element records which is not explained by  
782 ultradian changes in the animal's behavior.

#### 783 4.4.2 Short-term environmental changes and paleoweather

784 Outside of regular fluctuations caused by tidal, daily and seasonal cycles, changes in light and  
785 food availability at the hourly to daily scale are probably linked to circulation and weather  
786 phenomena. Previous studies show that enhanced vertical mixing during weather events such as  
787 storms, algal bloom events after wind-driven upwelling and pseudoperiodic dust deposition can  
788 temporarily increase the concentration of dissolved metals in surface waters, resuspend organic  
789 matter and temporarily increase primary productivity. (Lin et al., 2003; Al-Najjar et al., 2007; Iluz  
790 et al., 2009; Al-Taani et al., 2015; Komagoe et al., 2018). This will in turn lead to a shallowing of  
791 the redoxcline through increased organic matter load at the sediment-water interface, which can  
792 be recorded in the composition of giant clam shells (Yan et al., 2020). Interestingly, data in Yan  
793 et al. (2020) suggest that recording an extreme weather event in *Tridacna* requires wind speeds  
794 exceeding 20 km/h, a threshold which is almost never reached in the comparatively quiet Gulf of  
795 Aqaba (Manasrah et al., 2019), while such events are common in the stormier Bay of Brest (Hily  
796 et al., 1992; Chauvaud et al., 1998). This highlights another difference between the environments  
797 of pectinid and tridacnid specimens investigated in this study which could contribute to the  
798 variable expression of periodicity in the trace element composition of their shells. A plausible  
799 scenario therefore emerges in which aperiodic weather events cause short-term variability in both  
800 the chemistry and physical properties of the water column. These changes are subsequently  
801 recorded in bivalve shells, either directly because the weather events resuspend, remobilize or  
802 deliver trace elements like Mn and Ba (e.g., Dehairs et al., 1989; Gillikin et al., 2008; Mahé et al.,  
803 2010), or indirectly because environmental stress associated with the event affects behavior and



804 shell calcification, resulting in a change in the incorporation of alkali-group cations (e.g., Mg and  
805 Sr) into the shell biomineral (Carré et al., 2006; Takesue et al., 2008; **Fig. 7**). Our results therefore  
806 highlight the potential of high-resolution trace element records in bivalve shells to record short-  
807 term circulation changes and weather events, while prescribing caution in interpreting such  
808 records until the effect of true environmental changes on the sub-daily scale can be separated  
809 from aperiodic ultradian or behavioral patterns.

810



811 **5. Conclusions**

812 Our high-resolution trace element records reveal that short-term variability on the tidal or daily  
813 scale is recorded in the Mg, Sr, Mn, and Ba composition of shells of fast-growing mollusk species.  
814 The application of spectral analysis and variance decomposition on these trace element records  
815 is a useful tool to assess the influence of periodicity in the shallow marine environment on  
816 calcification in mollusk shells. Our statistical analysis reveals that tidal and daily variability each  
817 account for less than 10% of trace element variance in pectinids and tridacnids. In photosymbiotic  
818 giant clam shells, the amount of variance in Sr and Ba paced to the daily cycle is two times higher  
819 than in the non-photosymbiotic pectinids, suggesting that photosymbiosis in giant clams exerts  
820 some control on trace element composition in their shells. However, since only ~10% of the trace  
821 element variability in tridacnids is explained by diurnal variability, the recognition of  
822 photosymbiosis in the fossil record from diurnal variability in fossil shell composition will be  
823 complicated. In addition, differences between the mid-latitude environment of the pectinids and  
824 the tropical environment of the tridacnids likely account for part of the difference in trace element  
825 composition between the taxa. We propose that Ba and Mn composition in pectinids and  
826 tridacnids reflect short-term variability in primary productivity and sea water chemistry which  
827 control the mobility of these elements. Concentrations of Mg and Sr are likely controlled by short-  
828 term changes in growth and metabolic rate of the mollusks, which may be indirectly controlled by  
829 changes in their environment through circadian rhythms or behavior, explaining the pacing of  
830 trace element composition to the tidal and diurnal cycle. Most of the variance in trace element  
831 records in both taxa are not related to periodic behavior at the 12h or 24h scale, likely recording  
832 aperiodic events in the environment related to weather-scale phenomena or circadian patterns.  
833 We thus conclude that mollusk shell carbonate is a promising archive for recording weather-scale  
834 variability in shallow marine environments across latitudes, potentially recording weather-scale



835 phenomena in deep time, as long as these environmental effects can be separated by the  
836 influence of the animal's behavior.

837

#### 838 **Code availability**

839 Scripts used for data processing and to create figures in this manuscript were uploaded to an  
840 open-access repository on GitHub ([https://github.com/nielsjdewinter/TE\\_circadian](https://github.com/nielsjdewinter/TE_circadian)) and linked  
841 through Zenodo (<https://zenodo.org/record/6603175>).

842

#### 843 **Data availability**

844 Supplementary data and figures referenced in this contribution were uploaded to the online open-  
845 access repository Zenodo (<https://doi.org/10.5281/zenodo.6602894>).

846

#### 847 **Author contribution**

848 NJW designed the experiment after discussion with BRS, DK and LF. LF, DK, BRS and JT  
849 collected the samples. LF, DK and NJW together prepared samples for analyses and constructed  
850 shell chronologies using growth line counting. WB, LN, GJR and NJW carried out the LA-ICP-MS  
851 analyses and data processing. NJW designed and carried out the statistical analyses and wrote  
852 the R scripts guided by feedback from LN, BK, LN, WB and GJR. NJW wrote the first draft of the  
853 manuscript. All authors contributed to the writing process towards the final version of the  
854 manuscript.

855

#### 856 **Competing interests**



857 The authors declare that they have no conflict of interest.

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870

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