

Exploring the biomineral morphology of crossed-lamellar bivalve shells as a water temperature proxy

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Introduction

Bivalve shells serve as excellent high-resolution climate archives. Their periodic shell growth leads to the deposition of growth lines and increments (Fig. 1A) which can be used to align the shell record temporally.

The $\delta^{18}\text{O}$ paleothermometer (Grossman & Ku, 1986) is widely established in sclerochronological climate reconstruction. Recently, morphological variations of individual biomineral units (BMUs) were identified as an alternative temperature proxy, as larger BMUs are formed in warmer water (Gilbert et al., 2016, Höche et al., 2020, Milano et al., 2017). The new proxy is possibly more resilient against diagenesis (Brand & Morrison, 1987) and does not require knowledge of the isotopic composition of the paleo-seawater.

Bivalves can form a plethora of different shell ultrastructures. Like over 90 % of all mollusks (Almagro et al., 2016), the Glycymerididae form crossed-lamellar ultrastructure (Fig. 2) in their shells (here: outer shell layer and hinge plate). Species of this phylum have a long fossil record (Thomas, 1975), are long-lived (Reynolds et al., 2013) and inhabit coastal environments all over the world, qualifying them as an ideal study target.

Morphological changes of the BMUs (Fig. 2C) were assessed via SEM imaging in combination with automated image analysis. If correctly trained, automated image analysis can faithfully determine the morphology of the BMUs (Fig. 2D) and tremendously speed up the analysis procedure.

Here, we summarize data from a recent study and present preliminary data and interpretations from further proxy exploration and calibration.

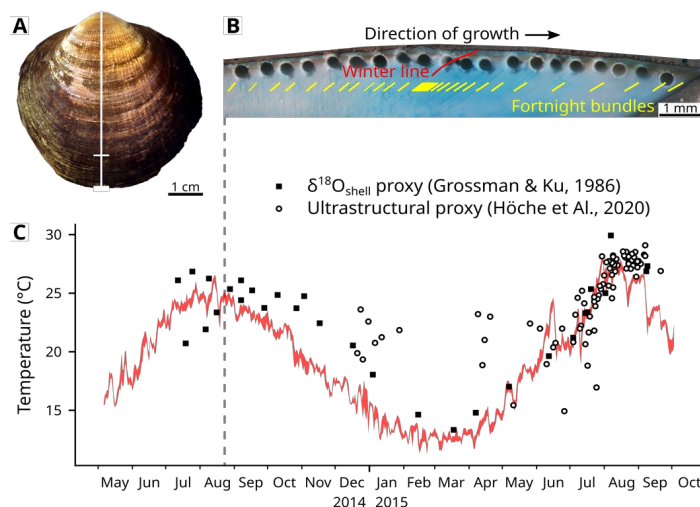


Figure 1 Sclerochronological temperature reconstructions via $\delta^{18}\text{O}$ and ultrastructural proxies in shells of *Glycymeris bimaculata* collected in the Adriatic Sea. (Höche et al., 2020; modified).

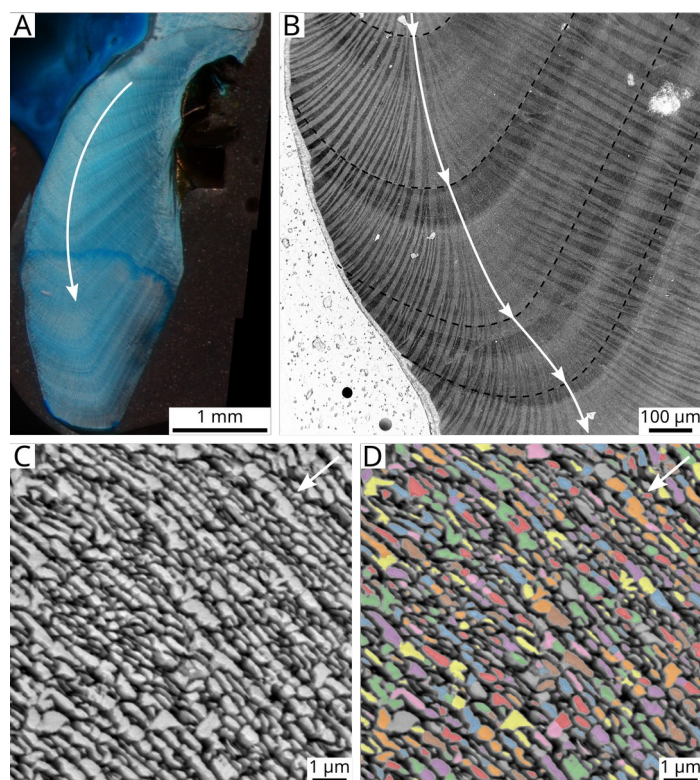


Figure 2 The crossed-lamellar ultrastructure of the hinge plate of *Glycymeris glycymeris*. Direction of growth indicated by white arrows. **A** Overview of a Mutvei-stained cross-section. **B** SEM micrograph of a portion of the hinge plate showing annual growth-lines (black dashed lines) as well as the 1st order lamellae (bright and dark gray stripes). **C** SEM micrograph of one 1st order lamella, showing their internal organization into 2nd and 3rd order lamellae (bright grains; individual BMUs). **D** Colored areas represent individual BMUs detected in image C via automated image analysis.

Further proxy exploration

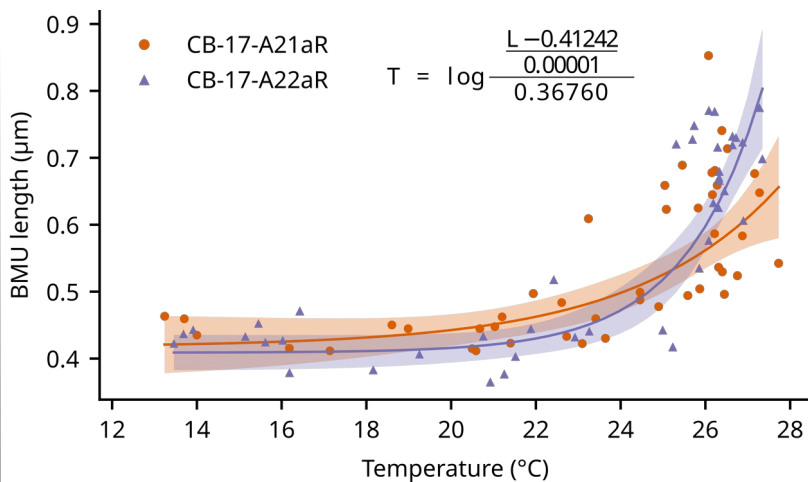


Figure 3 The length of BMUs in the outer shell layer of the shells of *G. bimaculata* correspond solely to temperature (Höche et al., 2020; modified). A logarithmic equation facilitates temperature estimates on the basis of BMU length ($r = 0.57$) with a precision of 2.3°C (1 σ) for temperatures over 18 °C (Höche et al., 2020).

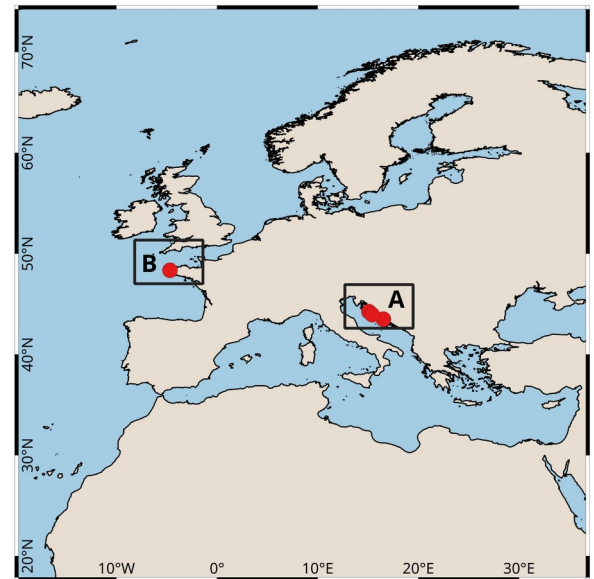


Figure 4 Map of collection sites. A: Pag bay, Pašman channel and Cetina river mouth, Northern Adriatic, Croatia. B: Porsmillin, Iroise Sea, France.

Aims

Thus far, only one species of *Glycymeris* was investigated for relationships of BMU morphology and environmental parameters. Can the new proxy also be applied to other species that also form CL ultrastructures in their shells?

Does the new proxy work in differing oceanographic and climatic regimes?

Do BMU morphologies vary between ventral margin and hingeplate of the shells?

In this presentation:

Fig. 4A – *Glycymeris bimaculata*, *G. pilosa*

Fig. 4B – *G. glycymeris*

Analyses

Investigate the ultrastructure of further bivalve species (*G. glycymeris*, *G. nummaria*, *G. pilosa*, *Venus verrucosa*, *Callista chione*) at the same locality.

Investigate shallow, coastal, restricted settings, (i.e., Adriatic Sea; 3-5m water depth), open, subtidal settings (Porsmillin, 21m) and the deeper shelf (Chatham Rise, 134m).

Compare the morphology of BMUs formed in contemporaneous portions of the hinge plate and ventral margin of the shells.

Results and Discussion

Adriatic Sea, Croatia

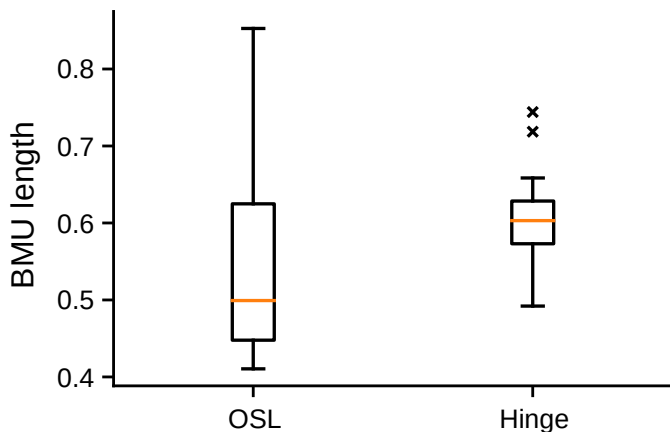


Figure 5 In shells of *Glycymeris bimaculata*, the length of biomineral units (BMUs) varies more strongly in the outer shell layer than in the hinge plate.

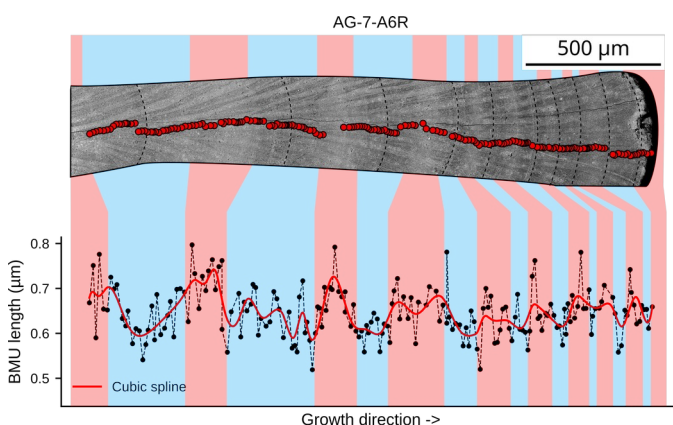


Figure 6 SEM composite image and associated BMU lengths of an imaged portion of a hingeplate of *G. pilosa*. Couplets of bright and dark gray growth increments are terminated by annual growth lines. The length of BMUs varied annually in images taken in growth direction (red dots).

G. bimaculata:

The length of BMUs of the outer shell layer corresponded solely to temperature (Fig. 3, Höche et al. 2020).

BMUs of the hinge plates of the shells exhibited significantly smaller seasonal amplitudes (Fig. 5), likely due to the condensed shell record and slower growth rate. For ultra-high resolution studies, the ventral margins of the shells should be targeted.

G. pilosa:

Under the SEM, hingeplate sections exhibited easily distinguishable annual growth features (Fig. 6). The length of BMUs varied concurrently with these growth features suggesting environmental forcing of seasonally varying environmental parameters.

Results and Discussion

G. glycymeris, Porsmillin, France

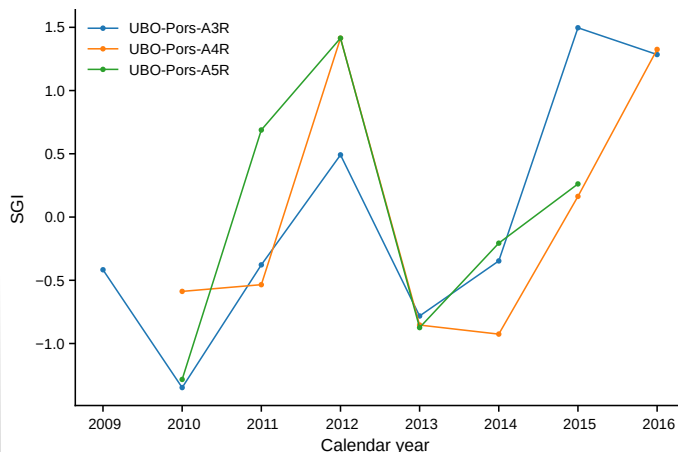
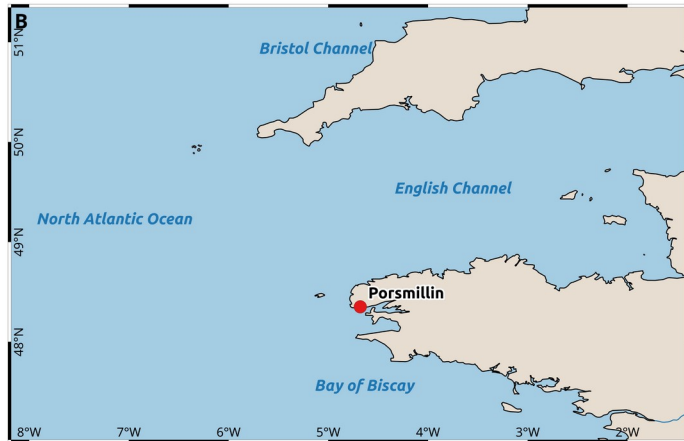


Figure 7 Standardized growth increment widths (SGI) show that the investigated individuals grew synchronously over the investigated time interval.

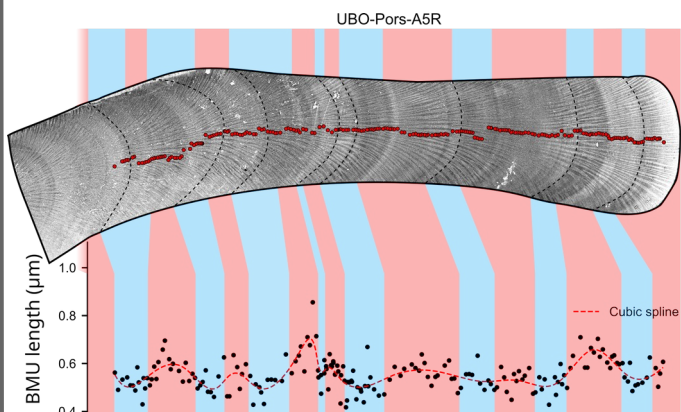


Figure 8 SEM composite image and associated BMU lengths of an imaged portion of a hingeplate of *G. glycymeris*. In the upper panel, couplets of bright and dark gray growth increments are terminated by annual growth lines. The length of BMUs varied annually in images taken in growth direction (red dots).

Under the SEM, couplets of darker and brighter bands were visible in the crossed-lamellar hingeplates (Fig. 8), that were terminated by one or multiple distinct growth lines of irregular simple prismatic (ISP) ultrastructure. Stable oxygen isotope values indicate that these couplets represent annual growth increments. Growth patterns of the investigated individuals of *G. glycymeris* indicate that the specimens of the population grew synchronously (Fig. 7).

The length of BMUs varied inter-annually and on seasonal time scales (Fig. 8). These variations likely correspond to seasonal temperature oscillations, but other factors also seem to be at play.

At the Bay of Brest, food availability (particularly nutrient-driven phytoplankton concentration) strongly governs shell growth in *G. glycymeris* (Royer et al., 2013; Featherstone et al., 2017) and possibly also BMU growth.

Conclusions

- In the outer shell layer of *Glycymeris bimaculata*, water temperatures could be derived by means of BMU length analysis with a precision of 2.3 °C. BMUs of the hinge plates show less variation and thus require a specific transfer function.
- The length of BMUs of crossed-lamellar hinge plates of *G. glycymeris* and *G. pilosa* varied on seasonal time scales, likely driven by temperature oscillations.
- The length of BMUs also varied intra-annually, suggesting that additional controls on shell growth (such as food availability) also control the BMU morphology. Possible reasons include the ecology and growth requirements of the bivalve species as well as the environmental conditions of the habitat.
- Slow growth rate leads to a condensed shell record and overprints seasonal variations of BMU morphology, especially in later stages of life and in the hinge plate (compared to the ventral margin).

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