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Disturbed by pH? Nacre tablet thickness of freshwater pearl mussels (*Margaritifera margaritifera*) is a poor temperature proxy

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ABSTRACT

Context. The ultrastructure of marine bivalve shells, specifically the thickness of nacre tablets has recently been identified to be related to water temperature. **Aims.** This study investigates whether the nacre tablet thickness (NTT) of freshwater pearl mussel shells can serve as a proxy for stream water temperature. **Methods.** Laboratory-grown juvenile and adult *Margaritifera margaritifera* from three streams were analysed using scanning electron microscopy to determine the relationship between NTT and water temperature. **Key results.** Neither laboratory-grown juvenile nor adult specimens from the field revealed consistent NTT trends with temperature. **Conclusion.** The NTT of *M. margaritifera* is largely uncoupled from stream water temperature. Presumably, fluctuations in stream water pH caused physiological stress and forced the animal to allocate more energy to homeostasis than to shell growth. The absence of a coupling between NTT of juvenile mussels and temperature is likely to be due to stronger physiological control on nacre tablet morphology during early stages of ontogeny, favouring thinner tablets with a larger proportion of organics *v.* $CaCO_3$, which increases the fracture resistance of the shell. **Implications.** Therefore, only if ambient pH remains stable, NTT of freshwater mussels beyond the age of five may serve as a temperature proxy, albeit being associated with a large error.

Keywords: biomineral unit, bivalve sclerochronology, Margaritiferidae, microstructure, nacre platelet thickness, organic matrices, paleoenvironmental reconstructions, physiological stress, scanning electron microscopy, shell growth, stream water bivalve, stream water pH, ultrastructure, Unionida.

Introduction

Temperature is a key ecological parameter in freshwater ecosystems. Among others, it controls the concentration of dissolved oxygen (Bunsen 1855), affects the rate of photosynthesis (Robarts and Zohary 1987; Singh and Singh 2015) and influences the physiology, growth and biogeographic distribution of aquatic organisms (Gunter 1957; Holtby 1988; Allan and Castillo 2007). To understand the natural thermal variability in streams, including seasonal to decadal changes, long-term trends and abrupt shifts, the current environmental change first has to be placed into context, as a prerequisite to testing, verifying, and optimising numerical simulations of future ecosystem and climate trajectories (e.g. Dugdale *et al.* 2017). To this end, high-resolution and temporally well-constrained reconstructions of pre-instrumental stream water temperature can be inferred from freshwater bivalve shells (Tomaru *et al.* 2002; Schöne *et al.* 2004, 2020).

Bivalves grow shell material on a periodic basis, resulting in the formation of distinct growth patterns, namely annual and daily growth lines (slow growth) and increments (fast growth) (Barker 1964; Dunca and Mutvei 1996). These growth patterns can be used to temporally align the growth record, add a calendar date to each shell portion if the time of death is known, and determine the ontogenetic age of the specimen (Jones and Quitmyer 1996; Mutvei *et al.* 1996). As demonstrated by annual growth-increment