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AN AUTOECOLOGICAL STUDY OF ANNUAL SHELL GROWTH INCREMENTS IN *MARGARITIFERA MARGARITIFERA* FROM LAPLAND, SUBARCTIC FINLAND

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ABSTRACT

Three shells of the freshwater pearl mussel (*Margaritifera margaritifera* (Linnaeus 1758)) were studied using sclerochronological methods. The long-lived shells were retrieved from a modern death assemblage beside a subarctic river in Lapland. An autoecological assessment of these bivalves was carried out by analyzing their annual shell growth increments. Subsequent to sclerochronological cross-dating, the incremental series were compared to each other and historical summer temperature records as observed at the local weather station between the years 1876 and 1979. Wavelet coherence, providing local correlation between the studied series in time frequency space, guided us to demonstrate that the shell growth of different bivalves has responded differently to climate fluctuations on separate time scales through the study period. Despite the incremental series showed distinct and positively high correlation with each other and climate (summer temperature) on sub-decadal scales, the shell growth variations of longer period pinpoint deviating growth fluctuations especially over the later half of the study period, since the 1930s. Over this period, the shell growth of one studied specimen started to follow the 18.6 year lunar nodal cycle. Interestingly, this bivalve experienced a shell damage/repair episode that perturbed its growth during the 1930s. Yet, the shell exhibiting the highest summer temperature correlation was also the shell with the highest growth level. Although strongest scleroclimatic associations can generally be found for local/regional increment chronology, our results demonstrate the insight of autoecological approach in studying archetypal sets of incremental series from a relatively small collection of molluscan fossil shell samples.

Key words : paleoecology, paleoclimatology, sclerochronology, malacology, freshwater pearl mussel

INTRODUCTION

When bivalve shell growth is periodically interrupted, the growth history of an organism can be traced back in time at resolution of that period. A pervasive feature of this type is formed in the bivalve shells as annual increments and the analyses of their widths reveal shell growth variations and their synchroneity (Marchitto et al., 2000; Rypel et al., 2008; Butler et al., 2009a). Moreover, the growth information from several individuals can be used to detail the environmental and climatic factors controlling the shell growth at level of studied population (Jones, 1981; Witbaard et al., 1997, 2003; Epplé et al., 2006). Apart from commonly studied marine bivalve shells (Marchitto et al. 2000; Strom et al., 2004, 2005; Butler et al., 2009a, b, 2013), freshwater bivalves of several species inhabiting rivers and lakes produce annual increments in their shells that can be reliable recognized and analyzed for building chronologies of multiple individual specimens (Rypel et al., 2008, 2009; Soldati et al., 2009; Black et al., 2010). Before calculating such chronology, the incremental series of individual shell specimens are compared to one another and to the mean series of other samples, to ensure correctness of the series in terms of their chronological dating. This process brings the methods of incremental growth research, sclerochronology (Hudson et al., 1976; Jones, 1983), close to tree-ring research, dendrochronology (Fritts, 1976), where the tree-ring series are routinely cross-dated before growth and environmental interpretations are to made.

Recent analyses of annual shell growth increments of different freshwater bivalve species have emphasized the complexity of their responses to a variety of environmental factors both on local

and regional level (Valdovinos and Pedreros, 2007; Black et al., 2010; Sansom et al., 2013). Moreover, an interesting approach could be seen arising from the field of tree-ring research, where recent analyses have concentrated on individualistic signals and responses of trees to external factors (Carrer, 2011; Rozas and Olano, 2013; Zhang et al., 2013). This approach could bear importance particularly on paleontological collections of shell materials. Compared to live-collected bivalves, the fossil bivalve shells as excavated from sedimentological sections may not exhibit overlapping lifespans. Thus, the construction of local or regional chronologies via cross-dating of growth increment series from several individual bivalves may not simply be possible in deep time.

In order to investigate the individualistic approach (Carrer, 2011) in more details, an autoecological analysis of annual shell growth increment series was conducted. To do so, we delve into the slerochronological data of *Margaritifera margaritifera*, a freshwater bivalve species from northern Europe (Helama and Valovirta, 2008a). There were several reasons to concentrate on this material. First, the shell collection used in this study represents an archetypal set of molluscan fossil shell samples and their incremental series (Helama et al., 2009a). The incremental series of this collection have previously been shown to cross-date systematically between the centennia-long sample series (Helama and Valovirta, 2008a; Helama, 2011) and the local chronology, built from a modern death assemblage, has successfully been cross-dated against the tree-ring chronologies from the same region (Helama et al., 2009b). Subsequently, the temporal variations of the produced annual shell growth increment chronology were shown to correlate strongly with variations in the historical summer temperatures in the region (Helama and Valovirta, 2008a; Helama et al., 2010; Helama, 2011). In addition, it has also been demonstrated that one of the bivalves has experienced a marked shell damage/repair episode (Helama and Valovirta, 2008a) during which the shell growth exhibited drastic fluctuations not recorded in other shells. This event could be specifically interesting in the autoecological context, in order to investigate the shell damage/repair impacts on correlativity between climate and growth. In this shell collection, the individualistic growth signals and their responses to environmental and climatic variations have, however, remained unanalyzed.

Here we compare the annual incremental series of three shells of *M. margaritifera* to one another, using both the linear correlations and the wavelet coherence (Torrence and Webster, 1999; Grinsted et al., 2004). These comparisons were complemented by analyzing the sclerochronological data in climatic context. In addition to summer temperature influence on the shell growth , an important driver of Arctic and thus of climate in the study region may originate from the lunar nodal cycle (Yndestad, 2006). Consequently, an attempt was made to additionally connect the incremental series with the lunar nodal time-series. Using the autoecological approach, the purpose of this study was to throw more light on the credibility of individual shell growth increments as recorders of their past aquatic environment.
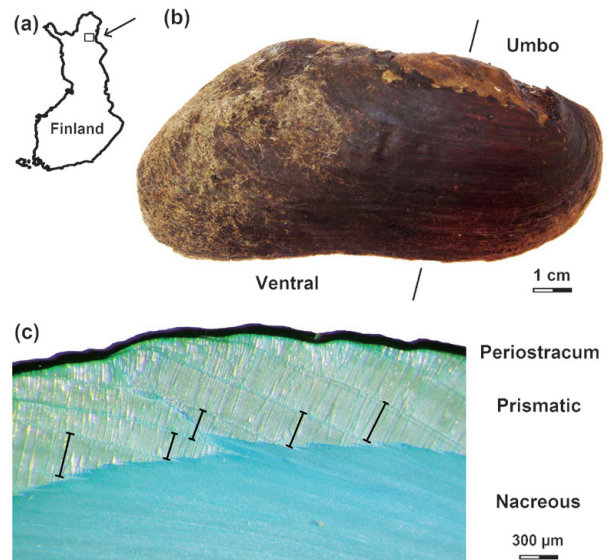

FIGURE 1. A map showing the collection point of specimens (**a**), a photo showing the cutting line from umbonal shell region towards the ventral shell margin (**b**), and microscopic view to prepared cross-section of a shell showing the periostracum, prismatic, and nacreous shell layers, with annual growth increment widths (bars), measured perpendicularly to winter-lines. Direction of growth is from right to left (**c**).

In so doing, the study demonstrates the benefits and pitfalls that may arise when individualistic data are used, instead of local or regional chronologies, for paleoecological or paleoclimatic interpretations.

<div align="center">MATERIAL</div>

Description of the shells

The studied material comprises three shells of the freshwater pearl mussel (*Margaritifera margaritifera* (Linnaeus 1758)), collected from beside a tributary of River Luttojoki in northeastern Finnish Lapland (latitude 68°36ʹN, longitude 28°14ʹE) (Fig. 1a). The mollusc species involved in this study, *M. margaritifera*, is an anthropogenically threatened invertebrate listed in Annexes II and V of the European Habitats Directive and Appendix III of the Bern Convention. *M. margaritifera* was protected by law in Finland in 1955, and Finland's Nature Conservation Act requires permission for any disturbance on living organisms and even for the collection of empty shells or fragments of dead mussels (Valovirta 1998). The shells of these dead mussels have previously been collected under license from The Lapland Regional Environment Centre and the material deposited in the collections of the Finnish Museum of Natural History (University of Helsinki). The lengths of the studied shells ranged between 120 and 126 mm (Helama and Valovirta, 2008a, b).

Production of the measurement series

Previous studies have demonstrated that the shells of *M. margaritifera* contain clear growth pattern of annual periodicity in the resulting increments (Mutvei et al., 1994; Dunca, 1999; Dunca et al., 2005). Later, Helama et al. (2007a) determined the specific characteristics of these increments from cross-sections of *M. margaritifera* shells. Following these instructions, the annual increments were measured from cross-sectioned shells. Shell specimens were cut along the axis of minimum growth from the umbo to the ventral margin (Fig. 1b). The sections were ground, polished and etched in Mutvei˙s solution, that comprise a 1:1 mixture of 25% glutaraldehyde and 1% acetic acid with added alcian blue, at 37–40°C for approximately 25 min (Mutvei et al., 1994). Following previous recommendations (Mutvei et al., 1994, Dunca, 1999), the increment widths between successive winter-lines were measured from photographic enlargements of known scale from the outer pristimatic shell layer, perpendicular to internal winter-lines (Fig. 1c).

ANALYTICAL METHOD

Cross-dating of the annual incremental series

Annual shell growth increment series were first cross-dated using sclerochronological methods (Helama et al., 2006). The three series were compared to one another for synchroneity of their wide and narrow increments. During the cross-dating process, any discrepancy in temporal placement between the conspicuous annual increments is suspected as a possible chronological error in that series. The suspected series are re-measured to pinpoint the measurement errors and to correct the chronology. Cross-dating ensures the correct temporal alignment of all annual increments to exact years in absolute calendric scale (Helama et al., 2006, 2007a). Thus, the sclerochronological cross-dating closely mimics the routinely applied cross-dating of treerings in the context of dendrochronology (Fritts, 1976). The cross-dating of the annual incremental series used here has been demonstrated elsewhere (Helama and Valovirta, 2008a) and it has also been confirmed that these shells exhibit super-centenarian ages as the number of annual increments in the shells A, B, and C were as high as 99, 162, and 137, respectively (Helama and Valovirta, 2008a). Such long annual incremental growth records further enabled a chronological comparison between the obtained sclerochronology and the tree-ring chronologies from the same region (Helama et al., 2009b). This comparison made it possible to statistically demonstrate that the increments under this study represent the calendar years 1819–1980 (Helama, 2011). The growth of the last year (1980) was not used here because of evidently incompleted growth in the middle of the season (Helama and Valovirta, 2008a).

Trend in the annual incremental series

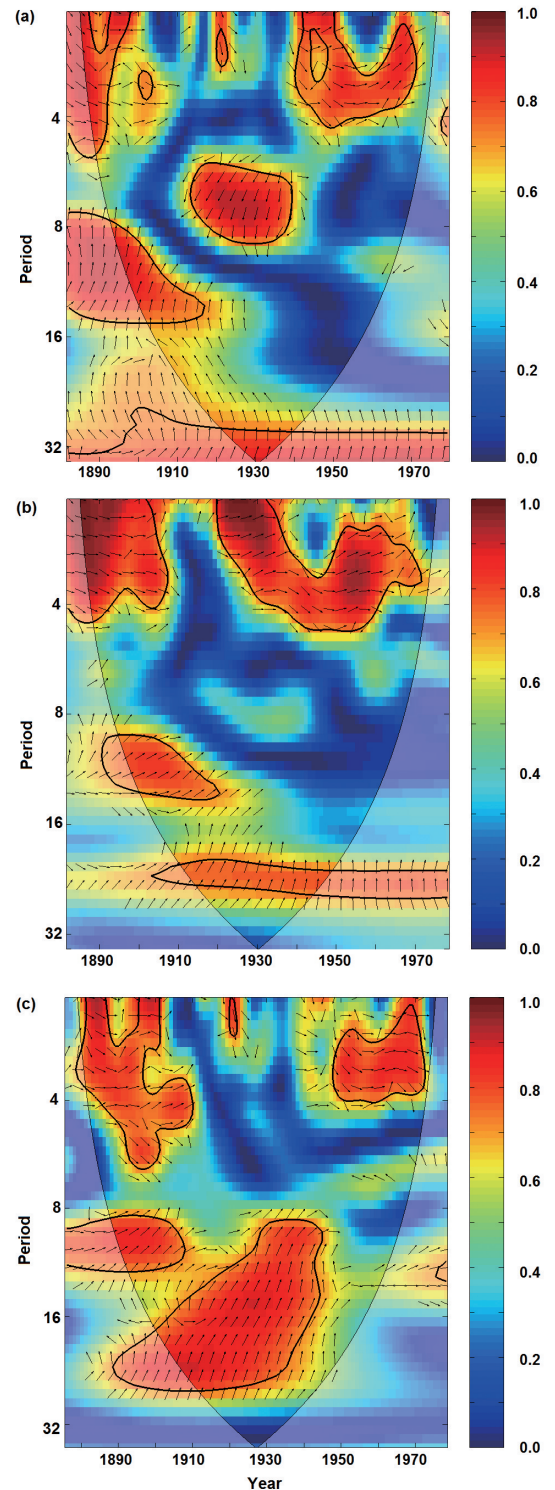Apart from year-to-year variations in the annual shell growth,

FIGURE 2. Squared wavelet coherence between the annual incremental series of the shells A and B (**a**), A and C (**b**), and B and C (**c**). In- and anti-phase relationships are shown using rightward and leftward arrows, the lagging and leading phases as upward and downward arrows. Areas with significant (p<0.05) coherence against red noise are denoted by a thick contour.
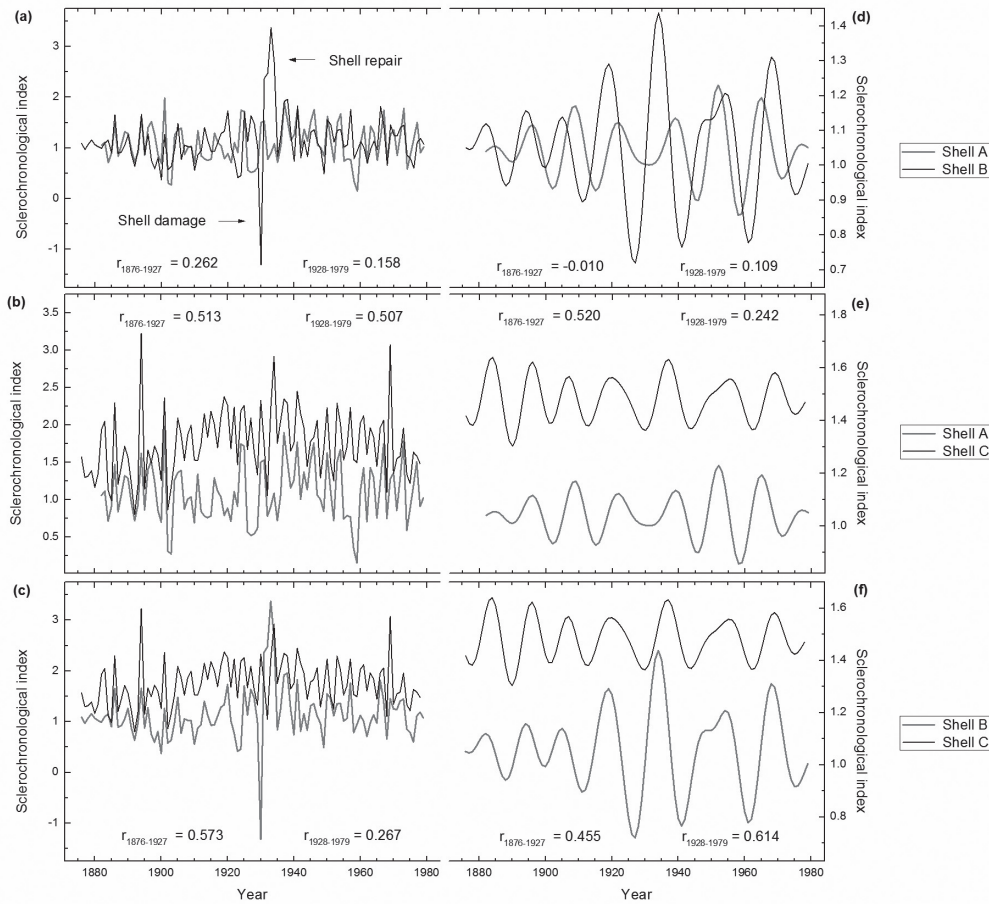
FIGURE 3. Visual and statistical comparison between the sub-decadal growth variations in the annual incremental series of the shells A and B (**a**), A and C (**b**), and B and C (**c**), and between the variations of longer term in the annual incremental series of the shells A and B (**d**), A and C (**e**), and B and C (**f**). Pearson correlations (r) were computed over the early (1876–1927) and late (1928–1979) periods.

the annual incremental series are known to contain an ontogenetic trend in their widths. Because of this trend, the biologically young increments (near the umbo) become considerably more wider than the older increments, with a growth decline until the ventral margin of the shell. For the studied *M. margaritifera* shells, this concave trend could be quantified using a modified negative exponential function (Fritts, 1976) as follows,

$$y_x = 2.979e^{-0.0307x} + 0.553$$

where y_x is the annual increment width (expressed in mm x 10) for annual increment number x (Helama et al., 2010). Using this function, the cross-dated annual incremental series were detrended and sclerochronological indices derived as ratios between the measured annual increment width and the width value as expected by the ontogenetic trend model. This method of trend removal follows the dendrochronological theory whereby the longtime trend present in the tree-ring series (here, annual

shell growth increment series) can be defined empirically for a restricted sample of trees (here, bivalves) and that the same trend can be subsequently removed from the series under investigation (Melvin and Briffa, 2014). Again, the applicability of the tree-ring methods for incremental data has been demonstrated through the previous sclerochronological analyses of shell growth (Strom et al., 2004, 2005; Helama et al., 2007b, 2009a, 2010; Black, 2009; Black et al., 2009; Rypel et al., 2008, 2009; Helama, 2011).

Evaluating environmental effects on shell growth

Annual incremental series of the shells A, B, and C were compared with the regionally representative summer temperature record and the lunar nodal time-series. Temperature record originated from the weather station of Karasjok (latitude 69° 28′ N, longitude 25° 31′E). Previous sclerochronological studies, correlating the summer temperature records and the mean and median chronologies of annual shell growth increments, have

evidenced a consistent connection between the shell growth and the mean temperature of June through August season over various temporal scales (Helama et al., 2009a, 2010; Helama, 2011). Here we build upon these findings and seek for the linkages between the individual series of the shell growth and the June-August temperature. Moreover, the annual incremental series were compared with the time-series of lunar nodal cycle amplitudes, as defined in a previous study detailing the linkages between this cycle and Arctic climate (Yndestad, 2006).

Annual incremental series were analyzed using wavelet coherence (Torrence and Webster, 1999; Grinsted et al., 2004), which represents the local correlation between the series under investigation in time frequency space. This means that the correlativity between the analyzed series can be calculated on multiple time-scales and for sliding intervals of time. Wavelet coherence belongs to the family of wavelet based time-series analysis (Torrence and Compo, 1998) and can be used to define the locally phase locked behavior of two series. In this study, the wavelet coherence was calculated between the incremental series, between these series and the temperature record, and between the incremental series and the lunar nodal time-series using the published algorithms (Grinsted et al., 2004).

In addition to wavelet coherence, the incremental series were plotted for visual comparisons with temperature and lunar nodal time-series. Moreover, the relationships were quantified using the Pearson product-moment correlation coefficient (r). Pearson correlation measures the linear relationship between two time-series. Following the results from the wavelet coherence, the correlation analyses were targeted separately on different time-scales. That is, the series were correlated for their short- (high-frequency) and long-term (low-frequency) variations. Hence, the incremental, temperature, and lunar nodal time-series were band pass filtered (Christiano and Fitzgerald, 2003) to depict their variations on sub-decadal (wavelengths less than 10 years) and decadal and longer time-scales (wavelengths more than 10 years). These components of the total variations thus represented the high- and low-frequency bands of the studied time-series.

RESULTS

Comparison of annual incremental series

Annual incremental series of the three shells were compared pair-wise using the wavelet coherence. Common to all of the comparisons was that the high-frequency (short-term and -period) variability in the series showed strong in-phase variations and therefore a consistent phase relationships (Fig. 2). These variations occurred on sub-decadal and characteristically on very short time-scales. In addition to their high-frequency agreement, the incremental series indicated growth fluctuations of longer term that did not show such in-phase variations. Instead, these variations, occurring on roughly decadal and longer scales, evidenced highly inconsistent phase relationships. That is, the low-frequency (long-term and -period) growth variability appeared poorly synchronous in comparison to the high-frequency
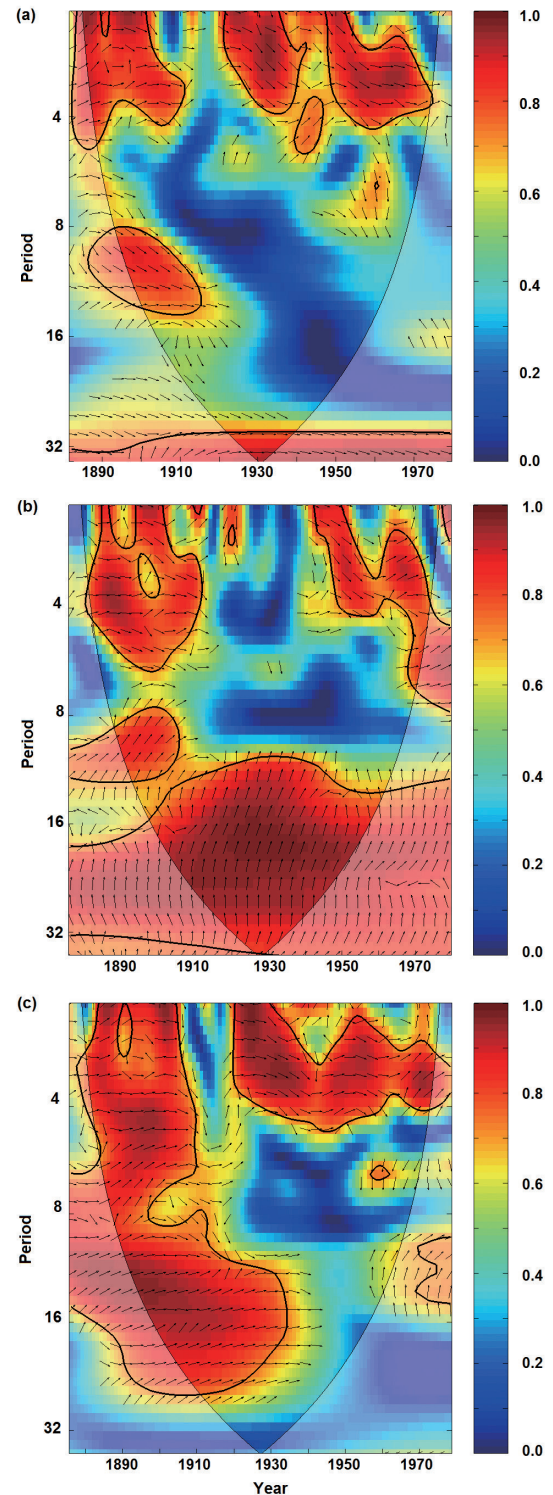

FIGURE 4. Squared wavelet coherence between the summer temperature and incremental variations in the shells A (**a**), B (**b**), and C (**c**). For further explanations, see Fig. 2.
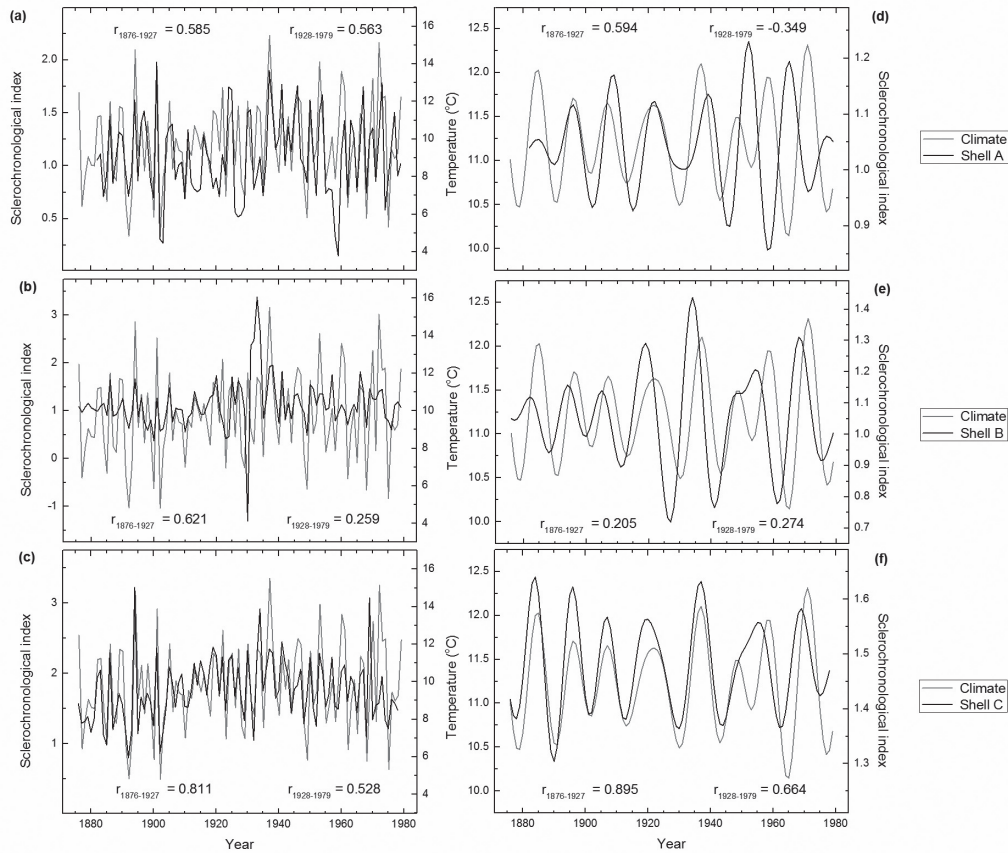
FIGURE 5. Visual and statistical comparison between the sub-decadal variations in summer temperatures and in the annual incremental series of the shells A (**a**), B (**b**), C (**c**), and between the variations of longer term in summer temperatures and the sample series A (**d**), B (**e**) and C (**f**). Pearson correlations (r) were computed over the early (1876–1927) and late (1928–1979) periods.

growth variability.

Guided by the outcomes of the wavelet coherence, the full spectrum of incremental variations was divided into its high- and low-frequency components for visual and further statistical comparisons (Fig. 3). On sub-decadal time-scales, the incremental series correlations averaged r = 0.449 and r = 0.311 over the early (1876–1927) and late (1928–1979) periods, respectively (Fig. 3a–c). These figures could be compared with the low-frequency correlations, those averaging r = 0.322 over both halves of the study period (Fig. 3d–f). It is also notable that the growth of the shell C exhibited considerably higher growth level over the full study period, in comparison to the shells A and B. With these regards, the incremental series of specimen C is also correlated with substantially high coefficients (r ~ 0.45) with both of the other series, A and B. In comparison the incremental series of the specimens A and B are correlated with a grand mean of r = 0.130.

Summer temperature and shell growth

Comparison between the annual incremental series and the climatic records evidenced similarly strong high-frequency coherence (Fig. 4). Namely, all of the three incremental series were seen to exhibit rather consistent in-phase relationships with the June-August temperature record especially on sub-decadal scales. In addition to these relationships, the shell A indicated low-frequency growth variations on multi-decadal scales through the study period. On the other hand, the specimen B showed highly inconsistent phase relationships on decadal and especially longer scales, suggesting that among the three shells studied, the growth variations in this specimen B were poorly connected to low-frequency temperature variations. Moreover, the specimen C showed strong in-phase variations with decadal and longer temperature variations, at least over the first half of the study period, until the 1930s.

The analyses of the wavelet coherence suggest us to isolate the

high- and low-frequency components of the annual incremental and temperature records for further visual comparisons and correlation analyses (Fig. 5). On high-frequency band of variations, the incremental series is correlated well with the summer temperature record with a mean correlation r = 0.561 (Fig. 5a–c). In this context, the annual incremental series of the specimen B is correlated rather poorly with climate over the late period (r = 0.259), although its climatic correlation over the early period is considerably high (r = 0.621). In comparison to these correlations on sub-decadal scales, the low-frequency correlations evidenced more complex relationships between the shell growth and climate variability, thus confirming the view obtained through wavelet coherence. While the annual incremental series of the shell A is correlated positively with temperature variations over the early period but negatively over the late period (Fig. 5d), that of the specimen B is correlated with low coefficients (r ~ 0.2) over the both halves of the study period (Fig. 5e). In contrast to these observations, the annual incremental series of the shell C shows markedly high correlation with the temperature record through the study period (Fig. 5f).

Seek for lunar signals

Wavelet coherence between the annual incremental series of the shells A and C did not exhibit statistically significant connections to the lunar nodal time-series (Fig. 6). Instead, the annual incremental series of the specimen B evidenced statistically significant coherence with this record over the later half of the study period. These results suggest that the growth variations of this specimen only followed the lunar fluctuation, at least since the 1930s. Further visual and statistical comparisons between the incremental series and the lunar nodal time-series on decadal to bi-decadal time-scales demonstrate that all the three series show positive correlations between the shell growth and the lunar nodal time-series, over the later half of the study period (Fig. 7). However, only the annual incremental series of the shell B could be linked with the lunar nodal time-series with clear in-phase linkage (Fig. 7b).

DISCUSSION

Comparisons between the annual incremental series of *M. margaritifera* evidenced similar shell growth variations between individuals, although the growth characteristics of different specimens exhibited also deviations. Following the wavelet coherence, the similarity of annual growth variations among the shells were most evident in their high-frequency band. Namely, the areas of significant in-phase relationships between the annual shell growth variations occurred robustly at time-scales less than ten years (Fig. 2). In fact, these are the time-scales on which the cross-dating can successfully operate by comparing the temporal growth synchrony between the consecutive increments (Helama et al., 2006). Similarly to these findings, the isolation of short-term variations were seen beneficial for the sclerochronological cross-dating of *M. margaritifera* and Arctica islandica annual increment
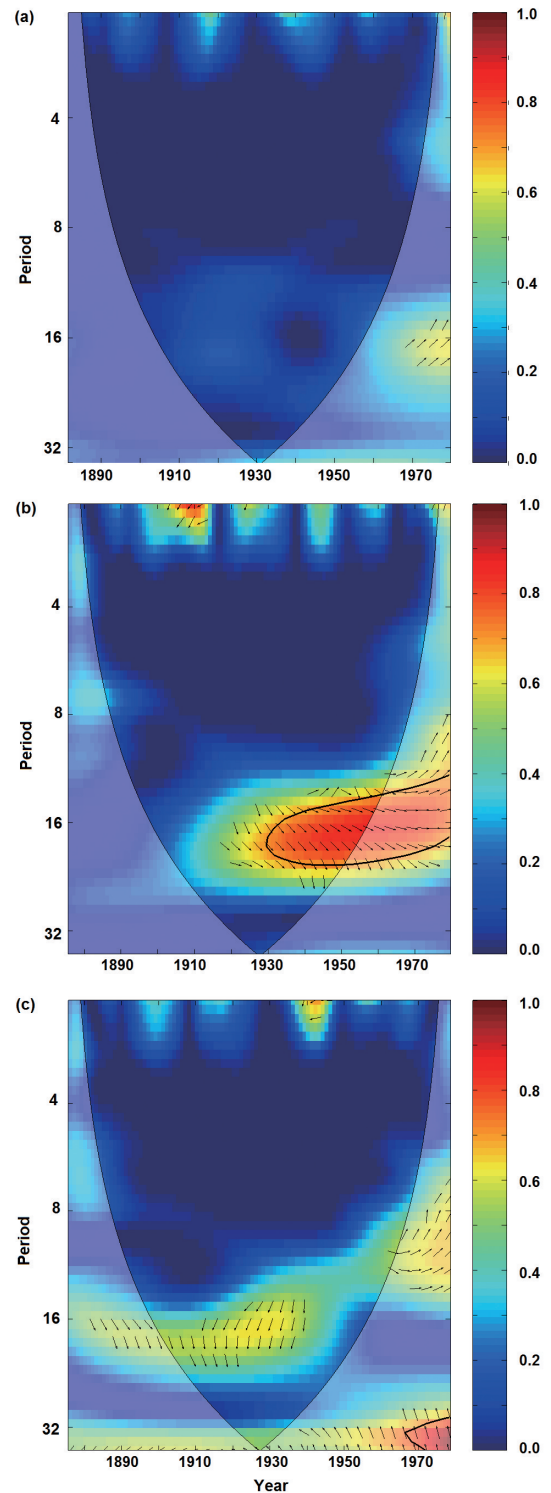

FIGURE 6. Squared wavelet coherence between the lunar nodal time-series and incremental variations in sample A (**a**), B (**b**), and C (**c**). For further explanations, see Fig. 2.
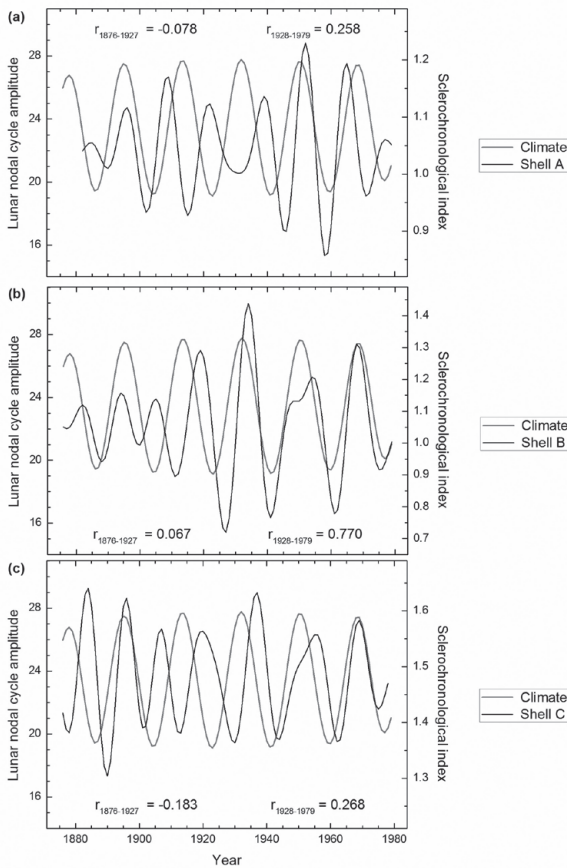
FIGURE 7. Visual and statistical comparison between the lunar nodal time-series and growth variations between the sample series A (**a**), B (**b**), and C (**c**) on decadal to bi-decadal time-scales. Pearson correlations (r) were computed over the early (1876–1927) and late (1928–1979) periods.

series (Helama et al., 2006). In fact, these delineations follow the commonly agreed approaches in the field of dendrochronology, in which the importance of high-frequency variations for cross-dating has been frequently emphasized (Yamaguchi, 1986; Wigley et al., 1987; Grissino-Mayer et al., 2010).

Highest correlations among the incremental series were obtained between the annual incremental series of the shells A and C. As previously suggested, the shell B experienced shell damage in the middle of its life (Helama and Valovirta, 2008a). Consequently, the increment that should have formed in 1930 was missing in this shell, with following shell growth anomalies characterized by markedly and moderately wide increments over the post-disturbance period, that continued for 5 and 8 years, respectively. Notably, an influence of this anomaly became noticeable also in the wavelet coherence, appearing as a non-significant area in corresponding time frequency plots over the 1930s (Fig. 2a and 2c). While no similar event was observed in other shells (Helama and Valovirta, 2008a), it could be postulated that the correlations between the sample B and other series

were possibly deteriorated owing to this event on similar sub-decadal scales, particularly over the late period (1928–1979). Simply omitting the most anomalous growth increment values in connection to the mentioned shell damage/repair event (1930–1935) from calculations actually elevated the correlations between the shell B and other series considerably (Fig. 8). These observations evidence the influence of disturbance, that only an individual organism may have encountered in the past, on the estimation of common signals on population level.

The shell damage/repair event could be detected also in the connections between the incremental and climatic variations. Clearly, there appeared an area with non-significant coherence between the shell B and summer temperature particularly over the 1930s (Fig. 4b), whereas no similar lack of significance could be observed in the case of the other two shells. Instead, the annual incremental series of the shells A and C both showed strong in-phase relationships with sub-decadal temperature variations with corresponding areas of statistically significant coherence over the 1920s and 1930s (Fig. 4a and 4c). Thereafter, it was the shell B that showed a linkage between shell growth and lunar nodal time-series, as evidenced both using wavelet coherence (Fig. 6b) and correlations (Fig. 7b).

Possible influences of the 18.6-year lunar nodal cycle (Yndestad, 2006) have previously been noted in the context of North American (Cook et al., 1997) and North European tree-ring chronologies (Linderholm, 2001; Edvardsson et al., 2011; Edvardsson, 2013). Moreover, late Holocene chronology using the time-series analysis of cross-dated *M. margaritifera* implied a periodicity that mimicked the lunar nodal cycle (Helama and Nielsen, 2008). Typical to this signal has been its weak appearance as well as its presence in treerings of trees growing on wet peat soils or bogs (Linderholm, 2001; Edvardsson et al., 2011; Edvardsson, 2013). Likewise, the lunar influence has been postulated to impact the growth through hydroclimate variations (Cook et al., 1997) that may consistently alter the groundwater levels particularly in habitats with wet substrate (Linderholm, 2001; Edvardsson et al., 2011; Edvardsson, 2013). In mountainous regions of Sweden, where summer temperature had strongest influence on tree-ring growth, with a relatively weaker implication of lunar influence, the lunar tidal maxima coincided with growth peaks (Linderholm, 2001). This setting was notably similar to our sclerochronological context, where the shell growth of *M. margaritifera* correlated well with summer temperatures with an in-phase relationship with lunar cycle. While the lunar signal remains a speculative signal, relative to the well-demonstrated temperature influence on *M. margaritifera* shell growth (Dunca, 1999; Helama et al., 2009a, 2010; Helama, 2011), the obtained in-phase relationship could indeed indicate a possible linkage through food supply. The studied river meanders through marshy landscape and the lunar nodal cycle could modify the concentrations of microbial biomass and algae from the river surroundings through changes in the water-table levels. Elevation of such concentrations could be seen benefitting the diet of the suspension feeding bivalves (Rypel et al., 2009). Putatively, the repairing of the shell B damage may have resulted in lingering
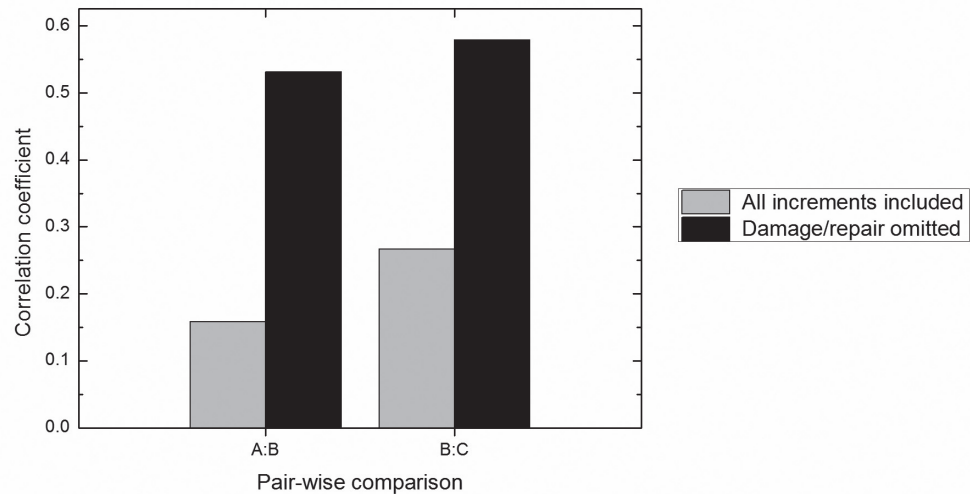
FIGURE 8. Correlativity change between the annual incremental series of the damaged (shell B) and undamaged shells (A and C) when calculating the correlation over the full late period (1928–1979) and after omitting the years (1930–1935) with damage/repair anomalies.

effects of higher food demand over the subsequent decades. Alternatively, the ecological position of this individual could have changed at the sampling site during the damage, with concomitant effects on its post-damage growth fluctuations.

It was found out that the annual incremental series of the shell C correlated markedly well with those of the other two shells. In comparison to the other two shells, this shell also portrayed considerably higher growth level over the full study period (Fig. 3). This was also the shell that correlated with generally highest coefficients with summer temperatures (Fig. 5c), in comparison to the other two shells examined. These lines of evidence suggest that although climate variability evidently controls the annual and decadal growth fluctuations, the climatic factor does not appear correspondingly limiting the overall growth rate of the shells. Instead, a set of additional factors may actually play a role behind the life-long shell growth levels. Again, these observations are suggestive of intrinsic (i.e., reproduction, sex, genetics) or ecological influence on absolute growth rate of individual shells, rather than straightforward influence of climate, that clearly, on the other hand, influences the relative growth variations. This interpretation would follow a global analysis of tree-ring data in that the absolute growth level of a limited sample set may actually be a poor paleoclimate indication (Falcon-Lang, 2005). While the efforts to cross-date larger assemblages of fossil shells from Holocene marine (Butler et al., 2009b, 2013) and freshwater (Helama and Nielsen, 2008) archives are in progress, the smaller assemblages of incremental data may, if interpreted with the greatest care, contribute to achieve the information of high-resolution past climatic and environmental variations. Although the most reliable scleroclimatic correlations can be retrieved using local/regional increment chronology, the autoecological

approaches has their benefit for augmenting our understanding of processes that may have significantly influenced the shell growth of the modern and fossil specimens during their life history.

ACKNOWLEDGMENTS

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