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A 217-year record of summer air temperature reconstructed from freshwater pearl mussels (*M. margarifitera*, Sweden)

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Abstract

Variations in annual shell growth of the freshwater pearl mussel *Margritifera margritifera* (L.) were utilized to reconstruct summer (June–August) air temperatures for each year over the period AD 1777–1993. Our study is based on 60 live-collected specimens with overlapping life-spans from six different Swedish rivers. Individual age-detrended and standardized chronologies ranging from 10 to 127 years in length were strung together to form one master chronology (AD 1777–1993) and three regional mean chronologies (Stensele, Uppsala, and Karlshamn). Standardized annual growth rates and air temperature (river water covaries with water temperature) exhibit a significant positive correlation and high running similarity confirming previous experimental findings. Up to 55% in the variability of annual shell growth is explained by temperature changes. From north to south this correlation slightly decreases. We establish a growth-temperature model capable of reconstructing summer air temperature from annual shell growth increments with a precision error of ± 0.6–0.9°C (2SD). The validity of the model was tested against instrumentally determined air temperatures and proxy temperatures derived from tree rings.

Our study demonstrates that freshwater pearl mussels provide an independent measure for past (i.e., prior to the 20th century greenhouse forcing) changes in air temperature. It can be used to test and verify other air temperature proxies and thus improve climate models.
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1. Introduction

Climate models require long-term and high-resolution records of environmental conditions. Such information can decipher natural climate variability, help understand rapid shifts of climate, estimate the relative importance on anthropogenic forcing of the climate and can thus enable reliable climate forecasts. Unfortunately, observational data is spatiotemporally incomplete and inhomogeneous as it covers only the last 100–200 years and only parts of the world. For times and places without direct measurements, climate modelers thus rely on proxy data (Jones et al., 2001), i.e. natural recorders of environmental variability, in order to calibrate and validate models.

Summer air temperatures play an important role in modeling the climate of boreal, terrestrial ecosystems (Briffa, 2000; Slonosky et al., 2000; Cook et al., 2002; D'Arrigo et al., 2003). Beyond instrumental measurements such data is almost exclusively inferred from variations of tree ring width and density (dendrochronology) (Briffa et al., 1990; Schweingruber et al., 1991; Grudd et al., 2002; Linderholm et al., 2003). The annual ring widths of trees growing near the timber-line, for example Scots pines (*Pinus sylvestris* L.) in northern Fennoscandia (Briffa, 2000; Gunnarson and Linderholm, 2002; Grudd et al., 2002), exhibit a significant positive correlation with summer (April–August; Briffa et al., 1990) warmth. This enabled the construction of a linear growth-temperature model capable of reconstructing summer air temperature proxies from tree ring data (Briffa et al., 1990; Briffa, 2000). In a recent paper such a model was applied to a 7400-year master chronology constructed from 880 contemporaneous trees with overlapping life-spans and provided

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information on annual summer temperature anomalies over this period (Grudd et al., 2002).

Other terrestrial proxies for environmental variables (e.g., Hammarlund et al., 2002, 2003) do not attain the same temporal resolution (i.e., annual). Hence, environmental reconstructions based on dendrochronology were never tested and verified by independent measures. However, such tests are strongly advised for several reasons given by dendrochronologists themselves (Grudd et al., 2002): (1) Tree ring widths are calibrated with known environmental variables. The calibration and validation periods, however, are only as long as the period for which observational data are available, i.e. in general 100–200 years. It remains unknown if air temperature controlled the growth rate of trees in the very same way during the reconstruction period which stretches over much longer time periods than the calibration period. (2) The reliability of environmental proxies decreases with decreasing sample depth (= number of specimens per time interval). The fewer the underlying specimens used in a proxy record, the less reliable is the reconstruction of environmental parameters. While the sample depth is large in most recent times, the mean chronology is based on lower sample size further back in time.

In the present study we present a new proxy for air temperature which has not yet received much attention as an environmental archive: Freshwater pearl mussels, *Margaritifera margaritifera*, from Swedish rivers.

Like many bivalve mollusks (e.g., Clark, 1975; Kennish and Olsson, 1975; Zolotarev, 1980; Jones, 1983; Jones et al., 1989), freshwater pearl mussels fulfill the prerequisites of environmental archives because they (1) grow by periodic accretion and produce annual (Hendelberg, 1961; Mutvei et al., 1994; Hastie et al., 2000) and daily growth increments (Dunca and Mutvei, 2001), (2) record the environmental information during growth as variable increment widths in their shells (Bauer, 1992; Dunca and Mutvei, 2001) and (3) exhibit long life-spans (Bauer, 1992; Bauer and Wächtler, 2001; Mutvei and Westermark, 2001), and (4) exhibit a broad biogeographic distribution (Hopkins and Buck, 1995).

Similar to trees, periodic production of skeletal hard parts results in distinct growth patterns that segment the bivalve shell into time intervals of near equal duration (Pannella and MacClintock, 1968; Hall et al., 1974; Richardson et al., 1980). Periodic growth structures provide an excellent dating control and enable us to assign precise calendar years to each portion of the shell (Dunca and Mutvei, 2001; Schöne et al., 2002, 2003a). Major growth lines of the *M. margaritifera* specimens used in our study were deposited during winter and resulted from sharply reduced growth rates (Hendelberg, 1961; Dunca and Mutvei, 2001). These lines were referred to as etch-resistant (see Section 2 for explanation) or winter lines. Experiments indicate that

no shell is laid down below 4°C (Dunca, 1999). The increment between two consecutive winter lines forms mostly during summer (Dunca and Mutvei, 2001). Hence, the growing season of *M. margaritifera* and Scots pines in Fennoscandia almost overlap. Like most other representatives of the Unionida (= naiads), shells of *M. margaritifera* grow faster at higher temperatures (Mutvei et al., 1994; Bauer and Wächtler, 2001). In combination with their distinct internal shell growth patterns, unionids in general may be extremely useful for climate reconstructions. While unionids exhibit a worldwide distribution (Bauer and Wächtler, 2001), *M. margaritifera* occurs only in Europe and northeastern North America (Hopkins and Buck, 1995). Its ontogenetic age increases from higher to lower latitudes: It grows 8–40 years old between Spain and Germany, but reportedly lives for up to 100 years (Bauer, 1992) in Scandinavia. Some individuals grow more than twice as old (Mutvei and Westermark, 2001; authors' observations). This makes *M. margaritifera* a perfect tool for long-term environmental reconstructions. Also, it enables the construction of composite chronologies that exceed the lifespan of an individual specimen. The respective methods were adapted from dendrochronology and have already been successfully applied to marine bivalve mollusk species. Some recent studies built master chronologies from different marine species (e.g., Witbaard et al., 1997) and inferred the interannual variability of water temperature over decades to two centuries (Jones et al., 1989: *Mercenaria mercenaria*; Marsh et al., 1999; Marchitto et al., 2000: *Arctica islandica*; Schöne, 2003: *Chione* spp.; Strom et al., 2004: *Panope abrupta*). Schöne et al. (2003b) used 22 long-lived specimens of *Arctica islandica* as a proxy for the North Atlantic Oscillation index over the past 245 years. Until now, only one study presented regional mean chronologies from freshwater bivalves. Mutvei et al. (1994) demonstrated that different individuals of *M. margaritifera* alive at the same time and in the same habitat exhibit similar variations in annual shell growth which are largely controlled by air temperature.

Here, we present the first long-term, annually resolved summer air temperature reconstruction based exclusively on live-collected shells of *M. margaritifera*. The almost unbroken shell growth record based on 60 specimens extends from AD 1993 back to AD 1777. We establish a growth rate–temperature model that enables precise reconstructions of summer air temperature form these data. Our study addresses the following questions: How precise are temperature reconstructions based on variations of annual growth rates of freshwater pearl mussels? How do the results compare to observational temperature data and proxy temperatures derived from trees? What are the advantages and disadvantages of using bivalves as proxies for environmental variables? Results of the present study can complement and verify

existing air temperature chronologies and contribute to further understanding of natural variability and anthropogenic forcing in the environmental history. Furthermore, our study aims at promoting the use of bivalve mollusks for long-term climate reconstructions.

2. Materials and methods

Sixty specimens of *M. margaritifera* were collected alive during AD 1853 and AD 1930 (stored in collections of the Swedish Museum of Natural History) and between AD 1986 and AD 1997 from six different rivers in northern, central and southern Sweden (Fig. 1 and Table 1). Samples were collected from shallow water settings (0.50–1 m, Pärlälven: 6 m). Following methods described by Dunca and Mutvei (2001), one valve of each specimen was cut from the umbo to the ventral

margin perpendicularly to the winter lines and along the axis of minimum growth (Fig. 2). Most other bivalve species do not permit this approach, because a complete growth record was only found along the axis of maximum growth. However, Dunca and Mutvei (2001) counted the exact same number of growth increments in shells that were cut in either direction. In order to clarify inter-annual growth patterns, the sections were ground (800 and 1200grit metallographic grinding paper) and polished (3 μm diamond paste) and then etched in a solution of 0.5% acetic acid, 12.5% glutaraldehyde and 5 g alcian blue powder at 37–40°C for ca 25 min, carefully rinsed in de-ionized water and allowed to air-dry (Mutvei et al., 1996). While acetic acid dissolved the carbonate, glutaraldehyde dried the organic matrix and alcian blue stained mucopolysaccharids and glucosamids in the shell. This treatment results in excellent three-dimensional preservation of the growth structures
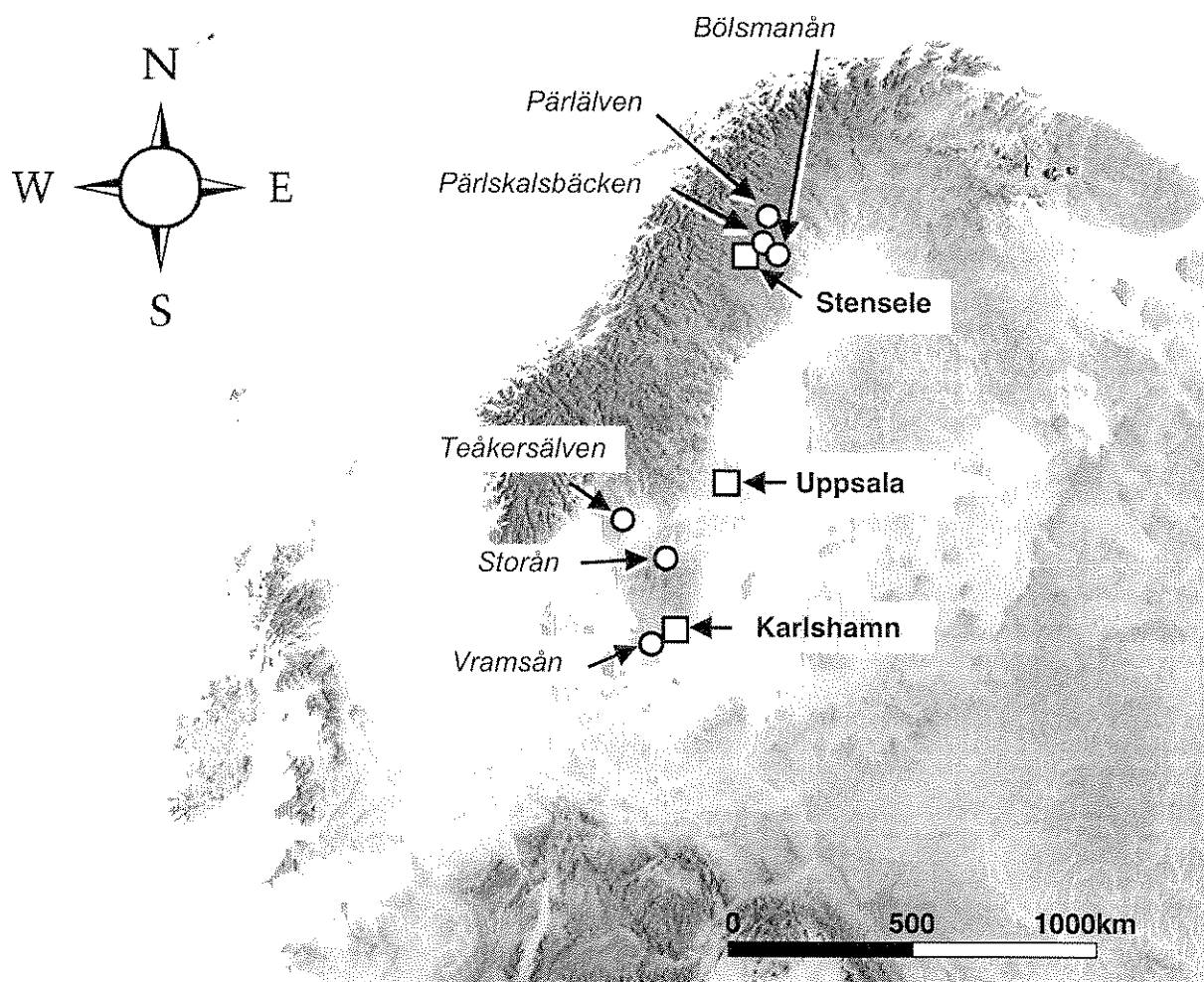

Fig. 1. Map showing sample localities (circles) of *M. margaritifera* shells and meterological stations (quadrangles). The rivers Pärlälven (N66°33′, E19°12′), Pärlskalsbäcken (N66°14′, E19°30′) and Bölsmanån (N65°45′, E20°15′) represent the northern region (Stensele), Teåkersälven (N58°29′, E12°12′) and Storån (N57°20′, E13°48′) the central region (Uppsala) and the Vramsån river (N56°05′, E13°50′) the southern region (Karlshamn). Mean summer temperatures (AD 1850–1996) are 12.16°C for northern Sweden, 15.22°C for central Sweden and 15.77°C for southern Sweden.

Table 1
Shells of *M. margaritifera* used in the present study

| Population region	Locality	Individuals' dates of death	Number of specimens	Length and period covered (year AD)	
				Regional mean chronologies	Master chronology
Northern Sweden (Stensele)	Parälven	1986	5	134 years, 1860–1993	
	Pärlskalsbäcken	1993	5		
	Bölsmanån	1997	5		
Central Sweden (Uppsala)	Teåkersälven	1986	8	87 years, 1902–1993	217 years, 1777–1993 (gap: 1853–1859)
	Storån	1988	4		
Southern Sweden (Karlshamn)	Vramsån	1853, 1930, 1989, 1992, 1993	33	217 years, 1777–1993 (gap: 1853–1859)	
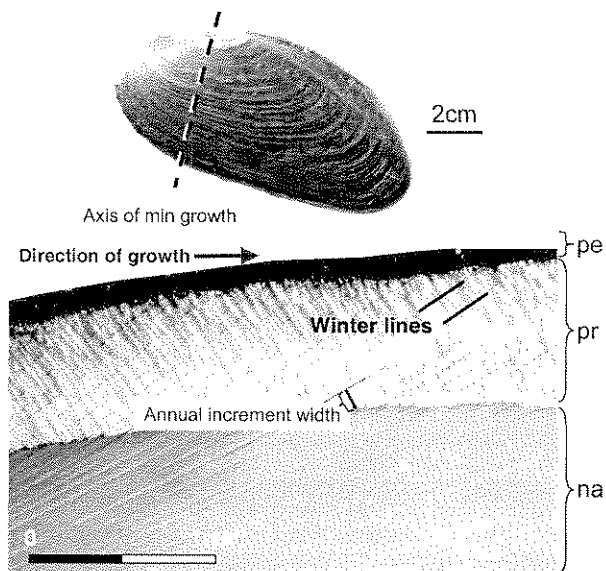
Fig. 2. Sclerochronology. Shells of *M. margaritifera* were cut along the axis of minimum growth and perpendicular to the winter lines. Etching of polished cross-sections with a glutaraldehyde–alcian blue–acetic acid-solution reveals the internal growth structures. Etch-resistant (or winter) lines limit growth increments that form during the summer months. The widths of the growth increments were measured from the boundary between the prismatic (pr) and nacreous (na) shell layer perpendicularly to the previous winter line. pe = periostracum.

with distinct, etch-resistant, blue-coloured winter lines (Fig. 2).

2.1. Growth increment width measurements

For precise determination of growth rates, annual increments were viewed under a reflective light binocular microscope (magnification up to 400 ×), digitized with a Nikon Coolpix® 995 camera and their widths were measured to the nearest 1 μm with Scion/NIH version 4.0.2 beta image analysis software (available free at http://www.scioncorp.com). Measurements were conducted in the outer shell layer as shown in Fig. 2. The average growth increment width is 370 μm.

2.2. Detrending, standardization and filtering

The growth of most organisms is controlled by physiological constraints and environmental conditions. Analysis of environmental signals in growth increment time-series requires removal of ontogenetic growth trends, predominantly age-related growth trends. As the shell grows older, the rate and the year-to-year variance decrease. Statistical methods for detrending were developed by dendrochronologists (for a review see Cook and Kairiukstis, 1990). In the present study we used logistic growth functions and second-order polynomials to estimate the growth curves and age trends. Detrending retained most of the decadal and multi-decadal periods of climate variability. We calculated growth indices (GI) by dividing measured by predicted (estimated) growth values at each year (= age-detrending). Then, the GI data were standardized (standardized growth indices = SGI values) by subtracting the mean of the GI time series and dividing by the standard deviation of the GI time series. Methods are described in more detail in a variety of publications (e.g., Cook and Kairiukstits, 1990; Schöne, 2003). For visual comparison of the SGI mean chronologies, we performed an extra step and digitally filtered the data with a Savitzky–Goley filter (windows length: 20 years) and thus removed the high-frequency oscillations.

2.3. Statistical evaluation of agreement between chronologies

The agreement of year-to-year changes between SGI master chronologies or subsets thereof and measured or tree-ring width-based proxy records of air temperature

was quantified by three different statistical tests: (1) linear correlation, (2) *t*-statistic after Baillie and Pilcher (1973), and (3) Huber's (1943) running similarity (*Gleichläufigkeit*) test.

Linear correlation analyzes how similar are growth rates of two chronologies. Growth values of one chronology are plotted on the *x*-axis, whereas the values of the second chronology are plotted on the *y*-axis.

Baillie and Pilcher's (1973) *t*-statistic measures the strength of agreement between two chronologies using the correlation coefficient *r*, the coefficient of determination R^2 and the sample size *n*:

$$t = \frac{r\sqrt{n-2}}{\sqrt{1-R^2}}.$$

Huber's (1943) running similarity test checks for agreements of growth patterns between two chronologies employing a binary system. If the growth rate increases (positive sign) or decreases (negative sign) from one to the following year in both chronologies a value of one is assigned to that year. If the growth rate increases in one chronology and decreases in the other, or vice versa, a value of zero is given. The sum of (sign) agreements between two chronologies over a given period of time is expressed as percent agreement. In addition, this test provides information on the statistical significance of the match between two chronologies employing confidence intervals based on standard deviation units SD. Huber (1943) provides an empirical equation, where $1SD \approx 50/\sqrt{n}$:

$$G = 50 + \frac{s50}{\sqrt{n}}.$$

For 2SD (95%) variable $s = 2$, for 3SD (99%) $s = 3$. Two time-series are in statistically significant agreement (here 2SD) if the percentage of agreement is higher than the running similarity value *G*.

2.4. Environmental variables and air temperature proxies

Monthly air temperature records for the three regions Stensele, Uppsala and Karlshamn were obtained from the Swedish Meteorological and Hydrological Institute. River water temperature data from Norrbottens län were provided by Lisa Lundstedt (Länsstyrelsen). In addition, our study utilized air temperature proxies derived from tree-ring (Scots pine) width data from (Torneträsk chronology: Briffa et al., 1990; Briffa, 2000; Grudd et al., 2002; downloadable at http://www.cru.uea.ac.uk/cru/people/briffa/qsr1999/qsrfig1.xls). We compared SGI data of bivalve shells with observational and proxy records of air temperatures to resolve the control of temperature on growth rates. Previous studies already demonstrated that temperature plays an essential role in shell growth of *M. margaritifera* (Hendelberg, 1961; Bauer, 1992; Dunca, 1999; Dunca and Mutvei, 2001).

3. Results

A total of 60 specimens of *M. margaritifera* was used in the present study (Table 1). They lived between about AD 1750 and AD 1997. The highest sample depth (54 specimens) occurs during AD 1979–1986. Due to corrosion of the external shell layer (prismatic layer) in the umbonal shell portions, the first 30 or so years of each specimen could not be utilized (Fig. 2). Maximum and minimum length of the standardized annual growth increment width (SGI) chronologies were 127 years in northern Sweden and 10 years in central Sweden, on average 51.1 ± 6.8 years.

3.1. Mean chronologies of M. margaritifera

The mean chronology of all 60 live-collected specimens covers the period of AD 1777–1852 and AD 1860–1993 and exhibits an SGI range of 2.79 standard deviation units (Fig. 3A). We refer to this chronology as the master chronology (Table 1). SGI values of some time intervals stand significantly out, i.e. their 95% confidence levels do not overlap with the SGI values of the preceding or following time intervals. An interval of slower annual growth rates occurred, for example, during the 1950/60s, faster growth during the 1930/40s. In general, 95% confidence intervals of the SGI values become smaller in most recent years and with increasing sample depth (greater number of specimens arithmetically averaged per year). Narrow confidence bands also reflect a high level synchroneity in the interannual growth patterns of contemporaneous specimens (Fig. 3A). We did not find a correlation between the sample depth and SGI values ($R^2 = 0.001$, $p = 0.68$).

In addition, we constructed three regional mean chronologies from specimens of *M. margaritifera* in northern (Stensele chronology), central (Uppsala chronology) and southern Sweden (Karlshamn chronology) (Table 1). Despite regional differences were observed among the growth patterns (e.g., negative SGI values during 1941–1944 in central Sweden, but positive SGI values in southern and northern Sweden), similar multidecadal growth periods of about 30–40 years occur in all chronologies (Figs. 3B–D). Linear regression analyses between the low-pass filtered (Fig. 3) regional mean chronologies reveal the following statistics: Stensele–Uppsala: $r = 0.47$, Uppsala–Karlshamn: $r = 0.18$, Stensele–Karlshamn: $r = 0.43$.

3.2. Air versus water temperature

Water temperature records of the rivers in which the shells grew are scarce. Few available monthly data (April–September) cover the period of AD 1991–AD 1996 for four rivers in northern Sweden (near Stensele). However, air temperature records are abundantly
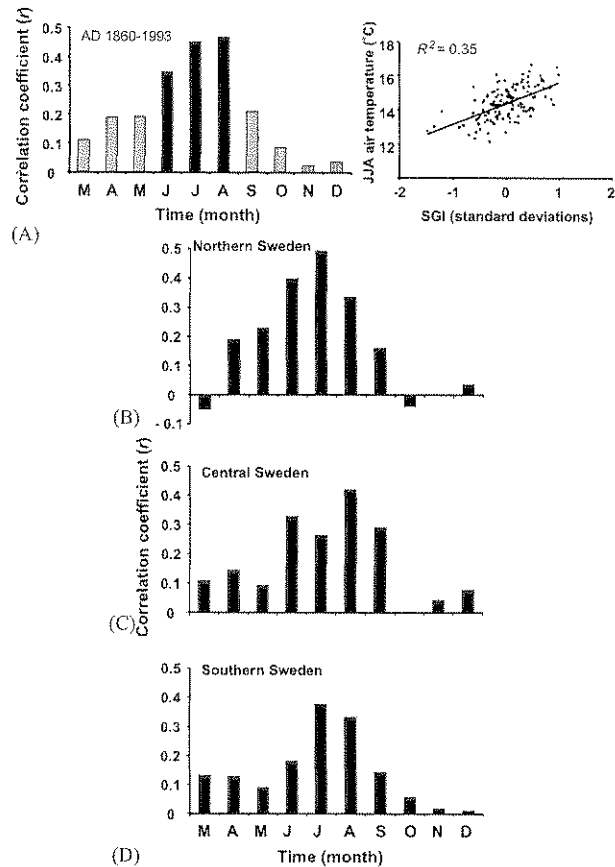
(A)

(B)

(C)

(D)

Fig. 3. A master chronology (A) and three regional mean chronologies (B–D) were constructed from age-detrended and standardized growth increment width (SGI) time-series of specimens with overlapping live-spans. For each year the arithmetic mean (thin black lines) and the 95% confidence levels were calculated (grey lines). In addition, data were smoothed (thick black lines) with a Savitzky–Goley (low-pass) filter (window length: 20 years; ends padded to prevent loss of data at the edges). The SGI master chronology stretches over the period of AD 1777–1993. Sample depth (number of specimens used for each year) is provided for the master chronology. Note that 95% confidence intervals are narrower for more recent times as the sample depth increases. Overall growth trends (smoothed data) are present in all chronologies.

available and reflect the contemporaneous variation in river water temperature very well. Previous studies (Mutvei et al., 1994) demonstrated that air temperature and annual shell growth of freshwater pearl mussels are highly correlated to each other. The correlation between monthly temperature data of four different rivers show a highly significant correlation ($r = 0.87$, $R^2 = 0.75$, $p < 0.0001$) with air temperature (Stensele record) and exhibit a slope of $m = 0.88$ (Fig. 4). Therefore, an increase in air temperature by 1°C is concurrent with a river water temperature increase of 0.88°C.

3.3. Annual shell growth and air temperature

Linear regression analysis revealed a positive correlation between annual shell growth and observed monthly
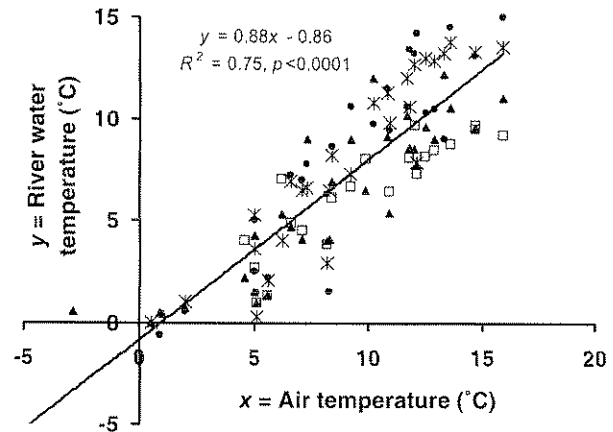

Fig. 4. A highly significant correlation exists between river water temperature and air temperature during April through September. Monthly river temperature data were obtained for AD 1991–1996 from four rivers (Kilankijok river: open squares; Bergmyrbäcken: filled triangles; Rokån: filled circles; Akkarjåkkå: asterisks) in northern Sweden adjacent to the site where the shells lived. According to the regression analysis, an increase in air temperature by 1°C results in a water temperature rise by 0.88°C. Because river water data are scarce and long-term record not available, air temperatures can be used a proxy for water temperature.

air temperature over the period AD 1860–1993 (period with reliable observational data for all three meteorological stations), notably during summer, i.e., June, July and August (Fig. 5A). Monthly air temperatures over this 134-year period were calculated as the arithmetic mean of three different stations in northern, central and southern Sweden (NCS) closest to where the shells grew, Stensele, Uppsala and Karlshamn, respectively. Thirty-five percent of the variation in annual shell growth rates over the period AD 1860–1993 is explained by summer air temperature (June–August mean, $r = 0.59$, $R^2 = 0.35$, $p < 0.0001$; Fig. 5A). Shells grow at significantly faster rates during warmer summers.

Furthermore, we explored the relation between shell growth and air temperature at the three regions (northern, central and southern Sweden). SGI values of each regional mean chronology were compared to air temperature data of the closest station nearby. While air temperatures during June, July and August are especially crucial for variations in annual shell growth in northern Sweden (Stensele chronology), temperatures during other months become increasingly important toward south (central Sweden: Uppsala chronology; southern Sweden: Karlshamn chronology), notably September (Fig. 5B–D). Accordingly, we observed a decreasing correlation between annual shell growth and summer air temperature from north to south. While 36% ($r = 0.60$, $R^2 = 0.36$, $p < 0.0001$) of the variability in SGI values of the Stensele chronology is explained by air temperature, this value decreases to 22% ($r = 0.47$, $R^2 = 0.22$, $p = 0.002$) and 17% ($r = 0.41$, $R^2 = 0.17$,

(A)

Northern Sweden

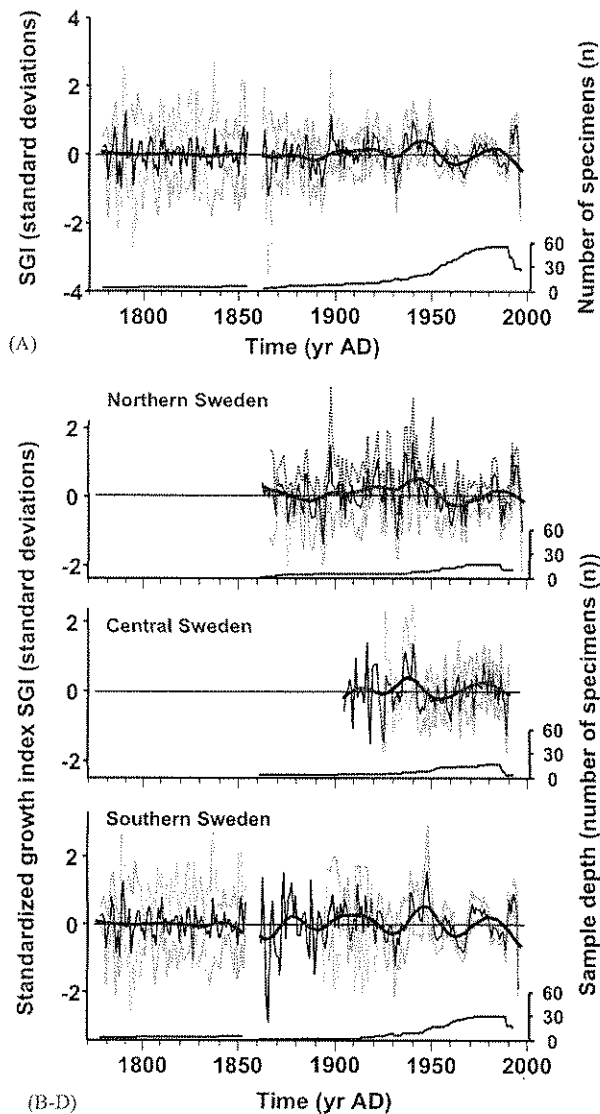Central Sweden

Southern Sweden

(B-D)

Fig. 5. Correlation between annual shell growth and air temperature. (A) Highest correlation among all studied regions exists with temperatures prevailing during June through August. Statistics were calculated for the period of AD 1860–1993 for which reliable instrumental measurements of air temperature are available for all three regions (NCS = northern, central and southern Sweden): $r = 0.59$, $R^2 = 0.35$, $p < 0.0001$. This coincides with previous findings on intra-annual shell growth and is hence not just a statistical relation. From north to south (B–D) June–August temperatures become increasingly less important, while temperatures during other months govern shell growth to a larger extent. This finding agrees with previous reports on an extended growing season toward lower latitudes.

$p < 0.0001$) in the Uppsala and the Karlshamn chronologies, respectively.

We also analyzed if and how the temperature of the preceding year controlled the actual annual growth rate (autoregressive model lag-1, AR-1 process). In a linear multi-regression model the SGI values at time t (SGI$_t$)

and those of the preceding year (SGI$_{t-1}$) were employed as predictors of air temperature. Results indicate that SGI$_{t-1}$ values had no significant control on temperature over the period of AD 1861–1993.

3.4. Growth-temperature model based on freshwater bivalves

Based on the finding that summer air temperature and annual shell growth at time t are significantly correlated to each other, we establish a model capable of reconstructing summer air temperature from shell growth of freshwater pearl mussels in Sweden (Fig. 6). We used the linear regression (SGI values versus NCS air temperature data) to estimate summer (June–August mean) air temperatures (T_{shell}) from SGI values of the master chronology of each year for the period AD 1926–1975 (= the calibration period; $r = 0.74$, $R^2 = 0.55$, $p < 0.0001$; Fig. 6A):

$$T_{shell} = 1.407\,SGI + 14.548. \tag{1}$$

By using the model (Eq. (1)), we calculated the summer air temperature from the SGI values for the period AD 1876–1925 (= the validation period) and for the period of AD 1777–1875 (= the reconstruction period) and for AD 1976–1993 (Figs. 6A–C). During the validation period the correlation of our *M. margaritifera*-based summer air temperature proxy and observational air temperatures still reveals highly significant values: $r = 0.59$, $R^2 = 0.34$, $p < 0.0001$ (Fig. 6A). The error (95% confidence level) in temperature inference from SGI values over the period AD 1860–1993 is $\pm 0.90°C$ and $\pm 0.62°C$ for the period of AD 1926–1975 (Fig. 6B). Instrumental air temperatures prior to AD 1860 are only available for one meteorological station (Uppsala) which is about 600 km south of the locality where most of the shells grew that constitute the pre-AD 1875 SGI time-series. Accordingly, the correlation is much lower, but still highly significant ($r = 0.36$, $R^2 = 0.13$, $p = 0.002$; Figs. 6A and C). Running similarity (*Gleichläufigkeit*) tests also confirmed the good agreement between observational and reconstructed air temperatures (Table 2).

For comparison, we re-calibrated the model using only the summer air temperature record from Uppsala for the period AD 1926–1975:

$$T_{shell} = 1.229\,SGI + 14.385 \tag{2}$$

with $r = 0.71$, $R^2 = 0.49$ and $p < 0.0001$. During the validation period the correlation statistics of our second model and observational air temperatures (Uppsala) return slightly lower values than for Eq. (1): $r = 0.52$, $R^2 = 0.27$, $p < 0.0001$.
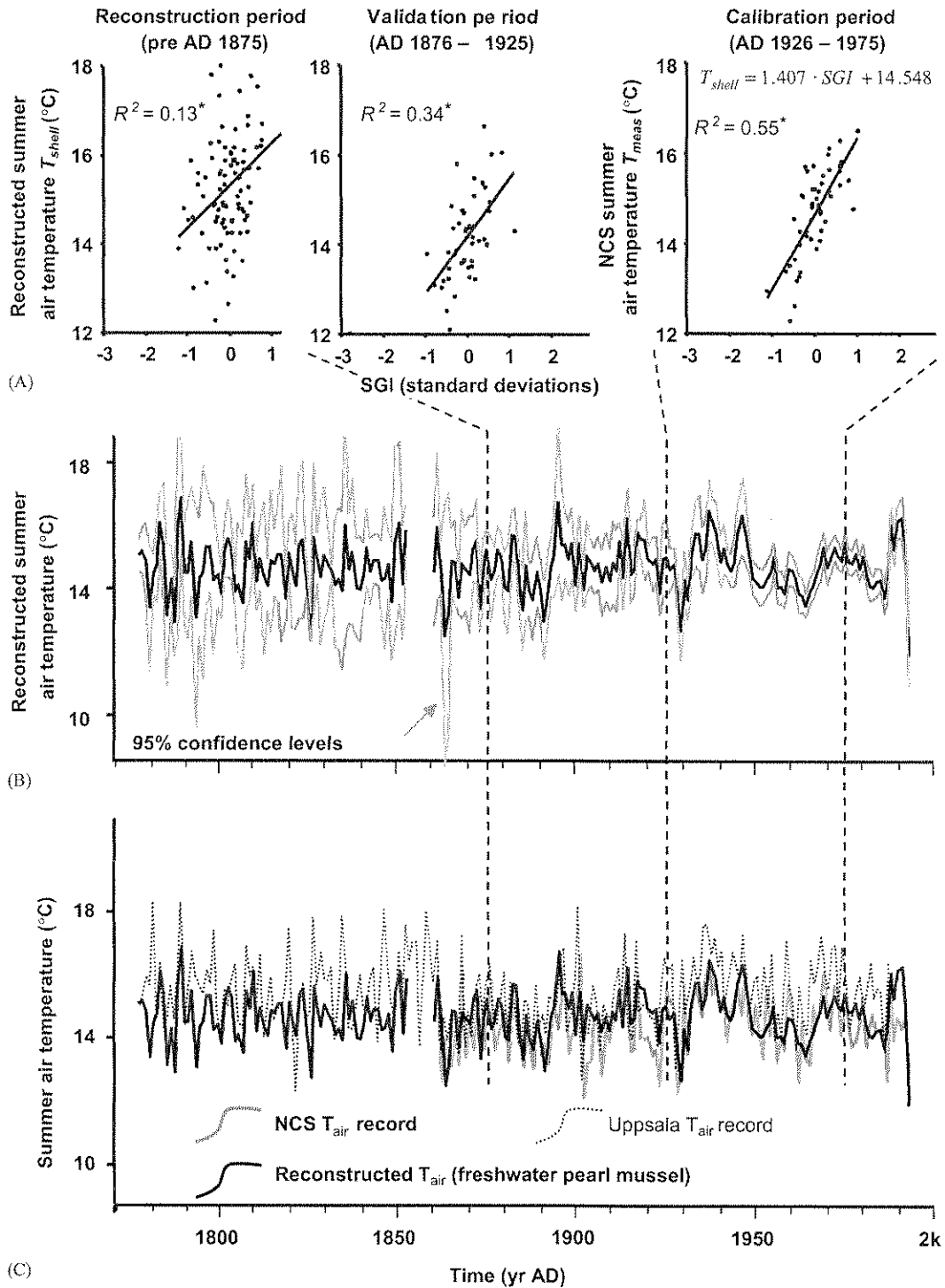
Fig. 6. Growth-temperature model and instrumentally determined temperatures. (A) The model was calibrated for the period AD 1926–1975 using the mean instrumentally determined air temperature record (T_{meas}) from northern, central and southern Sweden (NCS). Dendrochronologists used the same time period for calibration of tree data and measured environmental variables. The shell growth-temperature model was then applied to the validation (AD 1876–1925) and reconstruction periods (AD 1777–1875), respectively. (B) Using the model, we calculated temperatures from standardized annual growth rates SGI values (black) and 95% confidence intervals (grey) over the period of AD 1777–1993 and compared the results with observational data (C). Observational temperature record in (C) is depicted in grey, proxies in black. Note that the low correlation over the reconstruction period results from lower sample depth and less reliable air temperature data. Air temperatures prior to AD 1860 were only available for central Sweden (Uppsala). For further discussion see text. For abbreviations see Table 2.

Table 2
Statistics are based on variations in annual rates of the bivalve mollusk *M. margaritifera* (T_{shell}) and of Scots pines (T_{tree}) (dendrochronological data taken from Grudd in Briffa et al. (1990, 2000), Grudd et al. (2002)) as well as year-to-year variations in observational summer air temperature records (T_{meas})

Compared data	$T_{meas}-T_{shell}$				$T_{meas}-T_{tree}$				$T_{shell}-T_{tree}$			
Period (yr AD)	1777–1875	1876–1925	1926–1975	1777–1993	1777–1875	1876–1925	1926–1975	1777–1980	1777–1875	1876–1925	1926–1975	1777–1980
Length of period (years)	99	50	50	217	99	50	50	217	99	50	50	204
Number of data points	92	50	50	217	99	50	50	217	92	50	50	197
Number of shells	4–5	5–11	11–53	4–54					4–5	5–11	11–53	4–54
Correlation coefficient, r	0.36[†]	0.59[*]	0.74[*]	0.42[*]	0.54[*]	0.57[*]	0.70[*]	0.54[*]	0.20[‡]	0.55[*]	0.47[†]	0.34[*]
Variance explained, R^2	0.13[†]	0.34[*]	0.55[*]	0.18[*]	0.30[*]	0.32[*]	0.49[*]	0.29[*]	0.04[‡]	0.30[*]	0.22[†]	0.12[*]
Baillie & Pilcher's t-test	3.51[*]	4.60[*]	7.67[*]	6.72[*]	6.34[*]	4.74[*]	6.69[*]	9.11[*]	1.93[*]	4.53[*]	3.67[*]	5.10[*]
Huber's running similarity (or sign) test	65.22	60.67	72.92	72.92	74.23	64.58	81.25	72.77	58.43	68.75	56.25	59.28
(G-value, hit/ miss) [†]	135/72	54/35	35/13	35/13	72/25	31/17	39/9	147/55	52/37ns	33/15	27/21ns	115/79

Summer (June–August) temperatures over the period of AD 1860–1993 represent averages of three meteorological stations in northern, central and southern Sweden, data prior to AD 1860 came from Uppsala. [*]$p<0.0001$, [†]$p = 0.01$, [‡]$p = 0.05$, ns = not significant.

3.5. Air temperature proxies from Scots pine and bivalves

The exact same calibration period (AD 1926–1975) was chosen by dendrochronologists to reconstruct April–August air temperature from tree-ring width or density data (Briffa et al., 1990). For better comparison with our shell-based data, we re-calibrated their standardized tree-ring data with observational summer air temperatures (NCS record) to estimate June–August air temperatures (T_{tree}) from tree-ring width indices (x) (Fig. 7A):

$$T_{tree} = 0.863x + 14.311. \tag{3}$$

Eq. (3) explains 49% of the variability of annual tree ring width by air temperature during the calibration period, 32% during the validation period and 30% during the reconstruction period (Fig. 7A). Note that observational air temperature data for the reconstruction period were only available for central Sweden (Uppsala).

Fig. 7B depicts the summer air temperature proxy records based on shells (Eq. (1)) and trees (Eq. (3)) (Fig. 7B). Visual comparison reveals similar overall trends and a high degree of synchroneity between the two temperature reconstructions, especially during the last 140 years, the period with the highest sample depth and temporal coverage. Both series do not reveal any significant long-term temperature trends. This may be related to the "segment length curse" (Cook et al., 1995; see below). However, the number of cold summers was

higher prior to about AD 1900 as compared to the last 90 years (Fig. 7B). In order to statistically evaluate the similarity between the two proxy records, we employed linear regression analyses (tree-based versus shell-based temperatures) and running similarity tests. Shell-based proxy temperatures were the highest correlation found during the periods of AD 1926–1975 ($r = 0.47$, $R^2 = 0.22$, $p = 0.005$) and AD 1876–1925 ($r = 0.55$, $R^2 = 0.30$, $p<0.001$) and lowest during the pre-AD 1825 period ($r = 0.20$, $R^2 = 0.04$, $p = 0.05$). Between AD 1777 and AD 1980, the correlation between shell and tree growth is only 12% ($r = 0.34$, $R^2 = 0.12$, $p<0.0001$). According to the running similarity tests, SGI values and air temperature inferred from tree-ring width are significantly correlated during AD 1777–1980 and during the validation period (Table 2). During the other periods, p-values are slightly higher than 0.05.

4. Discussion

4.1. Annual shell growth: a proxy for summer air temperature

Results indicate that standardized annual growth rates of *M. margaritifera* shells reliably reproduce the inter-annual variability of summer air temperature shown by instrumental records. In any given year, all or most specimens studied here exhibit roughly similar growth responses (high running similarity or
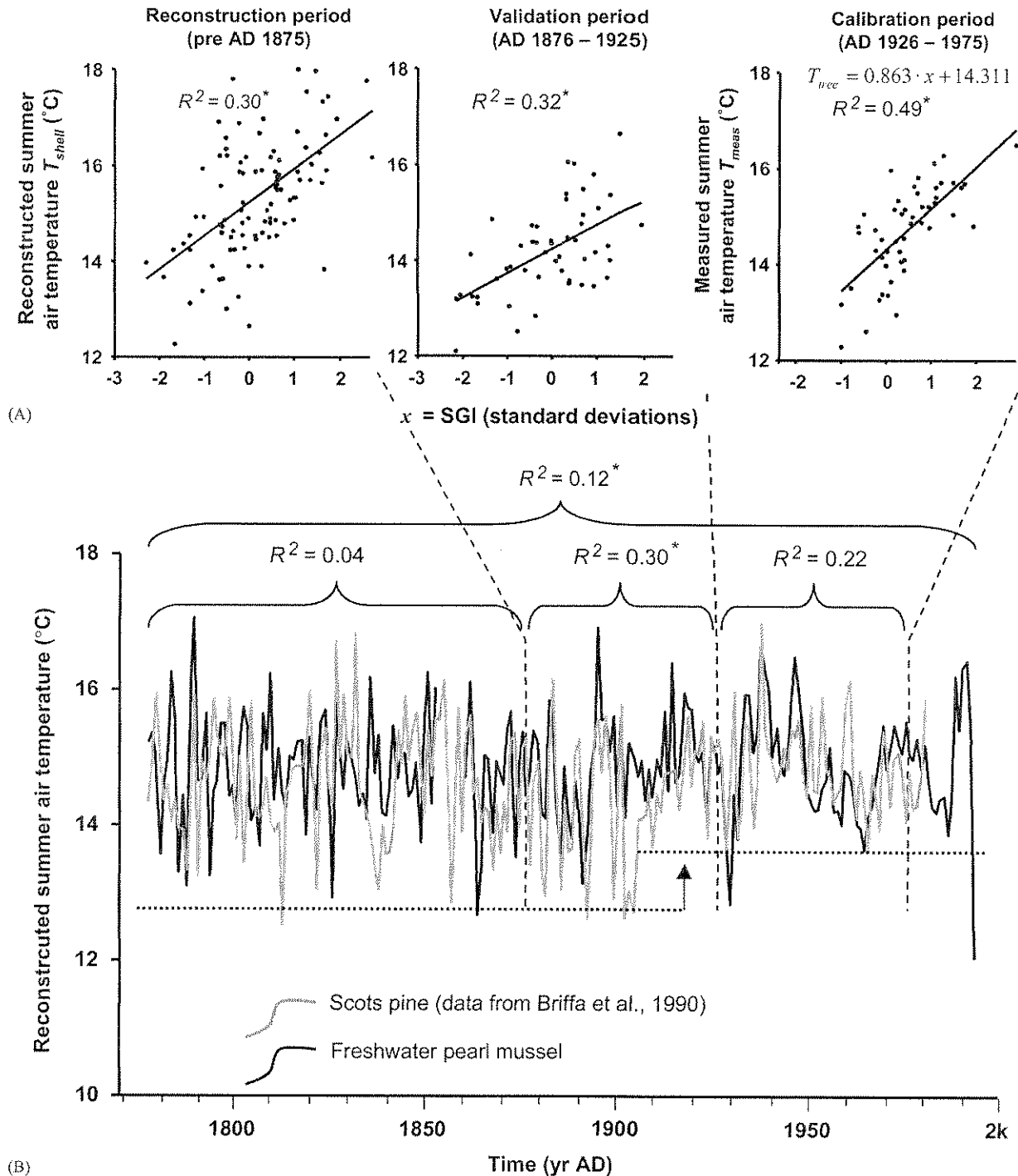
Fig. 7. Air temperature reconstructions based on tree-rings and comparison of the proxy records. (A) We re-calibrated standardized tree-ring width data by Grudd in Briffa et al. (1990) and Grudd et al. (2002), so that June–August temperatures can be inferred from variation in growth rates. The tree-based temperature model was then applied to the validation and reconstruction periods. Note, that the correlation statistics are similar to those obtained for shells (see Table 2) except for the pre-AD 1875 period. (B) Comparison of tree- and shell-based temperature proxy records reveal a reasonably good correlation over the period of AD 1876–1980. Notably, the tree- and shell-based temperature proxy records do not reveal significant temperature trends, but both records clearly show that cold summers were less frequent during the last 90 years (dotted lines). For discussion see text; for abbreviations see Table 2.

Gleichläufigkeit) as indicated by the narrow 95% confidence bands of the SGI mean values of the master and regional mean chronologies. The confidence limits

are especially narrow when the sample depth exceeded 10–15 specimens per time interval, i.e. during about AD 1920 to AD 1993. Prior to AD 1875, however, the

correlation between annual shell growth and measured or tree-based air temperature is much lower than after this period. We attribute this finding primarily to the low sample depth during the late 18th and early 19th century.

As indicated by the high correlation during the calibration and validation periods, the common annual growth response of the freshwater pearl mussel *M. margaritifera* is to a large extent controlled by summer temperature. Growth rates of shells increase as temperature rises.

The observed positive correlation between SGI and summer warmth is not surprising. Along a North–South gradient, Bauer (1992) found significant higher annual growth rates of *M. margaritifera* at lower latitudes (Spain and Massachusetts) than near the Polar Circle and concluded that higher temperature increases rates of shell production. Dunca and Mutvei (2001) reported higher daily growth rates in freshwater pearl mussels during summer. The shells grow at significantly faster rates (up to 2.5 μm per day) as soon as the temperature exceeds 10°C (Mutvei and Dunca, 2001). Similar findings on the close relation between shell growth and temperature have been reported for numerous other bivalve mollusk species (e.g., Henderson, 1929; Davenport, 1938; Kennish and Olsson, 1975, Schöne et al., 2002, 2003a). It is generally assumed that higher temperatures result in increased metabolic activity and hence faster shell production (Bauer, 1992).

4.2. Master and regional mean chronologies

While SGI master chronologies reflect the large-scale environmental variability, regional mean chronologies can reveal site/habitat-specific differences. In the current study, annual growth rates of populations of freshwater bivalves that grew in northern Sweden show a closer relation to fluctuations of air (and river water) temperature than those from localities further south. Presumably, this difference is mainly caused by differences in the length of the growing season and differences in food availability. Compared to northern populations, shells alive in central and southern Sweden show lower correlation with June through August temperature and higher correlation with May and September temperatures. This result is in agreement with previous findings which inferred the length of growing season from daily increment counts (Dunca and Mutvei, 2001). However, statistical analyses that took the extended growing season into account did not reveal significantly higher correlation coefficients. Hence, we assume that other environmental variables such as food availability are also important factors controlling shell growth (see Mutvei et al., 1996). The role of food on the growth rate of many bivalve mollusk species is well known (Ansell, 1962; Ansell, 1968; Schöne et al., 2003a). In addition,

the decreasing correlation between shell growth and temperature from northern to southern Sweden could result from a slightly different correlation between river water and air temperatures in central and southern Sweden. Our model assumes that river water and air temperatures show the same relation at all studied localities. Currently, we are unable to test this hypothesis, because river water temperature data was only available for northern Sweden.

4.3. Bivalve mollusk master chronologies: linking proxies

Up to now, the inter-annual variability of summer air temperature was almost exclusively inferred from tree-ring data. Freshwater pearl mussels provide the first independent high-resolution proxy for the exact same environmental variable. Once calibrated with instrumental measurements, relative annual rates of shell growth can be used to reconstruct warm season temperatures beyond times of direct measurements with approximately the same precision as trees (Jones et al., 1989; Grudd et al., 2002; Schöne et al., 2002). The explained variance of annual shell growth is approximately as high as that found for April–August air temperatures and tree-ring widths in Fennoscandian Scots pines (Briffa et al., 1990: 32–51%).

June–August air temperatures from annual tree-ring width data were very similar to those inferred from freshwater pearl mussels (Figs. 6B and 7), although running similarity between the two series was not always highly significant (Table 2). Such inconsistencies among the temperature proxies may result from slight differences in the vegetation period and from higher auto-correlation of tree-ring data (Fritts, 1976; Cook and Kairiukstis, 1990; Briffa et al., 1990). Despite of these problems, shells of *M. margaritifera* live in adjacent environmental settings as Scots pines and can thus potentially verify and test dendrochronological reconstructions. Our results (Table 2) clearly indicate that shells can reconstruct summer air temperatures with the same reliability as trees can. Shells can thus be used to infer air temperatures in regions where trees are not available or not sensitive enough to changes in temperature. Furthermore, freshwater bivalves could link with dendrochronologies in the non-tropical, terrestrial realm and with coral- and marine bivalve-based sclerochronologies. Such a holistic approach could lead to a better understanding of the climate history.

4.4. Bivalve mollusk master chronologies: perspectives for climate studies

Our present findings suggest that specimens of *M. margaritifera* alive at the same time and at the same place show similar growth patterns. This provides the

basis for the construction of longer chronologies which include dead-collected shells. Shells without known dates of death can be obtained from sedimentary deposits near Uppsala (Fredén, 1997) and be pre-dated with independent methods such as radiocarbon or amino acid racemization dating techniques (Goodfriend, 1992; Goodfriend et al., 1996, 1997). Standardized growth curves can then be cross-dated (Fritts, 1976) with the existing master chronology and potentially extend the length of the chronology. Similar studies were successfully applied to marine bivalve mollusks: Marchitto et al. (2000) and Schöne et al. (2003b) used live- and dead-collected specimens of *Arctica islandica* to built century-long master chronologies.

4.5. Advantages and disadvantages of using shells of M. margaritifera for climate studies

M. margaritifera is an extremely long-lived, widely distributed animal that records variations of temperature as sensitively as trees. Sub-fossil shells are available from sedimentary deposits. This makes it an excellent archive of past climate changes.

As many other bivalves, *M. margaritfera* offers several advantages over other environmental reconstruction based on accreted biological hard parts, especially trees and corals. First, shells of *M. margaritifera* provide multi-proxy records of environmental variables, such as natural and anthropogenic alterations of the environment (Dunca, 1999; Mutvei et al., 1996). Changes of environmental parameters are stored as variations in growth rates and geochemical proportions (Mutvei et al., 1996; Mutvei and Westermark, 2001). Second, *M. margaritfera* provides much higher-resolution environmental archives than trees as they grow by daily accretion of carbonate (Dunca and Mutvei, 2001). Third, *M. margaritfera* is apparently less severely affected by stand effects as tress. It is, for example, not necessary to sample only the "dominant" specimens of a population, i.e. the highest trees, or specimens from a specific ecotone, i.e. trees from near the timber-line (Schöne et al., 2003a).

Some disadvantages of using shells of *M. margaritifera* for environmental reconstructions are as follows: Growth structures are usually smaller than those of trees and thus analyses require higher optical resolution. In addition, the bivalves need to be sacrificed for studying internal shell growth patterns, whereas trees survive sampling (coring) without problems.

A problem described as the "segment length curse" (Cook et al., 1995) does not only affect tree-ring proxies, but also climate reconstructions based on bivalve shells. Though required for direct comparison of growth curves of different specimens of different ontogenetic ages, age-detrending and standardization removes not only age-related growth trends, but almost all low-frequency

signals related to climate changes. The maximum resolvable long-term trends (multi-decadal to century timescales) of the climate variability are related to the maximum length of the individual chronologies. As shown in Fig. 7, neither tree- nor bivalve-based temperature proxy records resolve clear low frequency trends such as a significant temperature rise over the last 150 years which many global climate models suggest. Current statistical techniques are unable to infer such climate information from tree or bivalve growth curves.

4.6. Implications and conclusions

Our study demonstrates that variations in annual growth rates of *M. margaritifera* can reliably reconstruct inter-annual variations of air temperature for time intervals and regions for which instrumental measurements are lacking. We (1) present the longest-ever-built master chronology of *M. margaritifera* shells, (2) demonstrate the usefulness of freshwater mollusk bivalve shells in reconstructing variations of summer air temperature, and (4) establish a model capable of predicting air temperature with a precision error of ± 0.6–0.9°C from standardized annual shell growth rates.

Freshwater bivalve mollusks can potentially provide a link between terrestrial (dendrochronology) and marine (bivalve mollusk-sclerochronology, Schöne et al., 2003b) proxies of environmental variables. Both shells of *M. margaritifera* and trees exhibit similar growing periods, i.e. they grow mainly during the warm summer months. Furthermore, annual growth rates of trees and freshwater pearl mussels are controlled by temperature.

We think that this new environmental archive will be of particular interest to climate modelers and ecologists. This new tool can provide records prior to the 20th-century greenhouse forcing and has the potential to further validate other air temperature reconstructions and thus improve climate models.

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