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Shell morphometry, pre-mortal taphonomy and ontogeny-related growth characteristics of freshwater pearl mussel in northern Finland

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Museum collection of endangered freshwater pearl mussel (*Margaritifera margaritifera*) shells was studied. The ontogenetic ages of the mussels were estimated to be between 12 and 178 years. Information from shell increments, morphometry and taphonomy was combined into age-dependent life-trait reconstructions that were modelled using linear and non-linear growth functions. Nearly all the life-trait records were best explained by non-linear models and only the shell weight was best modelled by the linear growth function. In accordance with the previously set theory about the plasticity of the species life-traits and their dependence on climate and hydrogeochemistry, the shells with northern origin reached relatively large sizes with slow growth rate. The ontogenetic age could be statistically predicted using the composite dataset of life-trait information. Based on the morphometrics, we theorized that the over 60-year-old mussels are better hedged against the potential hydrological changes resulting from climat change than younger individuals.

Introduction

Freshwater pearl mussel (*Margaritifera margaritifera*) is an endangered species which has suffered from pearl hunters, aquatic contaminants and eutrophication (Bauer 1986, 1988). Conservation plans and ecological study programs are conducted in several countries in order to enhance the potentiality of the species to survive over the 21st century threats (Young 1991, Araujo & Ramos 2001, Skinner *et al*. 2003, Valovirta *et al*. 2003). Increased knowledge of the habitat requirements and other ecological features of *M. margaritifera* are of crucial importance in the protection activity. Moreover, enhanced understanding of the species is important due to its extreme longevity since the biology of this species may provide keys to understand the physiological mechanisms sustaining the longevity and retard senescence (Ziuganov *et al*. 2000). In Finland the earlier threat to the species was profoundly pearl fishing while the modern threats are associated with the drainage of peatlands and silvicultural treatments that change the sedimentation rates and water quality of the rivers. Other factors include river dredging, eutrophication,

and construction of submerged dams for fishery purposes. Moreover, larval parasite of *M. margaritifera* is hosted by Salmonids and water power plants prevent the rise of these fishes to rivers. *M. margaritifera* was protected in 1955 in Finland but many of the populations are currently not breeding due to poor water quality (Valovirta *et al.* 2003).

Invaluable information about the bivalve ecology can be obtained from conchological studies. Shell morphology of many freshwater bivalves can be linked to the local hydrology (Ball 1922, Tevesz & Carter 1980) and the variations in shell growth, shape and size, of *M. margaritifera* has been shown to indicate the hydrology (Eagar 1977, Hastie *et al.* 2000a), hydroclimate and hydrochemistry (Bauer 1991, 1992). In addition, *M. margaritifera* forms distinct shell growth increments with an annual periodicity and the study of increments shows that the species may reach a maximum life span of more than hundred years (Hendelberg 1960, Timm 1994, Mutvei *et al.* 1994, 1996, Dunca 1999, Ziuganov *et al.* 2000). Internal growth structures are especially well visible in the cross-sections of the shells and serve as quantitative records that span over the lifetime of the individuals. For example, the growth variability of *M. margaritifera*, inferred from internal shell increments, correlates with summer temperatures while the aquatic pollution disturbs the climate-related growth signal in Swedish rivers (Dunca *et al.* 2005). The longevity of the species seems to increase towards north with decreased growth rates (Bauer 1992). Both of these variables, the general growth rates and the longevity, are of great importance for the conservational biology of *M. margaritifera* and in assessing the future scenarios of the species in different biogeographical settings (Bauer 1992, Hastie *et al.* 2000a, San Miguel *et al.* 2004).

We examined subfossil shells of *M. margaritifera* from northern Finland that were previously found empty in the proximity of the rivers, from anthropogenic deposits that most likely existed due to illegal pearl hunting (Helama *et al.* 2006a). This is to apply the principle of conservation palaeobiology (Flessa 2002) to study the endangered species without reducing the number of individuals in the existing populations. Our aims were to determine the maximal longevity of the species in the region, to estimate the influence of pre-mortal taphonomy on the ontogenetic age determination, to calculate the ontogenetic growth trends of the species by means of annual shell increments and morphometry, to create growth models that explain the three-dimensional growth of the species as a function of its ontogeny, to evaluate the possibility of statistically predicting the ontogenetic age of specimens based on ontogenetic morphometrics, and, to draw implications for the purpose of the conservation of the species.

Material

Shells of *Margaritifera margaritifera* are known to be collected from the proximity of three rivers in northern Finland, Kolmosjoki (municipality of Inari), Saukko-oja (municipality of Salla) and Kotioja (municipality of Taivalkoski). Empty shells of 24 specimens were found lying on the surface sediments on the river sides. It is likely that these were anthropogenic deposits existing due to illegal pearl hunting (Helama *et al.* 2006a). The samples now belong to the collections of the Finnish Museum of Natural History (Invertebrates Division), University of Helsinki. The exact years of death of the animals were unknown but the previous analysis revealed that the mussels that were collected from same deposit (river) had died at the same calendar year; moreover, the taphonomical analysis implied that the shells were unearthed not longer than probably couple of decades after the death (Helama *et al.* 2007).

Methods

Measuring the external shell dimensions

Each shell was measured with vernier calipers to the nearest 0.1 mm. Morphometric measurements follow the definitions of Björk (1962) and Tevesz and Carter (1980), the parameters express the posterior-to-anterior (p-a), dorsal-to-ventral (d-v) and dextral-to-sinistral (d-s) dimensions of the shells. The actual measures were length (p-a), posterior length (p-a), hinge length

(p-a), height (d-v), maximal thickness (d-s) and umbonal thickness (d-s) of the mussel. Weight of each shell was measured to the nearest 0.01 g. If only one valve was available, the thickness and weight of the individual were twofold.

Even in the smallest specimens the umbo was at least partly lost as a result of corrosion. The extent of pre-mortal shell taphonomy was determined by measuring the length (p-a) and breadth (d-v) of the corrosion. Shell morphometry and taphonomy data are given in Table 1. Great variability in the parameters implied considerable difference in the ontogenetic age of the samples. Age of each mussel was determined from annual shell-growth increments are described next.

Examining the internal shell growth increments

Growth lines can be observed directly on the external surfaces of shells, but shell cross sections provide much better resolution. As a matter of fact, several malacologists have documented difficulties in observing the narrowest increments near the ventral margin of the shell. Internal growth increments in turn were previously proved to provide reliable estimates of annual growth of *Margaritifera margaritifera* (Mutvei *et al*. 1994, 1996, Dunca & Mutvei 2001, Dunca *et al*. 2005, Helama *et al*. 2006, 2007). Following the methods described by Dunca and Mutvei (2001), one valve of each specimen was cut from the umbo to the ventral margin perpendicular to the winter lines and along the axis of minimum growth. Complete growth records for most species are found along the axis of the maximum growth. Dunca and Mutvei (2001), however, counted exactly the same number of increments in the axes of minimum and maximum growth sections with better visibility in the minimum growth section. The sections were ground (800 and 1200 grit metallographic grinding paper), polished (3 μm diamond paste) and then etched in Mutvei's solution at 37–40 °C for ca. 25 min, carefully rinsed in de-ionized water and allowed to air-dry (Mutvei *et al*. 1996, Schöne *et al*. 2005). This treatment resulted in an excellent three-dimensional preservation of the growth structures with distinct, etch-resistant, blue-coloured winter lines. Finally, annual growth increments were viewed under a reflective-light binocular microscope and digitally photographed. Widths of all the increments were measured from the outer shell layer, perpendicular to the winter lines, to the nearest 1 μm using the digital images. Helama *et al*. (2007) documented the measuring process of Kotioja and Saukko-oja specimens and more detailed description of the procedure can be found therein.

Estimating the number of corroded increments

The number of observed annual increments provided the minimum estimate of the ontogenetic age for each specimen. All specimens had however lost at least part of their umbonal prismatic layer due to corrosion. Correspondingly, an uncertain number of annual increments were unobservable. The problem of age estimation due to corrosion has been also pointed out in earlier malacological studies (Wellmann 1938, Hendelberg 1960, Björk 1962, Bauer 1992, Timm 1994). Basically, the number of lost increments

Table 1. Seven morphological (length, posterior length (LengthP), length of hinge, height, maximal thickness (ThickM), umbonal thickness (ThickU)), and two taphonomical parameters determined from the external shell dimensions. Extent of pre-mortal shell taphonomy was determined by measuring the length (LengthC) and breadth (BreadthC) of corrosion on umbo. Maximum (G_{max}), mean (G_{mean}) and minimum (G_{min}) values of measured parameters are indicated.

Dimension	Length (mm)	LengthP (mm)	Hinge (mm)	Height (mm)	ThickM (mm)	ThickU (mm)	Weight (g)	LengthC (mm)	BreadthC (mm)
G_{max}	125.8	101.9	67.8	63.4	22.7	22.7	70.7	60.9	29.8
G_{mean}	78.8	64.8	36.7	39.1	12.3	11.9	14.4	24.7	14.6
G_{min}	37.7	30.4	16.0	20.2	5.5	5.5	0.7	8.2	6.1

is a function of the breadth of the corroded area and the widths of the juvenile increments that were corroded. Previous studies have shown that the annual-increment widths in *M. margaritifera* are expected to be narrower with increasing distance from the dorsal margin (Dunca 1999, San Miguel *et al*. 2004, Helama *et al*. 2006, 2007). Such a non-stationary variation of shell increment widths complicates the estimation of the number of corroded increments.

The shells of *M. margaritifera* were divided into three categories based on the breadth of the corrosion: (i) shells with corrosion breadth smaller than 10 mm, (ii) shells with corrosion breadth greater than 10 mm but smaller than 20 mm, and (iii) shells with corrosion breadth greater than 20 mm. The first three measured increment widths in these three groups of shells were on average (i) 0.681, (ii) 0.583 and (iii) 0.290 mm, respectively. These widths indicate the mean distance from one winter line to the next one, measured perpendicularly along the cross-section, in a shell portion at different distances (d_{i} = 0–10 mm, d_{ii} = 10–20 mm, d_{iii} = 20–30 mm) from the dorsal margin.

Since the breadth of the corrosion was measured on external surface of the shell but the increment widths from cross-sections, we needed to create a quantitative relationship that could represent the relationship between the internal and external shell-increment widths. This relationship could then be used to estimate the number of increments within the corroded area. Relationship between the internal and external increment widths lies in the angle between the winter lines and the external shell surface. We measured this angle from cross-sections of sampled specimens near umbo and obtain the average of 17° (SD = 3.6°). That is to say that the typical winter-line converges the external surface (as well as the boundary between prismatic and nacreous shell layers) with rather low angle. The widths of the external shell growth increments could thus be estimated trigonometrically and the number of corroded increments could be estimated using the information about the breadth of the corrosion (which was measured from the external shell surface) and presumed increment widths (i, ii, iii) near umbo.

For example, the breadth of corrosion in sample 'T590' was measured to be as large as 15.9 mm. This distance (d) can be further expressed, according to our three distance categories (d_{i}, d_{ii}, d_{iii}) of corrosion extent, as follows:

$$d = d_{i} + d_{ii} + d_{iii} \quad (1)$$

which in turn for sample 'T590' gives:

$$d(\mathrm{T590}) = 10 + 5.9 + 0 \quad (2)$$

Thereafter, we derive the number of corroded increments (n_{corr}) using the aforementioned trigonometric relationships as follows:

$$n_{corr} = d_{i}/(0.681/\sin 17°) + d_{ii}/(0.583/\sin^{-1}17°) + d_{iii}/(0.290/\sin 17°) \quad (3)$$

For sample 'T590', n_{corr} could thus be estimated as follows:

$$n_{corr}(T590) = 4.30 + 2.96 + 0 = 7.26 \quad (4)$$

and thus the estimated number of annual increments that were lost by corrosion was 7 annuli for 'InL1'. The final age estimate of the sample is a sum of the number of corroded and originally observed increments (n_{obs}):

$$A_{est} = n_{obs} + n_{corr} \quad (5)$$

The number of originally observed increments in sample 'T590' was 31 annuli and thus A_{est} of 'T590' was calculated as follows:

$$A_{est}(T590) = 31 + 7 = 38 \quad (6)$$

This approach was used to solve the A_{est} for each of the specimen.

Modelling the growth characteristics

Ontogenetic age of each sample was associated with its morphometrical and taphonomical traits. This approach enabled us to study the morphometry and pre-mortal taphomony as a function of mussel ageing. General life-history was then modelled for the population using the linear regression and non-linear growth function of

von Bertalanffy (1938). The model with superior goodness-of-fit, judged by coefficient of determination (R^2), was chosen to represent the general growth pattern of each trait. The classical function of von Bertalanffy (1938) has traditionally been used to model the bivalve growth (Bauer 1992, Nyström *et al*. 1995, Hastie *et al*. 2000a, San Miguel *et al*. 2004). Hastie *et al*. (2000a) compared the von Bertalanffy (1938) model with the power and logistic models for Scottish *Margaritifera margaritifera* 'shell-length-at-age' data and found that the von Bertalanffy (1938) model performed generally the best with lowest residuals from their non-linear regressions. San Miguel *et al*. (2004) compared the von Bertalanffy (1938) model with a hyperbolic function and found that the two models were similar in performance and were both well fitted to Spanish *Margaritifera margaritifera* 'shell-length-at-age' data. However, the hyperbolic function appeared to be applicable only from 6 years of age onwards (San Miguel *et al*. 2004). One more obvious benefit of the von Bertalanffy (1938) function is that the growth model results are readily comparable between studies.

According to the original von Bertalanffy (1938: p. 186) growth function, the growth (G_A) of an organism at age (A) can be calculated as follows:

$$G_A = G_\infty - (G_\infty - G_0)e^{-kA} \quad (7)$$

where G_0 is the length at birth, G_∞ is the asymptotic growth measure, tending to infinity, and k is the growth rate from non-linear regression (Fig. 1). Realistically, G_0 ought to be a small positive value. Due to the curve fitting procedure, G_0 can also get a theoretical value that is negative. In our study, the growth function was applied to all morphometrical data (Table 1). In addition, we experiment fitting the non-linear function for taphonomical traits.

As a linearly progressing growth analogue for Eq. 7, regression line could be expressed as:

$$G_A = kA + G_0 \quad (8)$$

In addition to external shell measurements, internal shell growth increments were used to analyse the regional shell growth trends. Increments were aligned according to their ontogenetic age and the individual series were then averaged into one mean series. This is an approach often applied in dendrochronology, (Huntington 1914, Briffa *et al*. 1992, Helama *et al*. 2005), but has also been utilized in bivalve shell growth studies (San Miguel *et al*. 2004). This mean value function was further modelled using the modified negative exponential function of Fritts *et al*. (1969). This function creates model for expected increment width (I) at age (A) that can be expressed as:

$$I_A = ae^{-kA} + b \quad (9)$$

where constant a can be defined as determining the initial height of the curve, constant k controlling the concavity of it and constant b represent-

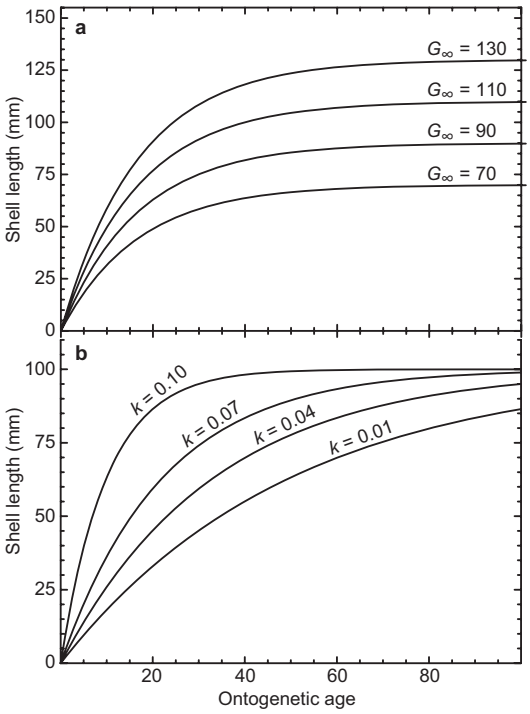

Fig. 1. Behaviour of the von Bertalanffy (1938) growth function exemplified by hypothetical parameters k and G_∞ (Eq. 7). (**a**) Four models of shell length history through the ontogeny with varying G_∞, and constant k = 0.06, and (**b**) with constant G_∞ = 100 and four different values of k. The hypothetical parameters are equivalent to the typical values for the shell length growth of *Margaritifera margaritifera* (Bauer 1992, Hastie *et al.* 2000a, San Miguel *et al.* 2004).

ing the translation of the time (tree age) axis (Fritts *et al*. 1969).

Predicting the ontogenetic age using morphometrics

Once the ontogenetic age of each specimen was determined and the life-trait characteristics were modelled, we experimented to statistically predict the true ontogenetic age of the specimens using purely the life-trait information. Bivalve demography is often estimated using the distribution of size frequencies, typically the measures of the shell length (e.g. Cerrato 1980). Thus, our goal was to statistically examine how reliable estimates of the true age of *M. margaritifera* the morphometrical variables, such as shell length, are.

In order to solve the ontogenetic age (A) from the von Bertalanffy (1938) growth function, we simply obtain the Eq. 7 in the form of

$$A = -\frac{\ln\left(\frac{G_\infty - G_A}{G_\infty - G_0}\right)}{k} \qquad (10)$$

Therefore, the ontogenetic age (A) could be theoretically solved using Eq. 10 among the populations for which the growth parameters (G_∞ and G_0) have been previously estimated and the G_A is the growth measure of the particular specimen for which the age is to be predicted. Likewise, if the relationship between the ontogenetic age and the life trait is found to be linear, we obtain the theoretical transfer function from Eq. (8) for the ontogenetic age:

$$A = (G_A - G_0)/k \qquad (11)$$

where G_0 and k are, similarly to Eq. 10, the predetermined growth parameters for the given population at ontogenetic age A, and the G_A is the growth measure of the particular specimen.

Results and discussion

Estimation of lifespan

The number of counted (and measured) annual shell growth increments ranged between 8 and 161 with the average of 37 (SD = 39). The umbo of *Margaritifera margaritifera* was lost due to pre-mortem taphonomical processes in all the studied valves. This is known to be a typical feature of *M. margaritifera* across its distributio areas (Linné 1806: p. 176). The number of observable annual increments was thus a minimum estimate of the lifespan of each mussel, the actual ontogenetic age at death being somewhat older. The number of lost increments was determined as a function of the breadth of the corroded area and the widths of the juvenile increments that were corroded and the estimated ontogenetic ages (A_{est}) were calculated as a sum of the number of counted and estimated increments.

The ontogenetic ages of the specimens based on A_{est} were on average 7 years longer than the ages based merely on the number of observed annual increments. The estimates of corroded increments were found to range between 3 and 19 whereas A_{est} ranged between 12 and 178, with average of 44 and standard deviation of 43 years. A_{est} of the three oldest specimens was on average 148 years. Ecology of the juvenile *M. margaritifera* may however bear some further implications on the aforementioned ages: subsequent to its larval parasite life-stage, mussels spend a number of years burrowed into the river sediment where its increments may grow exceptionally narrow: according to Buddensiek (1995), this may have generally caused an underestimation of approx. 4 post-parasitic years for the age determinations (*see* fig. 5 in Buddensiek 1995).

In addition, it should be however borne in mind that the mussels under the investigation were killed by man (Helama *et al*. 2007), hence even older specimens are expected to be found alive in nature. These northern mussels were evidently among the oldest recorded individuals of *M. margaritifera*.

The results indicating extreme longevity in the study region were in line with the observation of Bauer (1992) who concluded that the lifespan of the species tends to increase towards the high latitudes. Hendelberg (1960) studied the same species from Pärlälven, at the Arctic Circle in northern Sweden, and found two specimens over 100 years old (105 and 116 years). Björk (1962)

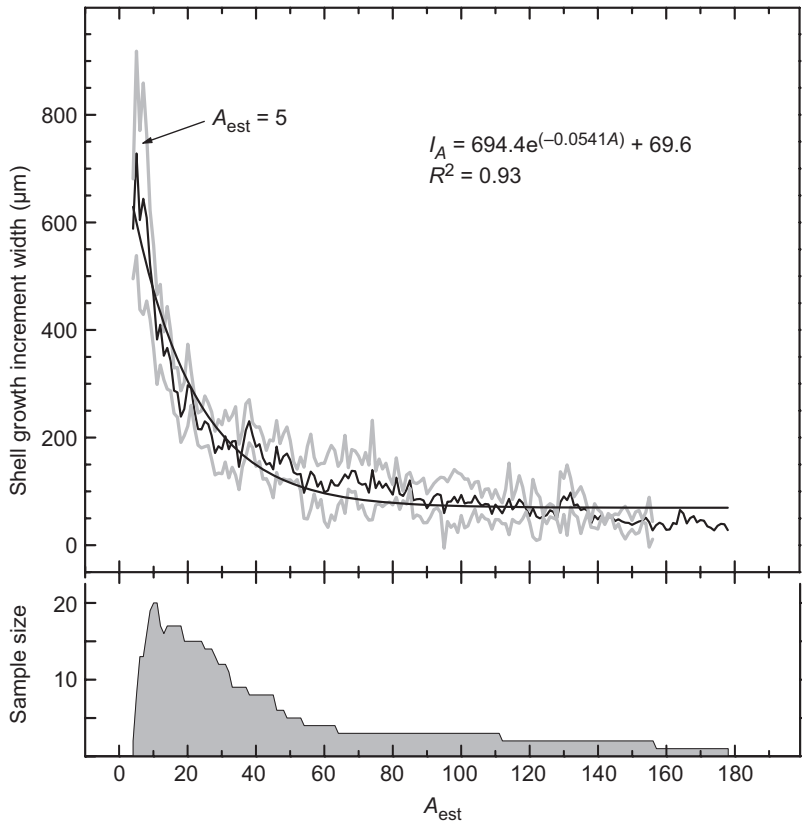

Fig. 2. Mean growth of the internal shell increments (black line) and its 95% confidence limits (gray lines) for the *Margaritifera margaritifera* from northern Finland, depicted as a function of ontogenetic age (A_{est}; Eq. 5). The mean function was captured by the growth function of Fritts *et al.* (1969) (Eq. 9) (upper plot). Sample size of the studied population is shown as gray area (lower plot).

studied populations of *M. margaritifera* from southern Sweden and, by comparing his results to those of Heldelberg (1960), concluded that the southern populations did not contain century-old individuals being thus probably considerably younger. Björk (1962) assumed this to be due to either climatic or anthropogenic factors. With regard to positive correlation between latitude and maximal age, Ziuganov *et al.* (2000) listed several very old specimens of *M. margaritifera* from arctic Russia (114, 155 and 190 years) but San Miguel *et al.* (2004) found a maximum lifespan of only 65 years among the populations in Spain. Century-old specimens can however be found also far south of arctic and subarctic areas as shown by Timm (1994) who determined the maximum age of 132 years for *M. margaritifera* found from Estonia, and Mutvei *et al.* (1996) who recorded a 100-year-old *M. margaritifera* specimen from south-western Sweden. According to Bauer (1992), the maximum biogeographical gradient in lifespan is probably linked to temperature-dependent variation of metabolism. In addition, aquatic pollution is likely to increase the mortality and thus decreases the longevity (Bauer 1992). Apparently, a single animal can reach very old age regardless of its position along the north–south gradient due to localized factors but the general tendency of longevity seem clearly to predict that the oldest specimens are likely to be found close to the northernmost limits of the species.

Ontogenetic trend in the shell growth increments

In order to study the age-dependent change in annual shell growth, the time series of the annual shell growth increment widths were aligned according to their ontogenetic growth years and averaged (Fig. 2). The mean series computed this way was expected to represent the growth variability due to ontogeny, physiological ageing and sizing of the organism (Huntington 1914, Briffa *et al.* 1992, Helama *et al.* 2005). The observed

growth trend was similar in behaviour to that in previously published data on populations of *M. margaritifera* (Dunca 1999, Helama *et al.* 2006, San Miguel 2004). The growth trend for northern Finnish *M. margaritifera* was modelled using modified negative exponential function (Eq. 9). The model quantified the characteristics of the growth trend, juvenile growth maximum, concavity of the growth decline and the mature growth level (Fig. 2). It further depicted the evolution of the increment growth as a function of bivalve age.

Shell increments of *M. margaritifera* from northern Finland exhibited widest annual increments at ontogenetic age of five years (Fig. 2). Interestingly, San Miguel *et al.* (2004) made identical observation when studying the shell growth of *M. margaritifera* in north-western Spain. San Miguel *et al.* (2004) observed the regional maximum growth at the ages of 5 and 6 years. Comparison of Spanish and Finnish populations is especially interesting as the two populations originate from near the southern and northern distributional limits of the species in Europe. Although the two populations exhibited the maximum growth at same ontogenetic age, the growth rates are however at different level. On average, Spanish populations reached the maximum annual growth of approx. 6.5 mm during the juvenile stage when measured on the external shell surface (fig. 1 in San Miguel *et al.* 2004). Accepting the aforementioned trigonometric relationship between the external and internal shell growth increments (with angle of 17°), we calculated that the maximum juvenile growth of Spanish populations was approx. 2.6 times higher than the maximum juvenile growth of *M. margaritifera* in northern Finland (Fig. 2).

After the juvenile growth maximum, growth trend exhibited exponential decline in annual increments (Fig. 2). The growth decline continued through the lifespan of the species. The observed growth trend and its overall shape were consistent with the results from Sweden (Dunca 1999, Helama *et al.* 2006) and Spain (San Miguel *et al.* 2004). This inter-population comparison implied that although the absolute growth rates were substantially different from north to south, the overall trend in growth behaviour through the ontogeny was similar in shape with exponential decline. Furthermore, the juvenile growth maximum occurred in phase with regards to mussel age. It would be difficult to explain the observed similitude by factors other than those internal to growth system, being probably related to the geometry of the shell.

Furthermore, the absolute narrowness of the oldest growth increments bears significance on the estimation of the longevity of the species. Previously, the ontogenetic ages of the *M. margaritifera* were identified by counting the annual growth increments in the ligament (Wellmann 1938, Hendelberg 1960, Bauer 1992, Semenova *et al.* 1992, Hastie *et al.* 2000a, 2000b) or by observing the internal increments in the shell cross-sections (Timm 1994, Mutvei *et al.* 1996, Dunca 1999, Dunca *et al.* 2005, this study). While the corrosion is the problem with all of the approaches, we emphasize the high resolution and visibility of the shell growth structures in the cross-sections. Previously, Timm (1994) compared the three approaches of growth increment counting using several freshwater species and found that counting the internal growth increments yielded higher number of annual increments than the two other approaches. In the populations from northern Finland, the ontogenetically oldest increments are often less than 50 μm, occasionally even less than 25 μm (Fig. 2). In this perspective, the carefully worked shell cross-sections appear appropriate medium to observing the narrowest (ontogenetically oldest) growth increments.

Three-dimensional shell growth and corrosion

Relationships between the different morphometrical and taphonomical traits indicated high degree of coincidence (Table 2) indicating that under three-dimensional inspection the mussels gained size more or less coherently. In addition, the corrosion seemed to get larger the larger and the heavier the shell gets.

Visual inspection of the life-trait variability showed that most of the morphometrical variables exhibited clearly non-linear development through the ontogeny (Fig. 3). Relationships between the ontogenetic age and morphometri-

cal and taphonomical variables were modelled with non-linear growth functions of von Bertalanffy (1938). Models explained 89%–94% of the observed growth variation due to ontogeny in all three shell dimensions (Table 3A). Linear models (not shown) were less effective in explaining the ageing in length, height and thickness of the shell. Non-linearity of the three-dimensional sizing of the shells was visually even well observable and the shells of *M. margaritifera* seemed to approach more or less asymptotic growth phase. In this stage, the three-dimensional sizing of the shells is seemingly not occurring any longer. The ontogenetic age, after which the greatest change towards asymptotic growth, differed slightly from trait to trait, but seemed to take place approx. between 70 and 100 years (Fig. 3). However, if the shell growth was presented increment-by-increment (Fig. 2), it became obvious that the shell growth does not actually cease even at age of 150–200 years but continues although with diminishing rate. The final, asymptotic, growth phase has implications for the morphometry based estimation of individual mussel age and thus for population demography; these issues will be discussed in this context below.

All the morphometrical traits bore relatively low growth rates; moreover, the mussels reached the asymptotic growth phase at rather late age.

Table 2. Relationships between the different morphometrical and taphonomical traits (Fig. 3) quantified by Spearman correlations. Correlations indicate high degree of similarity in the ageing process of different life-traits; mean correlation is 0.950 and the correlations are all significant ($p < 0.01$). The result is supported by Pearson correlations (not shown), having mean correlation 0.930. Abbreviations of the life-trait variables as in Table 1.

	Length	LengthP	Hinge	Height	ThickM	ThickU	Weight	LengthC	BreadthC
Length	1.000								
LengthP	0.993	1.000							
Hinge	0.983	0.992	1.000						
Height	0.953	0.962	0.959	1.000					
ThickM	0.950	0.947	0.934	0.943	1.000				
ThickU	0.962	0.955	0.945	0.942	0.980	1.000			
Weight	0.985	0.980	0.968	0.938	0.969	0.981	1.000		
LengthC	0.957	0.951	0.946	0.949	0.966	0.960	0.965	1.000	
HeightC	0.907	0.903	0.883	0.892	0.916	0.938	0.914	0.940	1.000

Table 3. Relationships between (**A**) the ontogenetic age and morphometrical variables (abbreviations are as in Table 1) were modelled by non-linear and linear growth functions (Eqs. 7 and 8), and (**B**) the comparison of the non-linear and linear approaches for modelling the progress in corrosion. Statistical fit of the models were quantified by explained variance (R^2). G_∞, G_0 and k are the obtained parameters of the fitted non-linear and linear models: G_∞ is the final length of the shell, G_0 is the initial length of the shell and k is the shell growth rate.

A	Length non-linear	LengthP non-linear	Hinge non-linear	Height non-linear	ThickM non-linear	ThickU non-linear	Weigth linear
R^2	0.943	0.939	0.936	0.893	0.931	0.922	0.936
G_∞	122.6	98.9	68.7	57.9	44.3	42.6	
G_0	–4.0	–10.1	3.0	4.5	6.3	5.7	–8.1
k	0.0363	0.0407	0.0221	0.0354	0.0199	0.0205	0.837

B	LengthC non-linear	LengthC linear	BreadthC non-linear	BreadthC linear
R^2	0.952	0.921	0.882	0.8
G_∞	72.7		30.4	
G_0	5.4	11.6	4.0	8.8
k	0.0090	0.297	0.0147	0.129

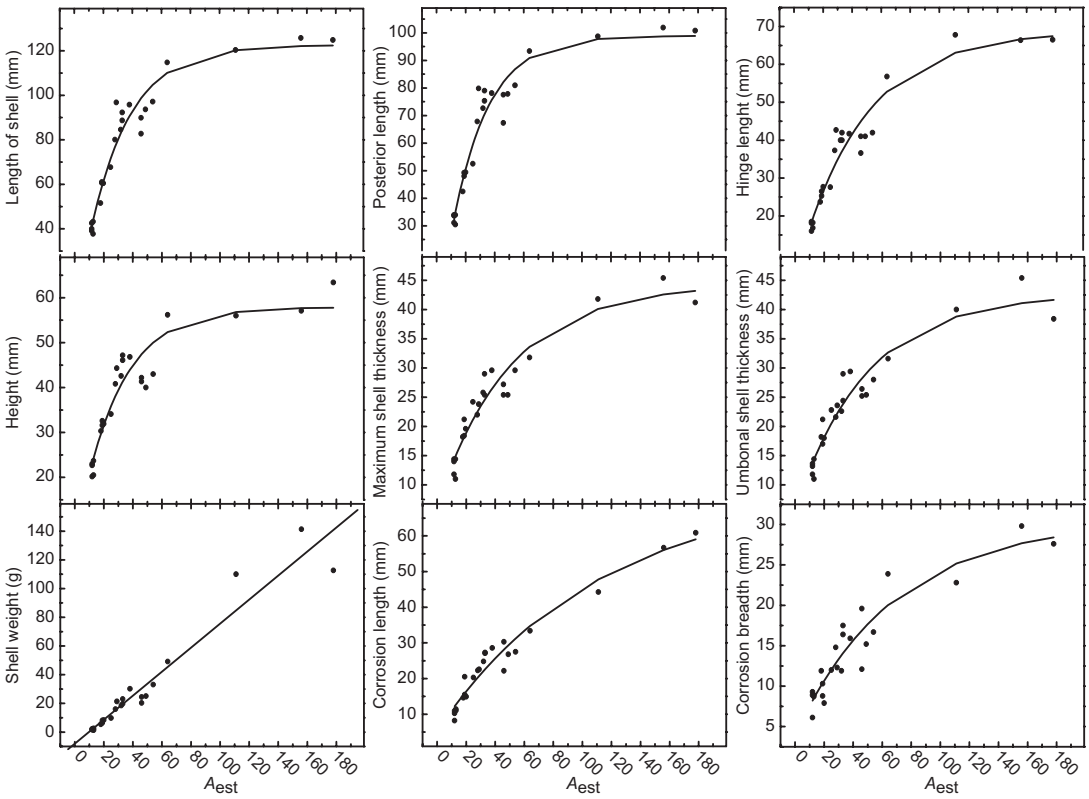

Fig. 3. Life-trait history of the different variables of *Margaritifera margaritifera* shell morphometry and pre-mortem taphonomy as a function of ontogenetic age (A_{est}; Eq. 5). The variation in individual specimens (circles) is further transferred into the population life-trait history (line) using the von Bertalanffy (1938) growth function (Eq. 7; Fig. 1). In one case (shell weight), linear function (Eq. 8) was used instead of the non-linear von Bertalanffy (1938) curve.

Both features were quantified by k in Eq. 7 (Fig. 1 and Table 3). In addition, the oldest of the studied shells reached relatively large size, indicated by both maximal (G_{max} in Table 1) and asymptotic G_{∞} (Table 3) size measures. Previously, the same non-linear growth model of von Bertalanffy (1938) was applied for *M. margaritifera* length growth data by Bauer (1992), Hastie *et al.* (2000a) and San Miguel *et al.* (2004). Since the growth rate comparison is expected to be most reliable between exactly same statistical models, the aforementioned studies and their results were chosen as a baseline for *M. margaritifera* shell length growth data from northern Finland. By comparison, Bauer (1992), who studied 48 populations across the species distributional areas in Europe and North America, found the range of k and G_{∞} for shell length as 0.018–0.108 and 83–138 mm, respectively. According to Hastie *et al.* (2000a), in Scotland the ranges of the estimates of k and G_{∞} for the shell length were 0.023–0.075 and 77–158 mm, respectively. In northern Spain, San Miguel *et al.* (2004) estimated ranges of k and G_{∞} for shell lengths 0.089–0.144 and 84–101 mm, respectively.

It is likely that the low rates of growth are related to the northern origin of the species. Already Björk (1962) compared the populations of *M. margaritifera* from northern (Hendelberg 1960) and southern Sweden and recorded the decidedly higher growth rates of his southern specimens. Using a dataset of *M. margaritifera* shell-length growth from large areas of Europe and North America, Bauer (1992) presented the negative correlation between the latitude and k value. Within the populations that were studied by Bauer (1992), the growth rate k varied markedly from approx. 65°N to 40°N, latitude explaining 55% of the spatial variance in k from north to south. That is to say that the northern

populations tend, in line with our observations, to growth at low rates and to attain the asymptotic growth phase at old age. Likewise, San Miguel *et al*. (2004) determined values of *k* higher than 0.1 for many southern populations of *M. margaritifera* in Spain. The obtained value of *k* for the growth of shell length in northern Finland was thus well in line with the previously demonstrated negative correlation between *k* and latitude (Björk 1962, Bauer 1992).

The study region is characterized by low annual temperatures, approx. between –0.4 and –2.0 °C (Helama *et al*. 2005). According to Bauer (1992), the major factor influencing *k* would be temperature with possible connection to the metabolism of mussels. Furthermore, the influence of temperature on *M. margaritifera* shell growth at a variety of sites was demonstrated by Semenova *et al*. (1992) and Dunca *et al*. (2005). Juvenile growth rates were shown to be at higher level in rivers with higher temperatures in northwestern Russia (Semenova *et al*. 1992) and the variability in diurnal and annual shell growth increments was positively correlated with summer temperatures in Swedish rivers (Dunca *et al*. 2005). More precisely, the highest correlation (0.59) between annual *M. margaritifera* shell growth increments of the compound dataset from northern to southern Sweden was found for June through August temperatures (Schöne *et al*. 2004) and the daily shell growth was found to co-vary with the growth season temperatures from April to October (Dunca *et al*. 2005). Since the shell increment growth seems to be positively controlled by summer temperatures, one could expect the same forcing to act on the overall shell accretion, and thus generally more slowly growing mussels ought to be found towards the north, in line with the suggestion of Bauer (1992).

Apart from climatic influence, the *M. margaritifera* shell growth rates could be associated with hydrochemistry. Comparing a total of 48 populations across the species distributional areas, Bauer (1991, 1992) found significant positive correlation between pH and G_∞ for shell length but significant negative correlation between pH and *k*, whereas the concentration of Ca was found to correlate significantly and negatively with *k* but not significantly with G_∞ for shell length. The spatial correlations of Bauer (1991, 1992) are parallel with temporal correlation of Mutvei *et al*. (1996) who found that in Swedish rivers the annual growth rates of *M. margaritifera* were significantly increased after an anthropogenic increase of pH and food supply. Referring to regional hydrogeochemistry, the study area is characterized by pH values of spring (and dug well) waters approx. between 5.8 (6.6). The concentrations of Ca in spring (and dug well) water are characteristically low, around 2–3 (8–10) ml l^{-1} and the waters are correspondingly soft (Lahermo *et al*. 1990). Interestingly, the regionally low concentrations of Ca and values of pH would thus be in contravention of observed low *k* and high G_∞ in northern Finland with regards to the aforementioned hydrochemistry–shell growth correlations of Bauer (1992). These results point to the predominance of climatic forcing on *k* and G_∞, with potentially minor influence from hydrogeochemical factors. Results from our sample would thus parallel with the observation of Bauer (1992) who emphasized the importance of temperature control on life-traits of the bivalve length growth.

The increase in shell weight could be well explained by regression line (Fig. 3). This indicates that adding the annual substance of shell material occurs in approximately constant rate regardless of the bivalve age and that the shell gains weight without actual asymptotic growth phase at ontogenetically old age, in contrast to three-dimensional sizing which occurs non-linearly. Observed linearity in shell weight increase is likely to be a result of inner and outer shell layers becoming thicker over the life-span of the mussels. Linear increase in *M. margaritifera* shell weight has previously been observed by Wellmann (1938) in Germanry (Lüneburg Heath), where annual increase was on average 1.2 g and by Hendelberg (1960) in northern Sweden, where the average annual increase fell between 0.85 and 1.4 g. Based on the regression weight *k* (Table 3), the annual increase in the present sample was estimated as 0.84 g. In the context of previous estimates, the shell growth in northern Finland thus appears relatively poor. This result is parallel to shell sizing for which the environmental interpretation was given above.

Non-linear models were found to be more effective in explaining the process of pre-mortem taphonomy than linear models (Table 3B). The difference in model performance was clear when comparing the two types of models that were used to explain the shell corrosion. The observed and modelled (Fig. 3 and Table 3B) non-linearity in the progressive shell corrosion may be due to the increasing thickness of the outer shell layer with increasing distance from the dorsal margin. As the area of corrosion becomes larger, the process involves with gradually thicker outer shell layer. It is thus probable that the corrosion is consequently retarded the larger the area it reaches. The hypothesis is supported by the observation that the benefit of non-linear model is relatively more distinct for modelling the corrosion breadth than length (Table 3B).

Some studies have emphasized the plasticity in the life-trait histories of *M. margaritifera* (Bauer 1991, 1992, Hastie *et al.* 2000a). For example, Hastie *et al.* (2000a) found the range of k between 0.023 and 0.098 from different subpopulations, mainly different rivers, in Scotland. Since we obtained a single regional estimate of k for shell length growth (0.034), the present sample cannot directly indicate the plasticity of the life-trait histories. We however note that the models explained (R^2 in Table 3) the regional life-trait variability at the level that was comparable to model fits of Hastie *et al.* (2000a) who obtained the von Bertalanffy (1938) models for shell length growth of different subpopulations with explained variance between 0.821 and 0.941. This, in turn, would indicate that the studied populations show rather homogenous life-trait histories within all the traits in the given region, at least between the studied rivers. More rivers from Lapland should, however, be studied to reach the final regional conclusion.

Converting the life-trait information into ontogenetic age

The correct determination of the population age structure is of great importance in studies that deal with species conservation. The status and the vitality of the endangered species in its environment is directly perceived from the demographical information and the age structure bears implications in outlining the future scenarios and potentials of the populations and species, such as *M. margaritifera* (Bauer 1991, 1992, Hastie *et al.* 2000b). Demographical studies are however often based on the distribution of size frequencies, and the shell size information is expected to mirror the supposed age classes of the species in the given environment. Typical indicator of bivalve age is the shell length. As compared with other life-traits, the shell length is, as a matter of fact, among the best measured variables describing the ontogenetic age (judged by R^2 in Table 3).

While the estimated population growth curve of any variable in Fig. 3 could readily provide visual means for the estimation of the age of the bivalves, we experimented with the statistical skill of life-trait information to predict the ontogenetic age of the specimens. In so doing, the life-trait information from Kolmosjoki and Kotioja was chosen as the calibration dataset. The remaining part of the dataset from Saukkoja was not used, and thus left for validation of the calibration model. That is, the age prediction model that was built using the specimens in the calibration was further evaluated by the specimens containing independent life-trait information that was not used to build the prediction model. Successful verification would imply that the age determination model is valid for independent shell material.

Furthermore, we built four different alternative transfer functions based on different predictors. Following Eq. 10 the shell length (L) was used as a sole predictor of ontogenetic age as follows:

$$A_L = -\frac{\ln\left(\frac{127.7 - L}{127.7 - 14.9}\right)}{0.0236} \qquad (12)$$

where A_L is the predicted age based on the shell length and G is the shell length of the particular specimen of an unknown age.

The ontogenetic age was predicted by Eq. 11 and thus solely by the shell weight (W) as follows:

$$A_W = (W - 5.268)/0.425 \qquad (13)$$

where A_W is the predicted age based on the shell weight and G is the shell weight of the particular specimen of an unknown age.

All eight non-linearly behaving morphometric variables were used in an integrated model. Since the measured variables were significantly inter-correlated (Table 2), the amount of data was reduced via principal component analysis (Jolliffe 1986, Hammer *et al.* 2001). After including the eight variables into the variance-covariance matrix, we obtained the first principal component (PC#1) that explained 97.4% of the total variance of the original data matrix thus indicating significant load of information in the PC#1. The ontogenetic age ($A_{PC\#1}$) of the mussels could thus be predicted with PC#1 inserted in Eq. 10 as follows:

$$A_{PC\#1} = -\frac{\ln\left(\frac{204.6 - PC\#1}{204.6 - 25.7}\right)}{0.0201} \quad (14)$$

where PC#1 is the first principal component from the variance-covariance matrix assigned to the particular specimen of an unknown ontogenetic age.

The combination of the linear and non-linear transfer functions was used to predict the ontogenetic age of the specimens. This prediction was based on PC#1 and shell weight. We obtain the compound transfer function for ontogenetic age ($A_{W,PC\#1}$) as follows:

$$A_{W,PC\#1} = 2.64 - 0.28A_W + 1.306A_{PC\#1} \quad (15)$$

where A_W and $A_{PC\#1}$ are the parameters solved in Eqs. 13 and 14.

In conclusion, all four different models showed similarly high degree of accuracy explaining 91.8%–99.6% of the variability in A_{est} among the calibration dataset and 94.7%–98.0% of the variability in A_{est} among the validation dataset, withheld from calibration (Fig. 4). The age predictions were in all except one case (shell weight) more reliable for calibration than verification datasets. This may be somewhat expectable result but at the same time it indicates that the prediction model becomes less accurate for populations that were not used in the actual calibration. The final model, predicting the age with maximal set of predictors (Eq. 15), seemed to improve especially the estimates of the oldest samples (Fig. 4) and on average, the calibration and verification provided age predictions that deviated ±3 years and ±10 years from the 'true' age estimates ($A_{est} - A_{pred}$), respectively. It is likely that, especially if applied for other population in the same region, the model provides more accurate predictions for ontogenetic ages that are under 100 years. Moreover, due to individual ageing-sizing process, the model could probably be better used to predict the population age structure (for example to transfer the demographical size frequency histograms to corresponding age estimates) than individual sample ages.

Although our multivariate analyses predicting the ontogenetic age of the mussels could be characterized as preliminary, we emphasize the significant skill of the model readily in its tentative form. Greater number of samples would be required to build an improved model.

Implications for conservation

The growth parameters and the ontogenetic age estimates are of great value for the understanding of conservation biology of *M. margaritifera* (Bauer 1991, 1992). In this respect, populations with high k, low G_{max} and low maximum ages have shown to be particularly vulnerable to extinction. These three parameters are coupled to fertility (the number of glochidia per gravid female) which is negatively correlated with k and positively with measures of age and size (Bauer 1991, 1992).

As evidenced above, the species may reach centennial longevity in northern Finland. Furthermore, the growth is characterized by relatively large shell size and low values of k. According to Bauer (1991, 1992), these are the typical features of populations that are least vulnerable to decline. Since the estimates of k tend to decrease and the maximum size and age tend to increase towards the high latitudes, one could expect to find less threatened populations in northern Europe. Even high level of fertility does not, however, support the species survival in the presence of aquatic contaminants that are detrimental for glochidia. In national scale, the water-quality related vitality of *M. margaritifera* amel-

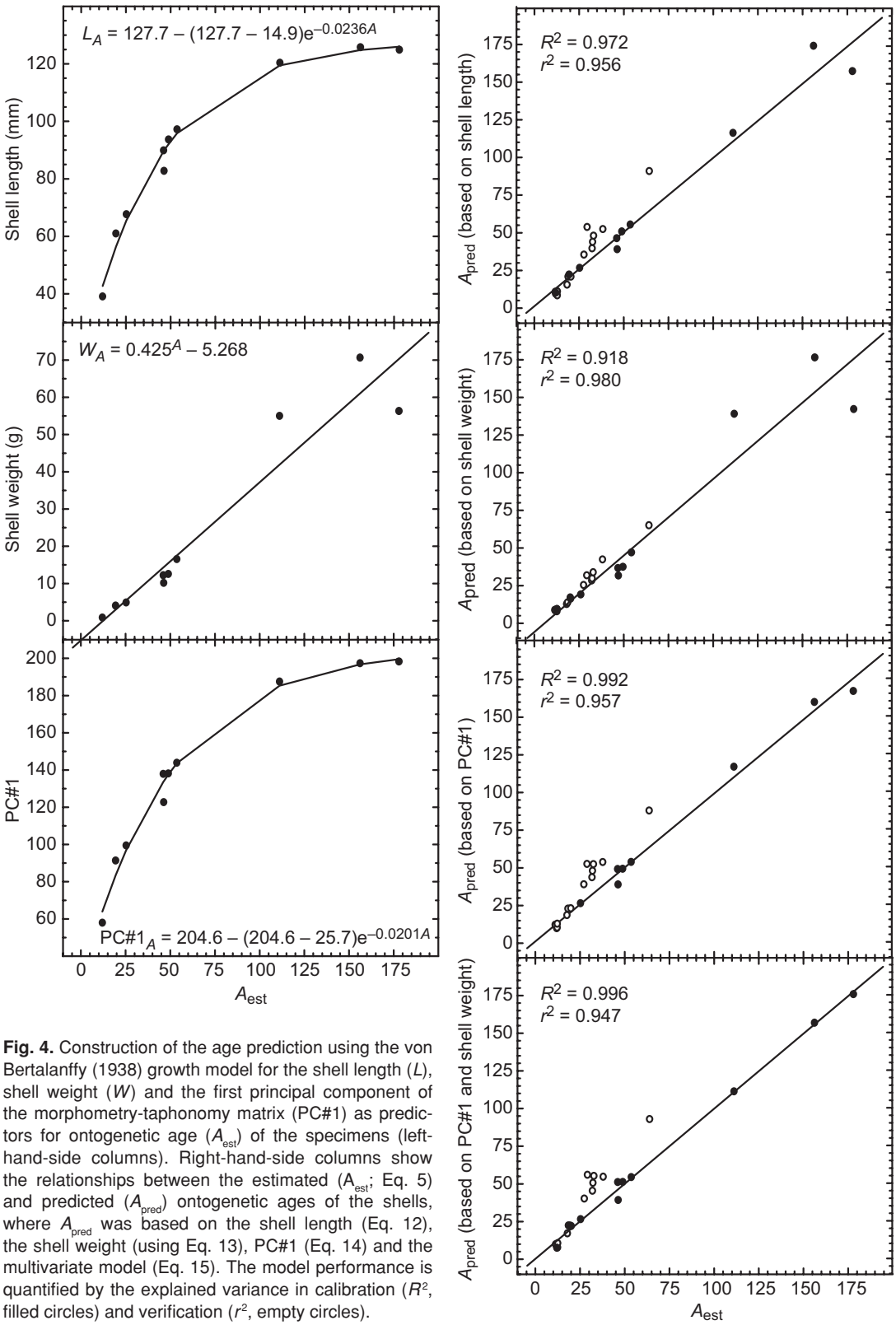

Fig. 4. Construction of the age prediction using the von Bertalanffy (1938) growth model for the shell length (L), shell weight (W) and the first principal component of the morphometry-taphonomy matrix (PC#1) as predictors for ontogenetic age (A_{est}) of the specimens (left-hand-side columns). Right-hand-side columns show the relationships between the estimated (A_{est}; Eq. 5) and predicted (A_{pred}) ontogenetic ages of the shells, where A_{pred} was based on the shell length (Eq. 12), the shell weight (using Eq. 13), PC#1 (Eq. 14) and the multivariate model (Eq. 15). The model performance is quantified by the explained variance in calibration (R^2, filled circles) and verification (r^2, empty circles).

iorates towards the north and accordingly the most vital populations are found from Lapland (Valovirta *et al*. 2003). The northern populations thus seem to inhabit the environment that interestingly appears to combine the favourable conservational elements: the harsh climate induces the extreme longevity along with high fertility whereas the overall water quality supports the reproduction and vitality. Moreover, the low growth value k can be theorized to support the population existence even under transiently deteriorated water conditions (Bauer 1991, 1992).

Additional threat for the species may however rise due to abrupt fluctuations in climate. According to Hastie *et al*. (2001, 2003), the changing climate has already and will have direct and indirect effect on the populations of *M. margaritigera* in northern Europe. More specifically, Hastie *et al*. (2001) described the influence of floods in the River Kerry (Scotland) in February 1998 that killed 4%–8% (50 000 mussels) of the internationally important *M. margaritifera* population due to channel reformation and large-scale movements of substrata. Since the amplitude of climatic fluctuations in Finlands is generally known to increase towards the north (Heino 1994), with corresponding amplification of ecological variations in the same biogeographical direction (Helama *et al*. 2005), the threat due to climatic perturbations will be at highest level in the northern latitudes, such as study region.

The regional climate of northern Finland is known to correlate with large-scale atmospheric variations (Hurrell 1995) with assumed increase in precipitation (Hurrell 1995, Jylhä *et al*. 2004) and river discharge (Peterson *et al*. 2002) due to currently observed climate trends (Hurrell 1995). These climatic relationships would imply increased risk of flooding also in the study region and concomitant threats to *M. margaritifera* populations. While the severest floods may be deleterious to the mussels, *M. margaritifera* may hedge against the moderate flooding by burrowing. According to Eagar (1977), the burrowing of the species is assisted by a strong ligament of which strength can be calculated from the surface area of the valve as projected on the sagittal plane using linear relationship

$$\mathrm{OM} = 936SA - 7419 \qquad (16)$$

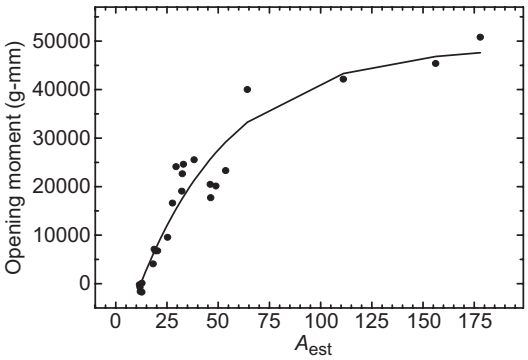

Fig. 5. Development of the opening moment of *Margaritifera margaritifera* as a function of ontogenetic age (A_{est}; Eq. 5). The moment was calculated by Eq. 16 using the product of the semimajor (posterior-to-anterior direction) and semiminor (dorsal-to-ventral direction) axes of the sagittal plane and π for surface area of the mussel.

where OM is the opening moment (g-mm) and SA is the surface area (cm^2). Applying this relationship to our morphometrical information (Table 3), we obtained a simple approximation of the burrowing strength for *M. margaritifera* from northern Finland (Fig. 5).

As compared with earlier life stages, the opening moment of the ligament does not seem to significantly increase after the ontogenetic age of 60 years. One could thus theorize that the mussels of approximately that age have somewhat stabilized their endurance against the possibly accentuating river discharge under the treat of amplified climatic perturbations, and that these mature individuals would thus be more hedged against the potential hydrological changes than younger individuals.

Apart from hydrological changes, the annual mean temperatures are projected to rise in Finland by 2–7 °C by the 2080s (Jylhä *et al*. 2004). As discussed by Hastie *et al*. (2003), the rise of mean temperatures may actually benefit the reproduction of *M. margaritifera* due to increased glochidial development in warmer waters. The critical upper thermal limits for survival and normal functioning in this species are however presently unknown. The projected increases in maximum temperatures and the frequency and duration of exceptionally warm periods in summer (Meehl & Tebaldi 2004) may be detrimental to mussels, particularly since they

typically inhabit small streams that tend to heat up rapidly (Hastie *et al*. 2003).

Conclusions

This study was based on the conchological life-trait information from subfossil shells of *Margaritifera margaritifera* from northern Finland, close to the northernmost distributional limit of the species. The gathered dataset included the number of counted annual shell growth increments (observed from the cross-sections of the outer shell layer), three-dimensional morphometry of the shell, shell weight and the pre-mortem taphonomy (measured as the extent of shell corrosion). The estimated variables of greatest importance included the ontogenetic age, the overall growth rate (k) and the asymptotic shell dimensions (G_∞). Based on these data we make the following conclusions:

1. The ontogenetic age of the mussels at the time of death was estimated adding up the number of counted annual increments and the estimated number of corroded umbonal increments. The oldest shells were found to be more than 100 years at the time of death and the oldest specimen was nearly 200 years old. The studied shells thus represented the mussel populations among the greatest longevity of the species.
2. Regional growth trends were modelled using the annual shell growth increments. Annual increments are significantly narrower (for ontogenetically oldest increments occasionally even smaller than 25 μm) in the study region than in the south, but the timing of the juvenile growth maximum (at the ontogenetic age five years) was identical from Finland to Spain.
3. Regional models were built using linear and nonlinear growth functions (von Bertalanffy 1938) for the different life-trait histories and pre-mortem taphonomy. The linear model proved to fit better only in the case of shell weight. As compared with those of the more southern populations, the growth rates (k) of the studied mussels indicate slow growth and the asymptotic growth length (G_∞ for shell length) was large.
4. The results indicating great longevity, slow growth rate and large asymptotic growth dimensions for *M. margaritifera* in northern Finland were parallel to the previous hypothesis that the oldest, largest and slowly growing populations can be found in the proximity of the northernmost distributional limit of the species. Whereas the severe climate bears major influence on the life-traits, the hydrogeochemistry probably plays secondary role in determining the characteristics in life-trait histories.
5. All individuals were umbonally corroded. The progress of shell corrosion decelerated the larger area the corrosion reaches. This is likely to be due to increasing thickness of the outer shell layer.
6. The ontogenetic age could be statistically predicted using the life-trait information. Our preliminary models predicted the ontogenetic ages with high accuracy for populations of which life-trait information was used in calibration (R^2 = 0.918 to 0.996). The prediction model became less accurate for other populations.
7. The theory predicts that the harsh climate induces the extreme longevity along with high fertility whereas the water quality supports the reproduction and vitality. The study region provides a climatic environment that seems to advantage the species conservation. Threat of decline is however present, currently and in the future, due potentially to stochastic climatic perturbations that may suddenly change the characteristics of the habitats.

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