

# Variation in the life span and size of the freshwater pearl mussel

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## Summary

1. Within the distribution area of the freshwater pearl mussel (*Margaritifera margaritifera* L.), the maximum observed life span attained in a population varies from 30 to 132 years and the maximum shell length from 80 to 145 mm. For both life-history traits, the growth constant  $k$  is a major determinant. The growth constant describes the shape of the average individual growth curve, the lower its value, the slower is the asymptote approached. Maximum size and life span increase as the growth constant declines and the maximum age almost equals the time necessary to complete the growth pattern.

2. With increasing latitude, from North Spain up to the polar circle, the growth constant declines, whereas age and size increase. This must be attributed to the close relationship between the growth constant and metabolism. As temperature decreases (towards the north), metabolic rate declines and the rate of growth decreases; the asymptote is approached slowly and this leads to a long life. Simultaneously, there is probably a shift in the anabolic-catabolic-balance increasing the asymptotic size and hence the maximum size.

3. The growth constant and maximum life span also respond to the productivity of the habitat. There is a negative correlation between growth constant and eutrophication, and the maximum life span is reduced as the concentration of nitrate increases.

4. Implications for Bergmann's rule and for the theory of ageing are discussed. It is concluded that this variability is a case of phenotypic plasticity with no adaptive value because: (i) plasticity must be attributed to unavoidable physiological responses; (ii) between populations the relationships between maximum life span, maximum size and reproductive output are positive, whereas trade-offs would be expected if variation in life-history tactics was the source of plasticity; and (iii) the demographic consequences of plasticity may be highly disadvantageous.

*Key-words:* life span, size, latitude, metabolism, plasticity.

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## Introduction

The correct interpretation of life-history variation is crucial for many problems in the theory of life-history evolution. One of them is the question of whether differences observed on the species level may be cited as evidence for life-history tactics, or whether tactics exist only at higher taxonomic levels (Stearns 1980). It is therefore of great importance to distinguish between variations arising from selection (the only variations representing different strategies) and variations caused by constraints (Stearns 1980; Begon, Harper & Townsend 1986).

Life-history traits closely linked with important ecological costs and benefits are life span and size.

Therefore, many authors have pointed out that both parameters should be under strong selective control (Hamilton 1966; McLaren 1966; Sauer, Grüner & Collatz 1986; Emlen 1970; Roff 1981; Forrest 1987; Langston *et al.* 1990). However, size and longevity may also respond passively to a number of environmental factors. It is often not clear to what degree variations are adaptive, to what degree they are caused by predation or competition without any adaptive value, or whether they are simply unavoidable physiological responses. For example, small size and short life span may be interpreted as an adaptive response to natural selection when mortality in all size-classes is high (Seed & Brown 1978), they may be caused by high mortality rates, reducing life

expectancy so that the maximum possible life span and size is simply never to be reached (Gilbert 1973; Bachelet 1980), or they may be a physiological response to high temperature (Beverton & Holt 1959). Only in the first case is variation attributable to a strategy. The growth strategy operates to maximize reproductive efficiency within a certain framework of heavy mortality. On the other hand, the other two cases may imply severe fitness losses, if the life-history strategy is not able to compensate for the disadvantages brought about by small size and short life span.

Size and life span are known to exhibit a considerable intraspecific variability, particularly in species that grow throughout their life, e.g. many cold-blooded vertebrates, many molluscs, etc. Here, I have investigated factors responsible for the variation of longevity and size of the freshwater pearl mussel (*Margaritifera margaritifera* L.). This species seems to be most suitable for a field study on this problem for three reasons.

1. It is one of the longest-lived invertebrates, attaining an age of more than 100 years (Comfort 1957; Hutchinson 1979; Grundelius 1987). When such an extraordinary life span evolves, this trait should be of particular importance for the fitness.
2. It is widely distributed from North Spain to the polar circle. Variations can therefore be analysed along a sufficient latitudinal scale, and a considerable gradient of environmental factors correlated with latitude must be expected.
3. There are some reasons to expect that variations in age and size are caused by only a few factors and not by an interplay of a multiplicity of factors, as is usually the case (Roff 1981). The pearl mussel is highly specialized. With a few exceptions, it occurs only in uniform habitats throughout its range: trout streams on primary rocks that are poor in nutrients and lime (Young & Williams 1983; Grundelius 1987; Bauer, Hochwald & Silkenat 1992). Therefore, environmental variability, such as water current, food supply, substrate type, etc., all of which are unrelated to latitude, must be expected to be low between the habitats. Furthermore, intra- and inter-specific interactions do not seem to play a role in the determination of life span and size. Competition surely does not occur today, as formerly the populations were stable at much higher densities (Israel 1913) and there are no other species in pearl mussel rivers with which it might compete (Bauer, Hochwald & Silkenat 1992). Life expectancy is high as the adult mussel apparently has no natural enemies and mortality rates are low under natural conditions. There are indications that most animals live out their allotted life span and die of old age (Bauer 1987). This suggests that the process of growth and ageing is determined more by intrinsic factors than by the rate of accidental mortality.

For this reason I have focused on intrinsic factors. I have analysed the variation of growth parameters within the distribution area and, based on these data, how maximum size and life span are determined by the process of growth. I have also investigated which environmental factors account for the variation of both traits and how these factors operate on the growth process.

Finally, I have tried to decide whether these intraspecific variations are adaptive or not. This decision relies on the mechanisms leading to variations, i.e. it is based upon whether the variations must be interpreted as being caused by constraints. Further arguments are the sign of the correlations between fitness traits when populations are compared (i.e. whether there are trade-offs or not), and the demographic consequences of plasticity.

### Materials and methods

Growth studies were conducted along a latitudinal gradient covering nearly the whole north-south distribution of the pearl mussel. The southernmost populations where growth was analysed are situated in Massachusetts and northern Spain, the northernmost at the polar circle. In each population, at least 10 empty shells of all size-classes were sampled, (emphasis was placed on finding the largest shell), except for some Swedish ones, where the analyses relied on published data (Hendelberg 1961; Grundelius 1987). Growth studies are based on annuli which, according to Hendelberg (1961), are suitable for age determination of freshwater pearl mussels. In order to make the annuli visible, the shells were placed into KOH (c. 5%) at 50°C, to remove the periostracum carefully. The following growth parameters were determined with these shells.

$A_{\max}$  is the maximum observed age in a population. It was estimated by counting the annuli. A problem arises with older shells, because considerable parts around the umbo (the oldest part of the shell) are corroded. Therefore, a growth curve was first established using young shells (where only small parts are corroded) and the number of annuli in the corroded areas of large shells was estimated from this curve.

$L_{\max}$  is the maximum shell length; this gives an indication of the size of the soft parts and is therefore closely related to reproductive traits (Bauer 1991).

$L_{\infty}$  is the asymptotic length of the average individual growth curve in a population.

$k$  is the growth constant, which determines the curvature of the growth curve, i.e. the rate at which the asymptotic length is approached (von Bertalanffy 1938). The lower the value of  $k$ , the slower is the asymptotic size approached.

The parameters  $k$  and  $L_{\infty}$  were estimated using Ford-Walford plots (Walford 1946). Every fifth annulus was measured along its longest axis. A

regression was then established for each population relating shell length at age  $t + 5$  years to shell length at age  $t$ :

$$L_{t+5} = a + bL_t$$

From this equation,  $k$  and  $L_\infty$  can be calculated.

$$k = -\ln(b)$$

$$L_\infty = a/(1 - b)$$

( $L_\infty$  is the intersection of the regression line with the bisector drawn through the origin)

To identify factors causing variations in age and size, I proceeded as follows. As a first step, the relationships within the growth parameters of all analysed populations ( $n = 48$ ) were investigated. I then developed a model predicting  $A_{\max}$  from the growth constant  $k$  and the proportion of  $L_\infty$  attained. To establish the model, I used growth data from 25 populations (these were simply the first that I analysed). The model is based on the von Bertalanffy growth equation which, according to Theisen (1973), gives a good fit to the growth of mussels above one-third of the maximum length (this can be confirmed for the pearl mussel; G. Bauer, unpublished). The model was tested with the data from the remaining populations ( $n = 23$ ), none of them being used to develop it.

The influence of two types of environmental factors on growth and age was analysed, namely latitude and physicochemical factors. To keep variability attributable to other factors low, only populations from typical pearl mussel habitats, i.e. rivers on primary rocks, were analysed. Populations from atypical habitats (e.g. sandstone) and populations where the geological substrate was unknown were omitted. Accordingly, the influence of latitude was tested for 33 populations. In order to analyse the effect of habitat variability not caused by latitude, data of 13 Bavarian populations were used, all of them being situated between  $45^\circ 35'$  and  $50^\circ 10'$ . For these rivers, long-term means of the following physicochemical parameters were available from earlier studies (Bauer 1988): discharge, conductivity, pH, BOD<sub>5</sub>, NO<sub>3</sub>, NH<sub>4</sub>, PO<sub>4</sub> and Ca.

Data analysis was conducted by means of correlation and regression analyses (SPSS-statistical package). In cases with a number of intercorrelated variables (relationships between the growth parameters, or between growth and hydrochemistry), I used path analysis (Sokal & Rohlf 1981) to quantify the effects between the variables. This method allows the construction of causal paths with a number of independent and dependent variables (Schemske & Horvitz 1988). Here I analyse the path coefficients (= standardized partial regression coefficients), which represent the magnitude of the direct effect of the independent variable on the dependent variable, with all other independent variables in the equation

held constant. (Indirect paths were found to be not significant or of minor importance.)

## Results

### THE GROWTH PROCESS

#### *Relationships among the growth parameters*

The maximum observed life span ( $A_{\max}$ ) differs considerably among the populations. There are populations for which an  $A_{\max}$  of only 30 years can be recorded, whereas in others this value amounts to 132 years (Fig. 1). A strong negative relationship between  $A_{\max}$  and  $k$  is evident, explaining 58% of the variation of  $A_{\max}$ . Furthermore, the maximum shell length correlates negatively with  $k$ . However, only 24% of the variance of  $L_{\max}$  is explained by this relationship. On the other hand, the correlation between  $L_\infty$  and  $k$  is stronger and exhibits a steeper slope. (It might be argued that both parameters are estimated from one regression line of the Ford-Walford plot, and therefore are not independent. However, there is no a priori reason why they should be linked on purely mathematical grounds (Beverton & Holt 1959)). The positive correlation between  $A_{\max}$  and  $L_{\max}$  (Fig. 1) shows that longevity tends to be higher in populations in which the animals grow larger. A strong relationship is evident between  $L_{\max}$  and  $L_\infty$ ; the points are scattered around the line  $y = x$ , indicating that the calculated asymptotic length and observed maximum length are largely coincident.

As all these variables are intercorrelated, a path analysis was conducted. Because  $k$  and  $L_\infty$  depend on growth throughout life, whereas life span and maximum size depend on the final point of the growth curve, it is assumed that  $k$  and  $L_\infty$  are basic parameters. Thus, the working hypothesis is that there may be an influence of the shape of the growth curve on life span and size, but not vice versa. The subsequent path analysis shows the following pattern (Table 1, Fig. 2):  $A_{\max}$  depends strongly on  $k$ . It is also influenced by  $L_{\max}$ , but not by  $L_\infty$ . There is no direct influence of  $k$  on  $L_{\max}$ , but there is an indirect one via  $L_\infty$ . Thus, as the growth constant  $k$  decreases, the asymptotic size  $L_\infty$  increases, leading to an increased maximum size  $L_{\max}$ . Simultaneously, the maximum age is increased. A moderate positive influence of  $L_{\max}$  is also evident for this parameter.

#### *A model for $A_{\max}$*

The strong inverse correlation between  $A_{\max}$  and  $k$  and the coincidence between  $L_{\max}$  and  $L_\infty$  (Fig. 1) suggest that the maximum life span equals the time necessary nearly to attain the asymptotic size. If this holds true, it would imply a causation between  $k$  and

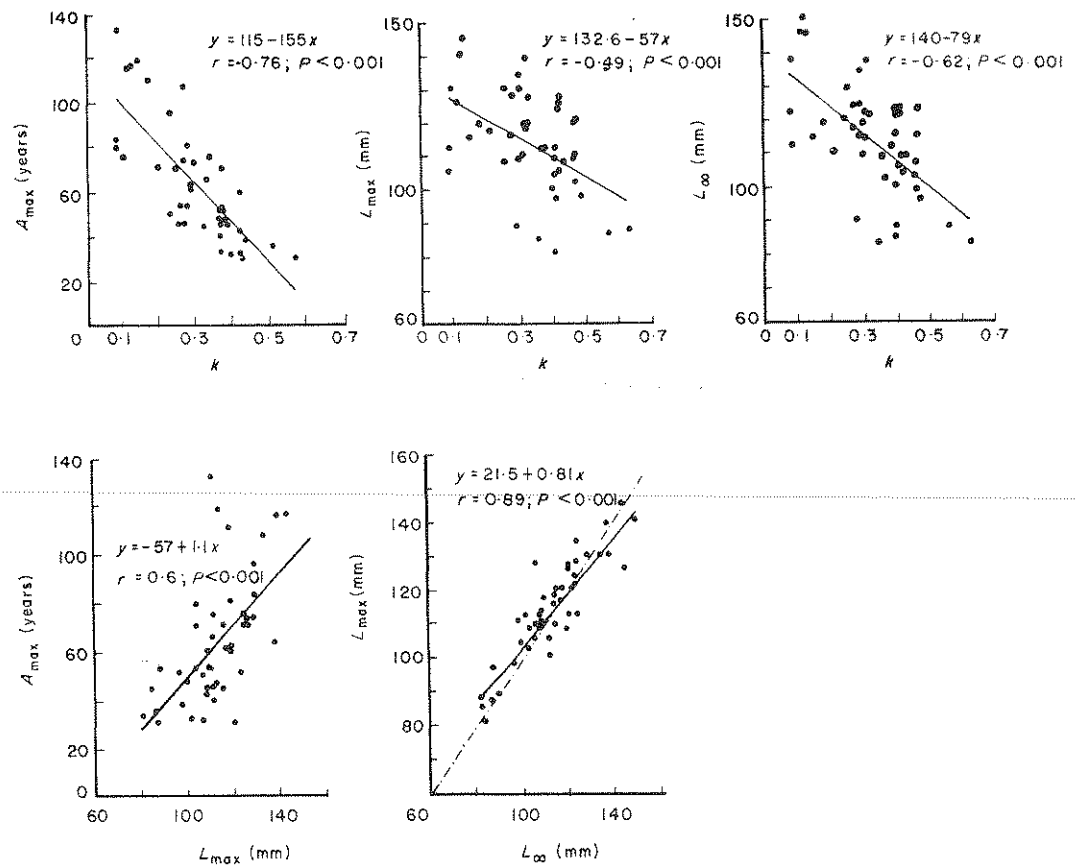


Fig. 1. Relationships between the growth parameters  $A_{max}$  (maximum age),  $L_{max}$  (maximum shell length),  $L_{\infty}$  (asymptotic shell length) and  $k$  (growth constant). (Each point refers to one population. The dotted line in the  $L_{max}$  -  $L_{\infty}$  plot is the line  $y = x$ ).

Table 1. Path coefficients and proportion of variation explained ( $R^2$ ) from linear regression of growth parameters

Dependent variable	Independent variable	Beta	$R^2$
$A_{max}$	$k$	-0.67***	0.59
	$L_{\infty}$	0.12	
$A_{max}$	$k$	-0.62***	0.66
	$L_{max}$	0.3**	
$L_{max}$	$k$	0.1	0.79
	$L_{\infty}$	0.99***	
$L_{max}$	$L_{\infty}$	0.8***	0.81
	$A_{max}$	0.15	
$L_{\infty}$	$k$	-0.48**	0.4
	$A_{max}$	0.18	

\*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

$A_{max}$ : the major determinant for  $A_{max}$  would be the shape of the growth curve, i.e. the rate at which the asymptote is approached. This hypothesis can be tested by means of a model. As a mathematical description of the growth process (e.g. the relationship between size and age), the von Bertalanffy equation is used.

$$L_t = L_{\infty}(1 - e^{-k(t-t_0)}) \quad \text{eqn 1}$$

where  $L_t$  is the length at time  $t$ , and  $t_0$  is a correction

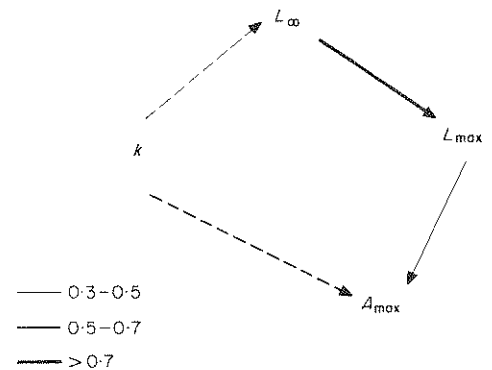


Fig. 2. Path diagram showing significant effects between the growth parameters. Positive effects are indicated by solid lines, negative effects by broken lines. The line width indicates the magnitude of the path coefficient as shown lower left. See Table 1 for the actual values and significance levels.

on the time axis. The maximum body size is expressed as the relationship between  $L_{max}$  and  $L_{\infty}$ , i.e. the proportion of  $L_{\infty}$  attained. Thus, the model is independent of the actual values of  $L_{max}$  or  $L_{\infty}$ . The deduction of the model, as given in the Appendix, yields the following equation for the calculation of the maximum age ( $A_{max}(c)$ ):

$$A_{\max}(c)(\text{years}) = 5 \left\{ \frac{[-\ln(0.012/k)]}{k} \right\} \quad \text{eqn 2}$$

This model is presented graphically in Fig. 3. To test the model,  $k$  and  $A_{\max}$  were determined in 23 populations. Using equation 2,  $A_{\max}(c)$  was calculated and compared with the observed values. Although the slope of the regression line is slightly different from 1 ( $t = 2.6$ ;  $P < 0.05$ ), both values seem to be in good accordance (Fig. 4).

#### IMPACT OF ENVIRONMENTAL FACTORS

##### Latitudinal variation

When the growth parameters are compared along a south-north gradient, the following pattern is evident. The growth constant  $k$  shows the strongest relationship to latitude (Fig. 5): 55% of its variation is explained by this factor. The maximum observed age increases considerably with latitude. At the southern border of the distribution area it is 30-40 years, whereas at the polar circle it exceeds 100 years. Latitude explains slightly less of the variance of  $A_{\max}$  than it does of  $k$ . The least explanation yields latitude for the variation of the size parameters; however, it is still evident that size is positively correlated with latitude. Thus, the growth constant of pearl mussels declines markedly northwards, maximum age and asymptotic size increase considerably. This tendency is less strong, but still significant, for the maximum size.

##### Physicochemical factors

Differences among the productivity of pearl mussel rivers depend mainly upon the degree of pollution (Bauer 1988), which in Bavaria ranges from nearly unpolluted ( $\text{NO}_3\text{-N} = 0.9$  ppm,  $\text{BOD}_5 = 1.2$  ppm) to

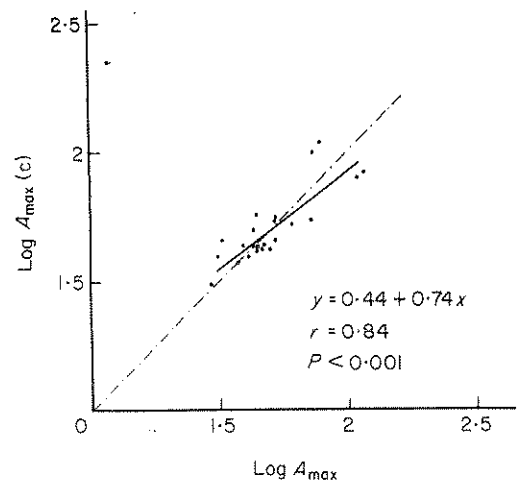


Fig. 4. Comparison between observed ( $A_{\max}$ ) and calculated maximum age ( $A_{\max}(c)$ ). (Each point refers to one population).

moderately eutrophic ( $\text{NO}_3\text{-N} = 3.3$  ppm,  $\text{BOD}_5 = 4$  ppm). When only populations from this area are considered, the regressions of  $A_{\max}$ ,  $L_{\max}$  and  $L_{\infty}$  on  $k$  are not significant (Table 2). An analysis with physicochemical factors reveals the following pattern (Table 2):  $A_{\max}$  does not respond to any of the factors.  $L_{\max}$  shows a weak tendency of being positively correlated with some eutrophication factors. This tendency becomes more evident when  $L_{\infty}$  is considered, whereas  $k$  correlates negatively with these factors.

There are two possibilities regarding the way in which life span and size might be influenced by physicochemical factors. On the one hand, these factors might operate indirectly via  $k$ , according to the mechanism presented in Fig. 2. This would mean that the shape and final point of the growth curve are altered. On the other hand, these factors might operate directly, i.e. only the final point of the

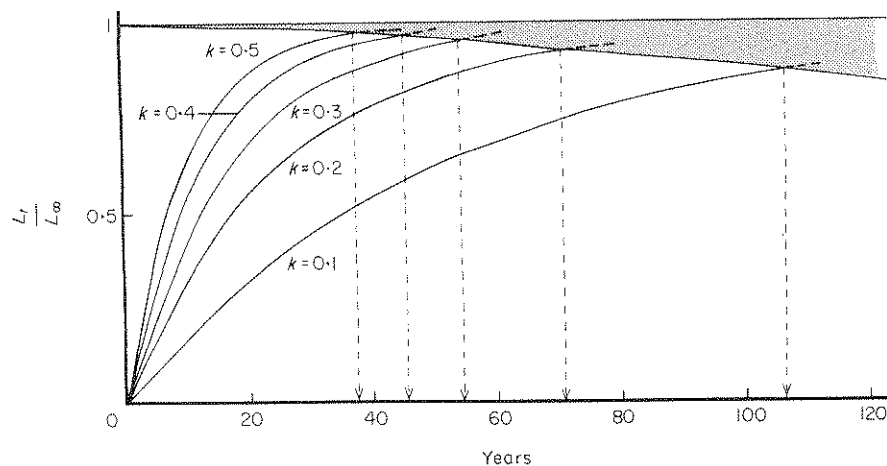


Fig. 3. Graphical presentation of a model for calculating the maximum life span of pearl mussels growing at different growth constants  $k$  ( $L_t$  = shell length at time  $t$ ). The maximum age equals the time the growth curves require to enter the shaded area near the asymptote.

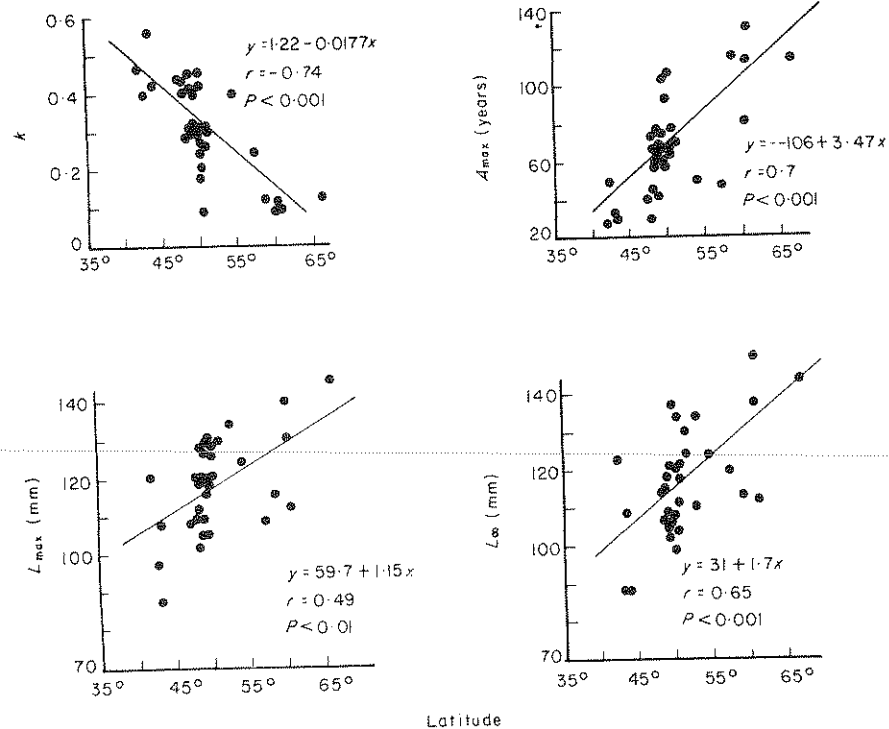


Fig. 5. Relationships between growth parameters and latitude. For the calculation of the regressions, the latitude was transformed according to the decimal system. The southernmost populations are situated in North Spain and Massachusetts, the northernmost at the polar circle (only populations from primary rocks are considered).

Table 2. Correlation matrix for growth parameters and physicochemical factors. Q = discharge, cond. = conductivity

	$A_{max}$	$L_{max}$	$L_x$	$k$	Q	pH	Conductivity	BOD <sub>5</sub>	NO <sub>3</sub>	NH <sub>4</sub>	PO <sub>4</sub> diss.
$L_{max}$	0.49										
$L_x$	0.14	0.66*									
$k$	-0.36	-0.32	-0.44								
Q	0.06	0.24	0.12	-0.15							
pH	0.3	0.51	0.72**	-0.65*	0.03						
Cond.	0.12	0.47	0.50	-0.45	0.41	0.63*					
BOD <sub>5</sub>	0.16	0.34	0.55*	-0.78**	0.42	0.71**	0.76**				
NO <sub>3</sub>	-0.31	0.19	0.35	0.12	0.26	0.3	0.48	0.15			
NH <sub>4</sub>	0.12	0.52	0.45	0.1	0.26	0.22	0.59*	0.28	0.29		
PO <sub>4</sub>	0.22	0.54	0.47	-0.15	0.01	0.61*	0.77**	0.45	0.3	0.8***	
Ca	0.3	0.3	0.30	-0.67*	0.24	0.7**	0.86***	0.7**	0.16	0.25	0.62*

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

growth curve is altered. This problem was investigated by means of a path analysis. However, because of the low number of observations ( $n = 13$ ), the number of the independent variables was reduced. Out of the highly intercorrelated eutrophication parameters conductivity, pH, BOD, PO<sub>4</sub> and Ca (Table 2), only BOD was included because it is a good predictor of productivity in pearl mussel rivers (Bauer 1988). The path analysis confirms the negative relationships between  $k$  and eutrophication (Fig. 6, Table 3). This variation in  $k$  seems to have no influence on  $L_{max}$  (or on  $L_x$ , Table 3), whereas there is a moderately strong path coefficient from  $k$  to  $A_{max}$ . Moreover,  $A_{max}$  is influenced directly by NO<sub>3</sub>. At increased

concentrations of this ion,  $A_{max}$  tends to be reduced. With respect to the size parameters, the path analysis does not confirm the relationships with regard to eutrophication. These correlations (Table 2) must therefore be considered spurious.

## Discussion

### RELIABILITY OF THE AGE AND SIZE DETERMINATION

$L_{max}$  is a crucial variable for this analysis so it was of fundamental importance to estimate it with sufficient reliability. A comparison of  $L_{max}$  with the calculated

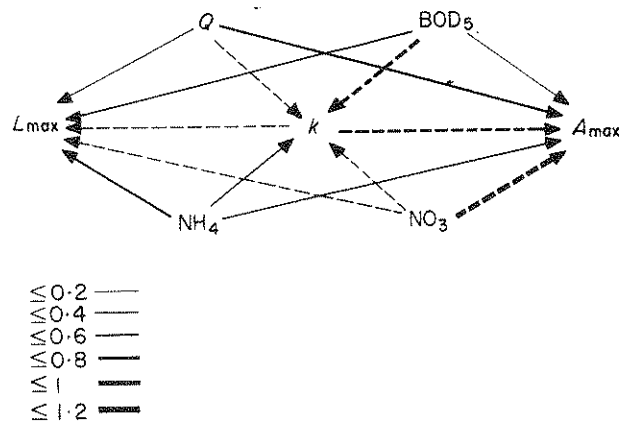


Fig. 6. Path diagram showing relationships between growth parameters and physicochemical factors for 13 Bavarian populations ( $Q$  = discharge). Positive effects = solid lines, negative effects = broken lines. The legend (lower left) gives the approximate magnitude of the path coefficients indicated by the different line width. See Table 3 for the actual values and significance levels.

Table 3. Path coefficients and proportion of variation explained ( $R^2$ ) from linear regression of growth parameters and physicochemical factors ( $Q$  = discharge)

Dependent variable	Independent variable	Beta	$R^2$
$k$	$BOD_5$	-0.98**	0.74
	$Q$	0.08	
	$NO_3$	0.13	
	$NH_4$	0.3	
$A_{max}$	$k$	-0.59	0.6
	$BOD_5$	0.05	
	$Q$	0.55	
	$NO_3$	-1.08*	
	$NH_4$	0.44	
$L_{max}$	$k$	-0.03	0.36
	$BOD_5$	0.34	
	$Q$	0.19	
	$NO_3$	-0.37	
	$NH_4$	0.52	
$L_z$	$k$	-0.29	0.45
	$BOD_5$	0.26	
	$Q$	-0.17	
	$NO_3$	0.01	
	$NH_4$	0.44	

\*  $P < 0.05$ ; \*\*  $P < 0.01$ .

$L_z$  reveals that indeed one of the largest shells must have been found in each population. The value for  $L_z$  should be relatively free of sampling errors as it depends only on the distance between annuli (see Methods). When comparing  $L_{max}$  and  $L_z$  one must consider that  $L_z$  is an average value for each population, whereas  $L_{max}$  is the absolute observed maximum length which, because of individual growth variation, may exceed  $L_z$ . Thus, if the maximum size is in the range of the asymptote and if a shell close to the true maximum has been found in each population, then the regression line between  $L_{max}$  and  $L_z$  should be slightly above the line  $y = x$  with a

slope of  $b = 1$ . This is indeed the case (Fig. 1;  $L_{max} - L_z$  plot). Most dots are above the line  $y = x$  and the reduced major axis regression slope is  $b = 0.91$ .

The problem of accuracy is more serious with respect to  $A_{max}$ . Age determination of shells is difficult for two reasons. Growth rates of pearl mussels during their early juvenile stage might be slower than at present assumed (Buddensiek 1991). Furthermore, the last annuli of the older specimens lie close together, a problem which is of particular importance for populations with extremely long-lived individuals. Thus, the values given here must be considered as minimum values. However, there are two reasons, suggesting that the estimation of  $A_{max}$  may be suitable at least for a comparative analysis. The first one is the sufficient estimation of  $L_{max}$ . Due to the asymptotic growth type the oldest specimens must be expected in the highest size-class. The second reason is the fairly good fit of the model for the calculation of  $A_{max}$  (equation 2). The model only depends on  $k$  which, like  $L_z$  should be largely free of methodical errors.

#### FACTORS INFLUENCING $k$

The growth constant  $k$  does not only describe the rate at which the asymptotic size is approached; it is also considered to be a 'coefficient of catabolism' (von Bertalanffy 1938; Beverton & Holt 1959), being closely related to metabolic rate. This is supported by an interspecific comparison among Unionoidea: growth constants of pearl mussels are definitely lower than those of unionids and the same pattern is found for  $O_2$ -consumption, e.g. metabolism (Bauer, Hochwald & Silkenat 1992). The hypothesis of a close relationship between  $k$  and metabolism is additionally supported by the strong negative correlation between  $k$  and latitude (Fig. 5), showing that in the south the asymptote is approached faster than in the north. This correlation must either be attributed to the length of the growing season or to a

temperature effect on metabolism. Similar results obtained from mussels (Taylor 1959; Theisen 1973; Bachelet 1980), crustaceans (Lonsdale & Levinton 1985) and fish (Beverton & Holt 1959), and the considerations regarding variations in  $L_{\max}$  presented below, argue strongly in favour of temperature. (The degree to which metabolic compensation for temperature (Bullock 1955; Conover & Present 1990) plays a role is unknown.)

A second complex set of factors influencing  $k$  is the productivity of the habitat. The growth constant correlates negatively with various eutrophication factors (Table 2). These relationships are confirmed by a path analysis (Table 3, Fig. 6) and by Alimov (1974), who also found a relationship between  $k$  and calcium for pearl mussels. The causes for these relationships remain an open question. As there is no evident latitudinal trend in hydrochemistry (Bauer 1986; Grundelius 1987; Bauer 1988), the correlation between  $k$  and latitude (Fig. 5) can be used to compare the influence of temperature and hydrochemistry on  $k$ . Latitude alone yields a 55% explanation of variance. However, the unexplained variation cannot be attributed in total to the variation in hydrochemistry. One factor surely contributing to the unexplained variation is that the temperature regime of the rivers is not precisely related to latitude. It is modified by local conditions, such as altitude, local climate, distance to the source or shade. Thus, along the north-south distribution of the pearl mussel, the influence of temperature on  $k$  must be considered as being much greater than that of hydrochemistry.

#### SIZE VARIATION

##### *Factors influencing $L_{\max}$*

On a global scale, the maximum size correlates with  $L_{\infty}$ ,  $A_{\max}$  and  $k$  (Fig. 1). However, the path analysis suggests that the latter two correlations are spurious (Table 1, Fig. 2). In particular, the relationship between  $L_{\max}$  and  $A_{\max}$  must largely be attributed to intercorrelations. The fact that the asymptotic size is largely identical with the maximum size (Fig. 1), indicates that the maximum size can only be altered when the asymptote is altered. This is confirmed by the strong path coefficient from  $L_{\infty}$  to  $L_{\max}$  (Table 1, Fig. 2). With respect to factors influencing  $L_{\infty}$ , the relationships between  $k$  and  $L_{\infty}$  (Table 1, Fig. 2) and between  $k$ ,  $L_{\infty}$  and latitude (Fig. 5) are of importance. An explanation for these relationships offer physiological investigations on the dependence of the energy balance on body size and acclimation temperature. The shape of an asymptotic growth curve is determined by how long an animal can maintain a potential for partitioning energy into growth (Jørgensen 1976; Bayne & Worrall 1980; Vahl 1981a). This 'scope for growth' (Warren &

Davis 1967) declines with increasing body size and becomes zero at the asymptote. However, size has a different effect in different populations, less in the cold-adapted, more in the warm-adapted, so that northern animals can grow larger without the activity per gram body weight being depressed so far (Rao 1953; Bullock 1955; Ray 1960; Lonsdale & Levinton 1985). Therefore, in a cold-adapted population, the scope for growth is still positive at a body size where it would be zero under warmer conditions. This mechanism causes an increase of the asymptotic size in cooler areas, as a high slope of the growth curve can be maintained over a long period of time.

##### *Implications for Bergmann's rule*

This ecogeographical rule was originally formulated for homoiotherms, and states that, within a species, body size increases towards the north (Mayr 1956). The usual explanation for this rule is that large animals expend less energy for thermoregulation because of their small surface-to-volume ratio. It is therefore assumed that large size is a selective advantage in cold climates. Recently, there has been much criticism of this rule as many homoiotherms do not obey it, and it is argued that size variations are the result of factors other than heat conservation (McNab 1971; Murphy 1985). Furthermore, the rule's significance in terms of heat conservation is doubted (Scholander 1955), especially as there are data on poikilotherms, showing that body size increases at decreasing temperature (Beverton & Holt 1959; Ray 1960 and many references cited there). However, a latitudinal trend according to Bergmann's rule does not seem to exist in most poikilotherms (Park 1949; Gilbert 1973; Bachelet 1980). These confusing and contradictory results suggest two conclusions.

1. If Bergmann's rule exists, it apparently cannot be attributed to heat conservation, as body size also increases at lower temperatures in poikilotherms.
2. Body size is usually a complex syndrome of single effects. It may respond to various abiotic (Swan 1952; Ray 1960; Rhoads & Pannella 1970; Green 1972; Nevo 1973) and biotic factors (Nevo 1973; Roff 1981; Forrest 1987). Thus, Bergmann's rule should become all the more evident, when factors other than temperature are less important with respect to their effect on size. The rule works only 'other things being equal' (Mayr 1956). One example for this hypothesis is found regarding *Rana sylvatica*, which shows a negative relationship between size and temperature when reared in the laboratory (Ray 1960). However, this species does not follow the rule in the field where it lives in a variety of habitats, this variability operating on population ecology (Martof & Humphries 1959).

In contrast, the pearl mussel is highly specialized with respect to its habitat, and demography in the



adult stage is determined largely by intrinsic factors under natural conditions. Indeed, it obeys Bergmann's rule (Fig. 5, lower left). In connection with data on other poikilotherms, these results suggest that an increase in size correlated with decreased environmental temperature might be a phenomenon basic to the animal kingdom, as stated by Ray (1960). However, this relationship is not produced by selection, but rather by the underlying mechanisms of passive temperature-dependent shifts in the energy balance. But frequently this process is superimposed by responses of size to other factors.

#### LIFE SPAN VARIATION

##### *The extraordinary long life of pearl mussels*

The long life of pearl mussels is an outstanding feature of this species which contrasts sharply with the age attained by native unionids (10–20 years; Comfort 1957; Negus 1966; Hochwald & Bauer 1990). The fact that, among the unionids, metabolic rates and growth constants are also markedly higher than among pearl mussels (Bauer, Hochwald & Silkenat 1992) indicates a relationship between metabolism, rate of growth and life span. The same relationship is evident from the empirical data on the age of pearl mussels, showing a strong dependence of  $A_{max}$  on  $k$ , and a coincidence between  $L_{max}$  and  $L_x$  (Figs 1 & 2). They therefore suggest that the maximum life span of pearl mussels equals the time needed largely to complete the growth pattern. The slower the asymptote is approached, the longer is the duration of life. This is confirmed by the model predicting  $A_{max}$  from the shape of the growth curve. Thus, the low growth constant, i.e. the low metabolic rate, must be considered as the basis for the long life span of pearl mussels.

The theories about intrinsic causes of ageing and death (Hamilton 1966; Emlen 1970; Kirkwood 1977; Kirkwood & Holliday 1979) are mainly deduced from data gained from animals with determinate growth, e.g. groups with a marked senescent period. However, the conditions that are thought to be related to the process of ageing and death in these groups do not hold for groups with asymptotic growth. In the latter groups, a true post-reproductive phase is very rare (Beverton & Holt 1959). Fertility not only continues into old age (Bauer 1987); it frequently increases with age, as it is usually correlated with size (Vahl 1981a; Peterson 1986). Furthermore, mortality also frequently does not increase in old age, a pattern found particularly in long-lived species (Comfort 1957; Beverton & Holt 1959; Brousseau 1978; Bauer 1988).

The results discussed so far indicate that the life span of pearl mussels is fixed in terms of a developmental programme and the level of a death threshold. The growth curve acts as a physiological time-scale,

and the death threshold is near the asymptote, viz. at a size where the scope for growth approaches zero and tissue maintenance and therefore survival become increasingly difficult (Vahl 1981b; Bayne 1985). The same associations between growth and longevity are found in a number of unrelated groups with asymptotic growth (Beverton & Holt 1959). It is therefore probable that ageing in these groups differs fundamentally from that in species with deterministic growth. In the latter, senescent deterioration leads to death (Maynard Smith 1966; Lamb 1977), whereas in the former, death appears to be related to the attainment of a critical size, probably without a genetically controlled ageing programme.

##### *Factors influencing $A_{max}$*

As shown in Fig. 1, the long life span, as often mentioned in the literature, does not hold for all pearl mussel populations. In accordance with the above hypotheses regarding life span and death,  $A_{max}$  responds to the temperature-dependent variation of metabolism (Fig. 5). Towards the north of the distribution area, metabolic rate decreases and, consequently, the maximum life span increases.

The unexplained variation in the relationship between  $A_{max}$  and latitude (Fig. 5) may be attributable to different sources which are mentioned above. There is some inaccuracy in the estimation of  $A_{max}$  and the temperature regime is not determined by latitude only. Although the pearl mussel inhabits rather uniform habitats, there are some differences among hydrochemical factors. As shown in Table 2 and Fig. 6, there is a negative correlation between  $k$  and eutrophication and a relatively strong path coefficient from  $k$  to  $A_{max}$ . However, even if there is a trend towards an increased  $A_{max}$  at an increased eutrophication, there is an opposing effect. The negative path from  $\text{NO}_3$  to  $A_{max}$  indicates a reduced life span as the  $\text{NO}_3$  concentrations increase. This relationship has already been established using a different method. At high values of  $\text{NO}_3$  (c. 3 ppm  $\text{NO}_3\text{-N}$ ), mortality increases, so that not only the average, but also the maximum life span is reduced (Bauer 1988), apparently without affecting  $k$  (Fig. 6). This suggests that the growth curve is shortened, although its shape is not altered. The latter can be confirmed by the independence of  $A_{max}$  from  $L_x$  (Fig. 2). With respect to the former, the positive influence of  $L_{max}$  on  $A_{max}$  (Table 1, Fig. 2) has to be viewed. Compared with the growth constant,  $L_{max}$  adds only little (8%) to the explanation of variance in  $A_{max}$  but this amount is still significant. With respect to the growth curves in Fig. 3, if they are slightly shortened (by an increased mortality),  $A_{max}$  is much more reduced than  $L_{max}$ . In other words, a slight reduction of  $L_{max}$  reduces  $A_{max}$  considerably. This explains the significant path from  $L_{max}$  on

$A_{\max}$ , but its absence vice versa (Table 1, Fig. 2).

Thus, two mechanisms can be shown to operate on the maximum life span of pearl mussels. One is the temperature dependence of metabolism altering the developmental programme and hence the shape and final point of the growth curve. The other is caused by pollution increasing mortality rates and hence shortening the growth curve. Latitude alone explains 50% of the variation of  $A_{\max}$  (Fig. 5). The unexplained variation must be attributed in part to the scatter in the relationship between latitude and temperature, to the inaccuracies of  $A_{\max}$  and to variations in hydrochemistry. Thus, along the north-south distribution of the pearl mussel, the temperature-dependent variation of metabolism must be considered as the major determinant for life span, whereas hydrochemistry is of less importance.

#### ADAPTIVE OR NON-ADAPTIVE PLASTICITY?

Geographic patterns of intraspecific variations in life history have frequently been interpreted as an adaptation to local conditions (McLaren 1966; Schaffer & Elson 1975; Legett & Carscadden 1978). There are data showing that demography can influence life-history tactics on the species level (Barclay & Gregory 1982; Berven & Gill 1983); however, according to Smith-Gill (1983), non-adaptive plasticity is probably the most common form of environmentally induced variation.

The analyses of the factors causing variation of the pearl mussel's life span and size argue strongly in favour of the latter. This hypothesis is confirmed when the sign of the correlations between important traits is considered. The maximum shell length in a population is closely related to fertility. In a population with an  $L_{\max}$  of c. 90 mm, the average fertility amounts to  $1 \times 10^6$  glochidia per gravid female and reproductive period, whereas at  $L_{\max} = 150$  mm, fertility is  $5 \times 10^6$  glochidia (Bauer 1991). There is no relationship between the proportion of resting females (i.e. females which are not reproducing) and any of the reproductive traits (Bauer 1991) and, throughout the range, there is only one reproductive period per year (Smith 1978; Young & Williams 1984; Bauer 1987). Therefore, the number of reproductive periods available to a female is positively correlated with  $A_{\max}$ . Thus, total lifetime fertility is considerably affected by the components 'fertility' ( $L_{\max}$ ) and 'number of reproductive periods' ( $A_{\max}$ ). Calculations suggest that a small and short-lived female, growing at  $k = 0.6$ , attains only roughly 10% of the glochidia produced by a female that grows at  $k = 0.1$ , even if a reduction of the juvenile period of fast-growing individuals is considered (Bauer 1991). Accordingly positive relationships are found between the traits  $A_{\max}$ ,  $L_{\max}$ , present reproductive output of a particular age-class and expectation of future reproduction, when populations are compared.

However, according to the theory of life histories, trade-offs, and hence negative correlations would be expected between at least some of these traits if variation in life-history tactics was the major source of variation (Gadgill & Bossert 1970; Leggett & Carscadden 1978; Bell 1984; Noordwijk & De Jong 1986). According to the latter authors, positive correlations are observed when there is a large variation in the availability of resources for growth and reproduction, compared to the variation in the resource allocation, e.g. when there is only one life history strategy responding to the variation in the energy budget. A further conclusion of the model of Noordwijk & De Jong (1986) is that there should be populations that perform well and populations that perform poorly. The latter must be expected for pearl mussel populations whose individuals are forced to grow at high values of  $k$ . Indeed, there is good evidence that the life-history strategy of these populations barely ensured survival when conditions were optimal. However, slightly worse conditions (increased mortality of juveniles by pollution), could not be tolerated and led to quick extinction (Bauer 1991).

Thus, there is no evidence of any adaptive value of plasticity of the pearl mussel's life span and size. Plasticity must be attributed to unavoidable physiological responses to a temperature gradient and to the productivity of the habitat.

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## Appendix

The von Bertalanffy equation (1) can be solved to yield the time required to attain a given proportion  $x$  of  $L_{\infty}$  ( $x = L_t/L_{\infty}$ ):

$$t = t_0 - \left[ \frac{\ln(1-x)}{k} \right] \quad \text{eqn 3}$$

To estimate the maximum length of the growth curve, e.g. the degree to which the growth pattern is completed, the maximum proportion of  $L_{\infty}$  attained has to be determined. The asymptotic length was calculated and  $L_{\max}/L_{\infty}$  was plotted against  $k$  in 25 populations. According to Fig. A1, this factor depends non-linearly on  $k$ , being lower at low values of  $k$ . (This result will not be discussed here in detail. It might be a consequence of the Ford-Walford plot. The method might slightly overestimate the asymptote when the regression line becomes very steep, i.e. when  $k$  becomes very small.) The asymptote of the regression equation in Fig. A1 exceeds 1. The explanation for this is that  $L_{\infty}$  is the average asymptotic length in a population, whereas  $L_{\max}$  is the absolute observed maximum length which, because of individual growth variation, may exceed  $L_{\infty}$ . There are two possibilities for standardizing the equation to an asymptote of 1; viz. either by subtracting 0.07, or by division with 1.07. The first case yields

$$L_{\max}/L_{\infty} = 1 - \frac{0.013}{k} \quad \text{eqn 4}$$

the second

To decide which method should be preferred, both equations were solved for  $L_{\max}$  and, according to  $k$  and  $L_{\infty}$ ,  $L_{\max}$  was calculated for each population and compared with the observed values. With a correlation coefficient of  $r = 0.89$ , equation 5 yields a slightly higher explanation of variance than equation 4 ( $r = 0.88$ ). Therefore, equation 5 has been used for the model.

The correction constant  $t_0$  was determined by plotting  $\ln [(L_{\infty} - L_t)/L_{\infty}]$  against  $t$  for each population (Munch-Petersen 1973). Then,  $t_0$  can be calculated as the  $x$ -intercept of the regression line. An average value (mean  $\pm$  CI) of  $0.0009 \pm 0.03$  years was obtained, and no relationship between  $t_0$  and  $k$  was found. Therefore,  $t_0$  is considered to be zero.

A combination of equations 3 and 5, when considering that  $k$  was estimated for 5-year intervals, yields equation 2.

