Plasticity in Life History Traits of the Freshwater Pearl Mussel - Consequences for the Danger of Extinction and for Conservation Measures

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Abstract

In Central Europe, the freshwater pearl mussel (*Margaritifera margaritifera*) is threatened with extinction. It is shown how the danger of extinction is influenced by the plasticity of life history traits. The pearl mussel's life history strategy has been selected for a high lifetime fertility, which is attained by combining high life expectancy (= high number of reproductive periods) and high fertility. However, these two traits exhibit a considerable plasticity, which depends on the individual growth constant (i.e. the rate at which the asymptotic size is approached). The growth constant is influenced by a number of environmental factors: for example it increases with increasing temperature. An increased growth constant (= accelerated growth) leads to a reduction of life span, maximum size and fertility. These relationships reduce the lifetime fertility of individuals growing at a high rate. Populations consisting of such individuals should exhibit a high sensitivity to threats for two reasons: the growth rate of the population is low and the time until extinction is shortened due to the low individual life span. This hypothesis is confirmed by the population trend in different areas of the FRG. The results are discussed with respect to conservation strategies.

Introduction

Integrated Pest Management and species conservation do pursue opposite goals with respect to the target organism. However, both purposes require nearly the same detailed knowledge about the population ecology of the target organism. Investigations must therefore comprise the autecology as well as demographic processes in relation to extrinsic and intrinsic factors (BURGMANN *et al.* 1988). Ideally, such research programs should yield knowledge about minimum viable populations (SCHAFFER 1981), about weak points in the life cycle and about the most important factors affecting density. In the case of species conservation these data are then used to increase or stabilize the density of the target organism.

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However, such investigations are costly and take a lot of time and can, therefore, usually be conducted only at few localities. This raises the question whether or not the results can be applied to other populations of the same species. The problem does not only exist because the threats may be locally different. Populations may also differ with respect to their fitness due to plasticity in life history traits. On principle, all life history traits, like body size, longevity, fecundity, etc. may respond to a variable environment. However, usually some traits are fixed (are resistant to change) whereas others are highly plastic (BERVEN & GILL 1983). The fixed traits, the degree of plasticity and compensating mechanisms are not predictable but must be investigated for each species.

Plasticity may be adaptive or nonadaptive. Adaptive plasticity is an optimal response to a specific set of environmental stimuli which has a genetic basis, whereas nonadaptive plasticity is a nonspecific, passive variation of the phenotype due to physiological constraints of the environment (SMITH-GILL 1983). Particularly nonadaptive plasticity may be an important factor for the status of populations and for conservation strategies, but it is usually neglected in this context. The interplay of plasticity and threats as well as the consequences with respect to conservation shall therefore be described for the freshwater pearl mussel (*Margaritifera margaritifera L.*).

Biology of the freshwater pearl mussel

Freshwater pearl mussels inhabit exclusively running waters which are poor in nutrients. In late summer the females release glochidia. They can only develop into young mussels if they are able to attach to the gills of a suitable host fish, which they reach passively in the ventilating current of the fish. The only important host in Central Europe is brown trout (*Salmo trutta*, BAUER 1987a). The glochidia attach to the gills of the host and live as parasites for some weeks up to nine months. During this period they grow from 0.07 mm to 0.4 mm. Having completed metamorphosis the young mussels leave the host and presumably live for 3-5 years burrowed in the river bottom before they appear at the surface and begin their adult life.

Life history strategy

A very important factor influencing the evolution of the life history strategy are extremely high mortality rates of the glochidia. Out of one million glochidia only less than ten are lucky to be inhaled by a susceptible host (BAUER 1989, YOUNG & WILLIAMS 1984). To investigate the density relationships of this survival rate, the densities of parasitizing glochidia were plotted against the numbers of adult mussels present in the rivers (Fig. 1). The slope of the regression cannot be distinguished from $b = 1$, suggesting that in all populations the survival rate is the same (SOLOMON 1968). Therefore this relationship must be considered as density-independent in the investigated range of densities.
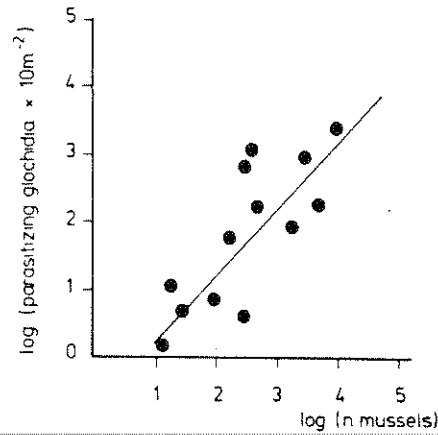
Fig. 1: Relationship between number of adult pearl mussels present in the river and density of parasitizing glochidia ($y = -0.5 + 0.92x$; $r = 0.78$; $p < 0.01$).
Each dot refers to one population

Furthermore, there is no evidence of any regulatory mechanism (BAUER 1989). So the chance of a female leaving descendants increases with the number of glochidia produced. Especially since the survival rates of glochidia are so extremely low and density independent, a strong selection pressure must be expected to produce as many glochidia as possible. In general, a high number of progeny can be achieved in two ways (Fig. 2): either a high life expectancy leading to a high number of reproductive periods, or a high fertility leading to a high number of progeny per reproductive period. According to most concepts about life history selection these traits represent alternative strategies (GREENSLADE 1983, SCHAFFER 1974, SOUTHWOOD et al. 1974, STEARNS 1976), but the pearl mussel combined them. The combination of a high life expectancy up to more than 100 years (GRUNDELIUS 1987) and a fertility of some million glochidia per reproductive period (BAUER 1987b) yields a very high lifetime fertility.

However, this is already too general because the two important traits "life expectancy" and "fertility" are considerably plastic. Therefore, in the following chapter, the correlations between parameters related to lifespan and fertility are analyzed.
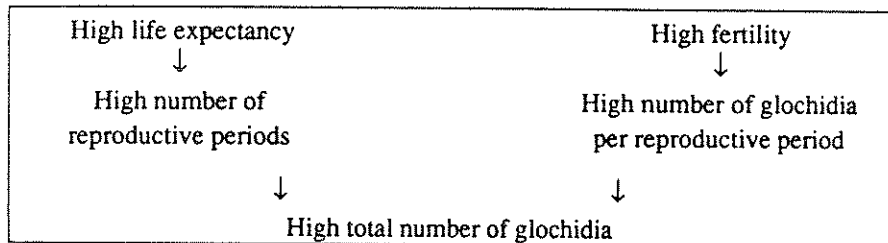
High life expectancy	High fertility
↓	↓
High number of reproductive periods	High number of glochidia per reproductive period
↓	↓
High total number of glochidia	

Fig. 2: Important traits in the pearl mussels life history strategy.

Plasticity

Growth studies

There is evidence that among poikilothermes life history traits like maximum size or life expectancy may be strongly influenced by the process of individual growth (BACHELET 1980, BEVERTON & HOLT 1959, GILBERT 1973, RAY 1960). Therefore growth studies were conducted along a latitudinal gradient covering nearly the whole north-south distribution of the pearl mussel. The analyzed populations are situated in Massachusetts (1 population), northern Spain (3), South Germany (16), Scotland (1) and Sweden (4). The geological substrate of all localities are primary rocks. In each population empty shells of all size classes were sampled, except for the Swedish ones, where the analyses are based on published data (GRUNDELIUS 1987, HENDELBERG 1961). The growth studies are based on the annuli. In order to make them visible, the shells were put in KOH (ca. 5%) at 50 °C, in this way removing the periostracum. With these shells three parameters related to growth were determined, namely the growth constant k, the maximum observed life span A_{max} and the maximum observed size L_{max}.

A basic parameter for the individual growth is the growth constant k, which determines the curvature of the average individual growth curve in a population, that is the rate at which the average asymptotic size is approached (BEVERTON & HOLT 1959). The lower its value the slower the growth. It was determined by measuring every fifth annulus along its longest axis. Then for each population, a regression was established relating shell length at age t+5 years to shell length at age t (Fig. 3, WALFORD 1946). The growth constant k is then:

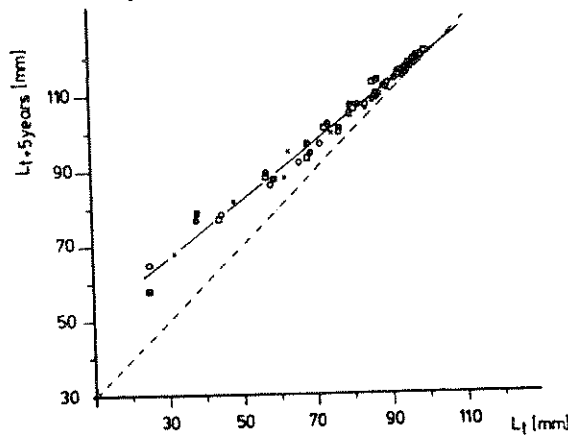$$k = - \ln (b), \quad \text{where } b = \text{slope of the regression}$$

Fig. 3:   Example of a Ford-Walford Plot for one pearl mussel population. Each symbol refers to one analyzed shell. The equation of the regression is:
$y = 28 + 0.77x; r = 0.99; p < 0.001.$

Tab. 1:   Correlation coefficients between growth constant, hydrochemical factors and latitude factors. (Between k and latitude the Spearmans rank correlation coefficient is given.

pH	BOD$_5$	Ca	Latitude
-0.65*	-0.78**	-0.67*	-0.78***

The maximum observed life span A_{max} is the maximum individual age recorded in a population. It was determined by counting the annuli. In this context it should be noted that under natural conditions mortality of adult pearl mussels is low, so that most mussels live out their alloted life span. Accordingly, the survivorship curve is convex (BAUER 1987 b). The maximum life span therefore must be considered as being more determined by intrinsic factors than by the rate of accidental mortality. Water pollution considerably alters the shape of the survivorship curve, but it has comparatively little effect on the maximum life span (BAUER 1988).

The third parameter, the maximum observed shell length L_{max}, indicates the maximum individual size attained in a population.

Fertility parameters

Fertility was estimated in nine populations. The number of glochidia per gravid female can easily be determined by keeping each mussel in a small bucket with only little water. This causes the release of glochidia which can then be counted. In contrast to most invertebrates there is usually no or at most a very weak relationship between fertility and age within a population (BAUER 1987b). Therefore, for each population an average fertility was calculated, i.e. the average number of glochidia produced by one gravid female per reproductive period. Since female pearl mussels do not reproduce every year (BAUER 1987b), the percentage of gravid mussels is also included in this analysis.

Correlations

The growth constant k shows relationships to a number of environmental factors (Tab. 1). It responds to hydrochemistry and to latitude. The latter relationship surely must be considered a temperature effect; at higher temperatures in the south, growth is accelerated.

When the relationships between k and the other traits are analyzed, the following pattern is evident (Fig. 4, Tab. 2):

At increasing growth constant the maximum life span decreases. Variation of this parameter is quite large;it ranges from 30 to 130 years (Fig. 4A). A similar relationship to k shows the maximum shell length (Fig. 4B), which again is related to fertility (Fig. 4C). In populations where the individuals are small, fertility is low compared to populations with

Tab. 2:   Correlations between growth constant (k), maximum observed age (A_{max}), maximum shell length (L_{max}),fertility and percentage of gravid mussels.

	k	A_{max}	L_{max}	Fertility
A_{max}	-0.75***			
L_{max}	-0.55**	0.59**		
Fertility	-0.79*	0.55	0.84**	
% gravid	-0.40	0.11	0.16	0.37

large individuals. Table 2 shows, that the percentage of gravid mussels is not related to any of the other traits. On the average, every year 64 % of all females take part in reproduction and 36 % are put in a pause (BAUER 1987b).
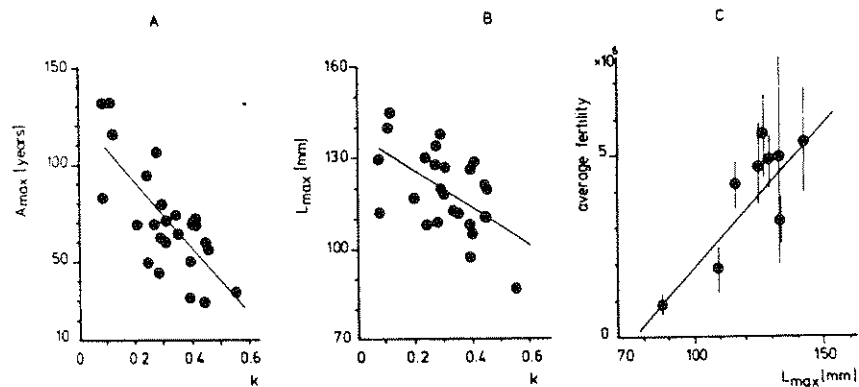

Fig. 4:   Relationships between
A: growth constant k and maximum age A_{max} (y = 125 - 168x;   r = -0.75; $p < 0.001$)
B: k and maximum shell length L_{max} (y = 139 - 62x; r = -0.55; $p < 0.01$)
C: L_{max} and fertility (= average number of glochidia per gravid female and reproductive period ± c.i.) (y = -6.2 + 0.08x; r = 0.84; $p < 0.01$).
Each dot refers to one population.

Plasticity and total reproductive output

Longevity and fertility are important factors for the number of glochidia produced by a female (Fig. 2). Since both parameters respond in the same way to k, A_{max} directly and fertility via L_{max} (Fig. 4, Tab. 2), a considerable reduction of the total reproductive output must be expected as k increases.

In Fig. 5 the total number of glochidia produced by one average female was calculated in relation to its growth constant k. The calculation is based on the relationships between k, A_{max}, L_{max} and fertility. Life expectancy is calculated according to a mortality rate of 10 % in ten years (BAUER 1988) and it is considered that the female pauses in 36 % of all reproductive periods. Furthermore, it is assumed that maturity starts when one fifth of the maximum life span has passed. This is largely an assumption. Since nearly all populations in Central Europe are overaged, this problem is very difficult to investigate. We know that in Scotland mussels attain an age of ca. 70 years and start reproducing at 12 - 13 years of age (YOUNG & WILLIAMS 1984). Presumably at increased growth constants the juvenile period is not reduced as much as is assumed here. But even in spite of this compensating mechanism a high growth constant leads to a large reduction of the total reproductive output. A female growing at k = 0.6 only attains roughly 10 % of the glochidia produced by a female which grows at k = 0.1.
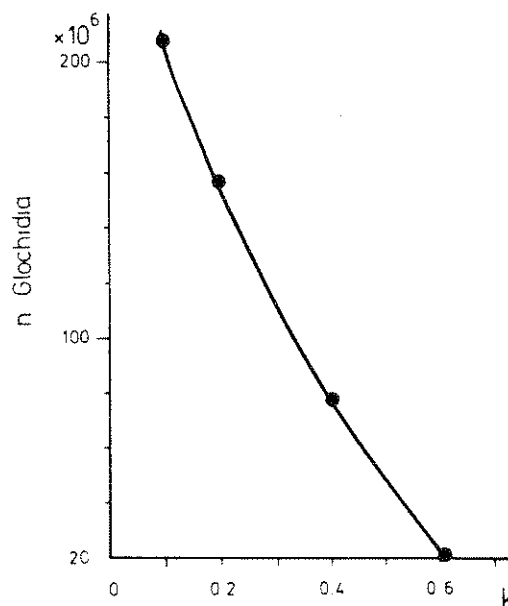

Fig. 5:   Total number of glochidia produced by one female pearl mussel in relation to its growth constant k

Plasticity and population growth

For the purpose of species conservation it is important to know how plasticity affects population growth. Therefore by means of a simple model the growth rate of the population (= r) is calculated in relation to the growth constant of the individuals (= k). The components of the model are presented in Fig. 6.

Adult stage (Fig. 6A)

The model operates with a constant age structure. As in the previous chapter, the mortality is 10% in ten years and maturity starts when one fifth of the maximum age has passed.

Glochidial and parasitic stage (Fig. 6B)

The complicated processes in this stage are combined in one equation. This equation describes the density of parasitizing glochidia out of the number of adult mussels. It is based on the data given in Fig. 1; however, a constant host fish density (the mean density recorded) is assumed in all rivers. The corresponding equation is $y = -0,6 + 0,97x$, ($r = 0,79$; $p < 0.001$). As the slope cannot be distinguished from $b = 1$, the model uses the equation $y = -0.6 + x$.

This equation can also be used to calculate the effect of different fertilities because two conditions are valid. The percentage of gravid animals as well as fertility are independent of age (BAUER 1987 b). The equation is based on field data from populations with an average fertility of 4 million glochidia per gravid female. If fertility x is used in the model, then log x/4 is added to the equation.

Furthermore, it is assumed that the river is 1 m wide, that the mussels are concentrated in one spot and that for 100 m downstream the chances of the glochidia finding a host are constant before dropping to zero. (The latter assumption surely is not far from reality, BAUER unpubl.).

Postparasitic stage (Fig. 6C)

The initial density of this stage is the density of parasitizing glochidia. (It has to be considered that the y-value of Fig. 7B only gives the density for one-year intervals.) A crucial point is the mortality during this stage as a mortality increase is the most important threat in Central Europe (BAUER 1988). YOUNG and WILLIAMS (1984) estimate this mortality in a healthy population at 95 %. To simulate the effect of an increased mortality the model uses rates of 95 %, 98 % and 99,995 %. The number of survivors finally yields the number in the first age class.

MORTALITY = 10% IN TEN YEARS

AGE

A

B

log [n paras larvae / 10 m²]

log [n mussels]
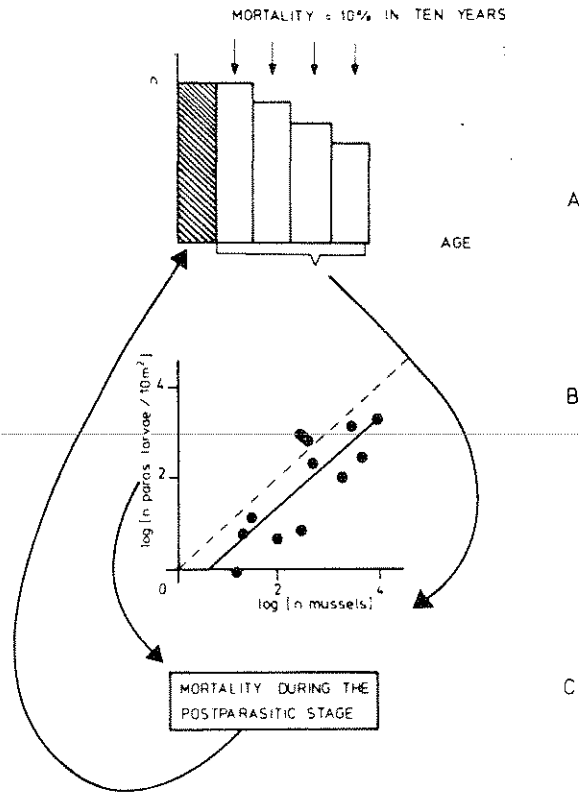
MORTALITY DURING THE
POSTPARASITIC STAGE

C

Fig. 6:   Schematic presentation of the model calculating the growth rate of a pearl mussel
population in relation to the growth constant of the individuals.
A = Adult stage;   B = Glochidial and parasitic stage;   C = Postparasitic stage
(See text for further explanation).

Calculation of r

For each k (0.1, 0,2 ... 0.6) A_{max} and fertility were calculated according to the
relationships in Fig. 4. With these values the growth rate of the population in ten-year
intervals was computed.

$$r = \ln \frac{N_{t+10}}{N_t}$$

The results (Fig. 7) suggest that there is a high risk of negative population growth if the
individual growth constant exceeds the value 0.5. Above this value there is a steep decrease
in growth rates. In this range there is also a strong effect of postparasitic mortality. Only at a
natural mortality of 95 % can positive growth rates be expected. Even a slight increase of
mortality leads to negative population growth. In general, the growth constant k seems to
have little effect at low values whereas at high values its effect on population growth is
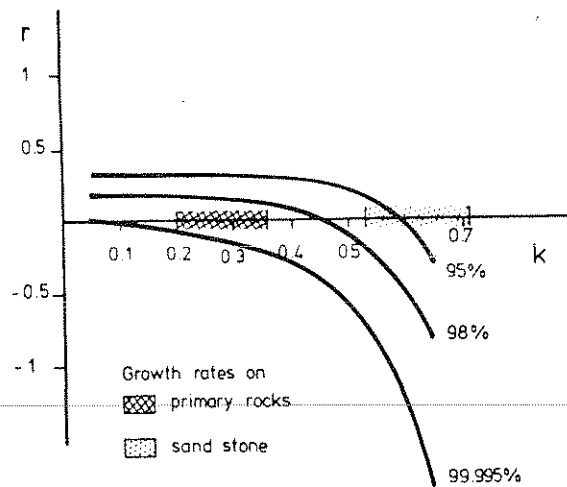tremendous.

Fig. 7:   Growth rates of the population (r) in relation to individual growth constants (k) at three different mortality rates in the postparasitic stage.
(The hatched and dotted area on the k-axis represent the 95 % c.i. of individual growth constants from two different localities in Germany).

Status of the freshwater pearl mussel in Central Europe

In many areas the freshwater pearl mussel formerly occurred at enormous densities (Fig. 8).

Fig. 8:   Formerly the suitable rivers in the Fichtelgebirge were plastered with pearl mussels.
(Photo by A. Ritter between 1930 and 1940).

In the Fichtelgebirge (North East Bavaria), suitable rivers were not only plastered for 20 - 30 km, frequently there were even two or three layers of mussels (ISRAEL 1913). However, since the beginning of the 20th century the numbers have decreased by more than 95 %. Nearly all of the remaining populations lack young mussels (Fig. 9) and will therefore become extinct within the next decades (BAUER 1983, WELLS *et al.* 1983).

The most important cause of decline is eutrophication, which already at very low levels increases the mortality of the postparasitic stage living in the river bottom. As Fig. 9 shows, in most cases the number of young mussels have decreased continuously during the last decades. Presumably the animals die because eutrophication leads to a high amount of detritus enriching the sediment with mud. In this way the river bottom becomes less and less suitable for the development of young mussels (BAUER 1988). The causal mechanisms leading to the death of the juveniles are unknown. Possible explanations are a shortage of oxygen or an increased predator density.

Also the adult stage is affected by eutrophication. Mortality at this stage is related to the nitrate concentration in the water (Fig. 10).

However, the adult stage is less sensitive than the postparasitic stage, i.e. as eutrophication increases first survival of the postparasitic stage is prohibited, then mortality of the adults rises. Thus, there are a number of populations which lack young mussels but mortality of adults still is low (BAUER 1988).

Fertility is remarkably independent of eutrophication and a subtle mechanism causing females to switch to hermaphrodites at low densities ensures a high fertility even in very sparse populations (BAUER 1987b).
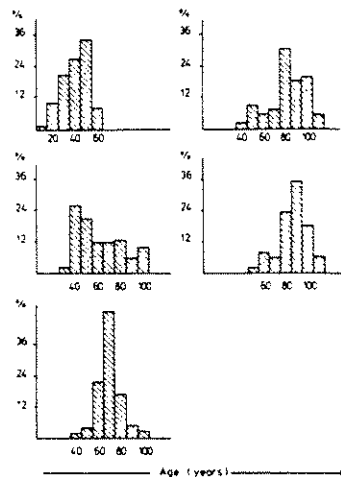

Fig. 9:   Some typical age structures of pearl mussel populations in Bavaria.

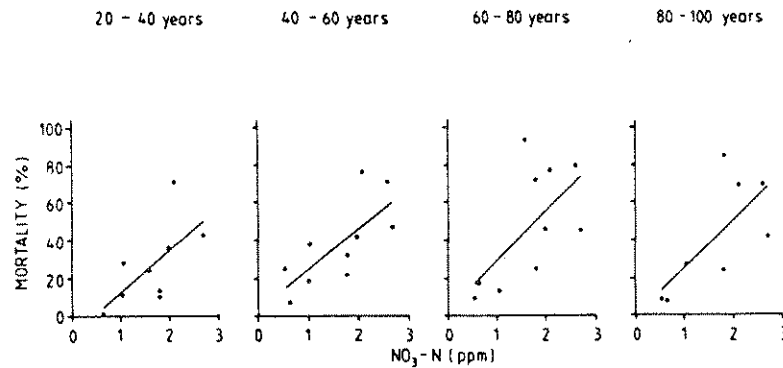20 – 40 years   40 – 60 years   60 – 80 years   80 – 100 years

Fig. 10: Relationship between age-specific mortality of adult pearl mussels and the nitrate concentration in the water for eleven populations. (From BAUER 1988).

20 - 40	years :	$y = -10.3 + 22.4\,x$;	$r = 0{,}68$; $p < 0.05$
40 - 60	years :	$y = 3.3 + 21\,x$;	$r = 0.74$; $p < 0.01$
60 - 80	years :	$y = 2.6 + 26\,x$;	$r = 0.66$; $p < 0.05$
80 - 100	years :	$y = -0.85 + 26\,x$;	$r = 0.74$; $p < 0.05$

Influence of plasticity on status and conservation strategies

The results given in the last chapter undergo a considerable differentiation when plasticity is taken into account. In fact only one statement is independent of plasticity, namely that concerning fertility. Hence it follows for conservation strategies: With respect to fertility there is no critical density. Since there are probably no feedback mechanisms, the problem of a Minimum Viable Population does not seem to exist for the freshwater pearl mussel.

All further consequences only result from a combination of plasticity and threats. These consequences concern the danger of extinction (i.e. the sensitivity to threats), and conservation strategies.

The danger of extinction

Plasticity affects the danger of extinction via two components, namely

a) the growth rate of the population:

Eutrophication causing increased mortality, during the postparasitic stage should have a strong impact if the individual growth constant k exceeds 0.5 (Fig. 7). Already at a very low eutrophication level such populations should decrease and overage.

b) the time until extinction of overaged populations:

Most populations in Central Europe lack young mussels. The time until extinction of such populations is proportional to the number of age classes present in the population. Populations consisting of shortlived individuals (high values of k) will become extinct very soon. Of course the nitrate concentration in the water also has to be considered in this context.

There is an example for these hypotheses.

The results presented so far were gained from populations on primary rocks, which are the main distribution areas of the freshwater pearl mussel. Another suitable substrate are sandstones which are poor in lime. In Germany a distribution area on primary rocks is the Fichtelgebirge, whereas Odenwald, Spessart and Rhön are examples where the pearl mussel occurrs on sandstone (Fig. 11). Both areas are similar with respect to industrialization, human population density, etc. SEIDLER (1922) gives the maximum shell lengths for a number of sandstone populations. When they are compared to the maximum shell lengths of populations from the Fichtelgebirge, it is evident that the mussels on sandstone are smaller (Fig. 12).
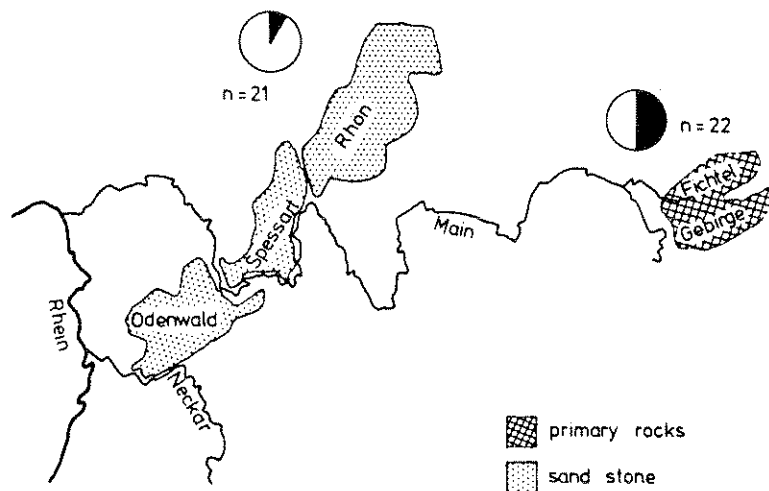

Fig. 11: Percentage of still populated pearl mussel rivers (black segments) in the Fichtelgebirge (primary rocks) and in sandstone areas (Odenwald, Spessart, Rhön). n = number of rivers which were originally populated. (Some rivers in the Odenwald were inhabited by mussels introduced from the Fichtelgebirge. They are not considered here).
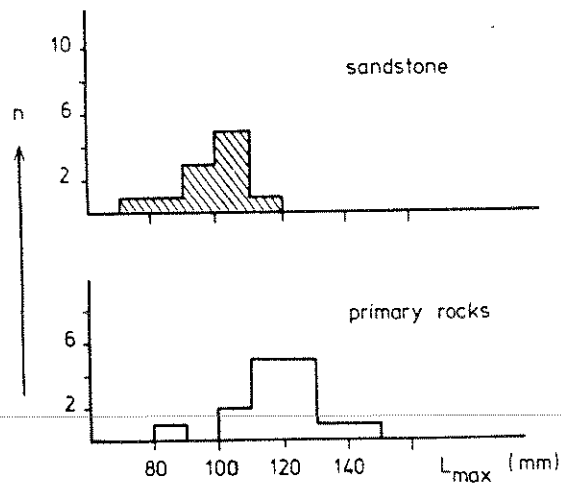
Fig. 12: Maximum shell lengths of pearl mussels on sandstone and on primary rocks (n = number of populations). The sandstone mussels are significantly smaller (t = 5.7; p < 0,001).

Converting their shell lengths into growth constants by means of the equation in Fig. 4B, yields an average of k = 0.62 ± 0.09, whereas in the Fichtelgebirge the average growth constant is 0.28 ± 0.09.

According to Fig. 7 a high danger of extinction must therefore be expected for the sandstone populations, whereas the populations in the Fichtelgebirge should be less vulnerable. This is confirmed by the present status (Fig. 11). Though in both areas nearly the same number of rivers had been populated, the pearl mussels have nearly disappeared from the sandstone mountains (HEUSS 1962, JUNGBLUTH 1986), whereas in the Fichtelgebirge half the populations still exist. Apparently, because of high growth constants associated with short life span and low fertility,the sandstone populations existed such that when conditions were optimal, the life history strategy barely ensured survival of populations. However, slightly worse conditions could not be tolerated and led to quick extinction. (Since most sandstone populations are extinct, I could investigate only one. The results were as follows: k = 0.63, A_{max} = 30 years, L_{max} = 88 mm and average fertility = 930 000 ± 30 000 glochidia per gravid female).

Conservation strategies

First of all, it is important that fertility depends neither on the age of the female, nor on population size. That means that all populations, even if they are very overaged or very

small, are able to reproduce. There is no population which could not recover if effective conservation measures were taken.

Analysis of mortality showed that there are two weak points in the life cycle. One is natural, namely the extremely low and density-independent survival rates of glochidia. The other one is strongly influenced by man. It concerns the increase of postparasitic mortality by eutrophication. Accordingly, two conservation strategies may be proposed: Increase of the density of parasitizing glochidia by introducing infected fish and (or) improvement of the water quality. The first measure is simple and cheap. Up to 1000 Glochidia are able to develop on one trout fingerling. Therefore, it is possible to increase the number of young mussels released by the hosts considerably. Improving the water quality is of course always a desirable measure. However, it is expensive and at present can only be enforced in a few cases (BAUER & EICKE 1986). Since most of the remaining populations will become extinct within the next decades, conservation measures are urgently necessary. As there is no way to improve the water quality of all remaining pearl mussel rivers quickly enough, even delaying extinction would be a success in many cases. Thus, one has to decide which measure has to be taken in which case. Where is an artificial infection of host fish appropriate? Where is the only useful measure an improvement of the water quality? Which populations have high priority?

To solve these problems, the following procedure is suggested. (All measures refer to overaged populations). For each population the following parameters should be recorded:

Maximum shell length, maximum age, age structure, population size and hydrochemistry (especially conductivity, pH, nitrate, phosphate, calcium, and BOD_5 (BAUER 1988)).

a) Populations with large shells and long individual life span

These populations will still exist for many decades unless they are very overaged or the nitrate values are high. If the latter is true one must seek counter-measures.

In a large population (more than 5000 individuals), the natural infection intensities of the hosts and thus the initial densities of the postparasitic stage are high (Fig. 1). Every year many young mussels enter the river bottom, however none of them survive. This indicates that mortality in the postparasitic stage is absolutely 100 %. The river bottom is totally unsuited for young mussels. Thus, the only efficient conservation measure is an improvement of the water quality.

In a small population, the density of the postparasitic stage is also small. Even if there are some suitable spots in the river bottom, the chances are very small that one of these few young mussels will be released from the host just above one of them. Particularly if the water quality is not too bad, hosts which are artificially infected with glochidia from this population should be introduced.

b) Populations with small shells and short individual life span

These populations will soon become extinct; therefore they have the highest priority. Conservation measures must be taken very soon.

Already very low eutrophication levels must be expected to have a strong negative impact. In this respect a crucial weak point is the low fertility, leading to a low density of the postparasitic stage. As in the last case there is hardly any chance of one of these few young mussels surviving, even if the river bottom is not completely unsuitable. Therefore artificially infected fish should be introduced, no matter whether the population is large or small. If this measure is conducted for some years with many fish, (at least 1000 per population and year), it might be sufficient to provide a stock of young mussels able to survive the postparasitic stage. In this way the quick collapse of the population could be prohibited.

Conclusions

Detailed knowledge about the population ecology of a threatened species is an important requirement for effective conservation measures. However, as the example of the freshwater pearl mussel shows, it is problematic to apply demographic results gained from a few localities to other populations of the same species. The long lifespan of the pearl mussel, which is often mentioned in the literature (COMFORT 1957, HUTCHINSON 1979), does not hold for all populations. In addition reproductive parameters and sensitivity to threats are different. Only if the relationships between the plastic reactions of life history traits are known, can especially vulnerable populations become evident and a catalogue of conservation measures with broad validity be developed.

Zusammenfassung

Am Beispiel der in Mitteleuropa vom Aussterben bedrohten Flußperlmuschel (*Margaritifera margaritifera L.*) wird gezeigt, wie die Plastizität bionomischer Komponenten den Gefährdungsgrad einer Tierart beeinflußt. Die bionomische Strategie der Flußperlmuschel zielt auf eine möglichst hohe Glochidienproduktion ab, was durch die Kombination einer hohen Lebenserwartung (= hohe Zahl von Fortpflanzungsperioden) mit einer ebenfalls hohen Fertilität erreicht wird. Gerade diese beiden Komponenten zeigen aber starke plastische Reaktionen in Abhängigkeit von der individuellen Wachstumskonstante. Die Wachstumskonstante, d.h. die Geschwindigkeit, mit der sich die individuelle Wachstumskurve ihrer Asymptote nähert, wird von verschiedenen Umweltfaktoren beeinflußt: sie steigt z.B. mit zunehmender Temperatur. Eine Erhöhung der Wachstumskonstante (= "schnelleres Wachstum") führt zu einer Verringerung von Lebenserwartung, Maximalgröße und Fertilität. Dieser Mechanismus hat eine starke

Reduktion der gesamten (=lebenslangen) Glochidienproduktion bei schnellwüchsigen Tieren zur Folge. Für Populationen aus schnellwüchsigen Individuen muß daher eine hohe Empfindlichkeit gegenüber Gefährdungsfaktoren erwartet werden, wobei zwei Gründe besonders wichtig sind: ein verringertes Populationswachstum und eine aufgrund der geringeren Lebenserwartung verkürzte Zeit bis zum endgültigen Aussterben. Diese Hypothese wird durch die Bestandsentwicklung in verschiedenen Gebieten der BRD gestützt. Die Ergebnisse werden im Hinblick auf Schutzstrategien diskutiert

Acknowledgements

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