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The freshwater pearl mussel in South Bohemia: Evaluation of the effect of temperature on reproduction, growth and age structure of the population

By JAROSLAV HRUŠKA[1]

The Czech Institute of Nature Conservation Prague and
Czech National Union of Nature of Protection Activists, District Committee
Prachatice

With 3 figures and 2 tables in the text

Abstract

The relationship between temperature of the medium and development of the population was studied in the freshwater pearl mussel (*Margaritifera margaritifera* L.) on the upper boundary of its vertical distribution in South Bohemia (760 to 800 m above sea level). The results of this study can serve as a basis for identifying trends in the development of the population in relation to climatic changes and to changes in the management of the upper reaches of brooks and rivers populated by the pearl mussel and for seeking other suitable localities where the mussel could be introduced or transferred to in order to save the population.

Introduction

The freshwater pearl mussel (*Margaritifera margaritifera* L.) is distributed from the holarctic reaches of North America to Eurasia; the 40th degree NL is its southern boundary (BAUER 1980). The average age of populations increases, the species is dying out. The pearl mussel's requirements for quality of the biotope and the possibilities of active conservation have been studied by a number of authors (BAUER & THOMAS 1980, BAUER 1983, 1986, 1988, DETTMER 1982, DYK 1974, HENDELBERG 1961, YOUNG & WILLIAMS 1984, WÄCHTLER 1986 and others). The basic requirements of the freshwater pearl mussel for chemical and physical quality of water have been identified, the course of reproduction and its limiting factors have been described, and practical possibilities of protection have been found. The factors which are responsible for limiting the vertical distribution of the freshwater pearl mussel have not yet been studied in detail. In the river Pärlälven in arctic Sweden, as far north as the Arctic Circle, the upper boundary of distribution of the freshwater pearl mussel is 360 m above sea level (HENDELBERG 1961), whereas in South Bohemia, the centre of

[1] Address of the author: JAROSLAV HRUŠKA, Česky svaz ochránců přírody, Okresní výbor Prachatice, 384 51 Volary 48, Czechoslovakia.

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Europe, this boundary is higher: 800 m above sea level. At this boundary of occurrence, most of the localities populated by the mussel are brooks running from areas exposed to south or from those, which are sparsely covered with forest.

Rapid intensification of farming causes rapid eutrophication of water courses, up to their upper reaches. As a result, the environment, where freshwater pearl mussels can live, has shrunk to a few places with their headstreams in the forest parts of the higher-altitude areas of the Bohemian crystalline region. The boundary of vertical distribution is an additionally limiting factor in these areas; this should be learned thoroughly if the last remains of the freshwater pearl mussel are to be saved.

Description of the territory studied

This study was carried out in the river Blanice (Prachatice district) in the mountain range of the Bohemian Forest. The river is a typical biotope of the freshwater pearl mussel in South Bohemia (Dyk 1974) with a total population of about 130 thousand individuals. The river is about 5 m wide, 20 to 60 cm deep, with a relative fall of 0.3 to 0.6 %. Its spring is located 970 m above sea level. Its upper reaches are lined by forests; only a small proportion of the landscape is farmed, and its human population is low.

The water has the following characteristics (average values):

conductivity	75 µS/cm	pH	6.8
BOD_5	1.6 mg O_2/l	Ca^{2+}	5.0 mg/l
NO_3^-N	0.7 mg/l	PO_4^{3-}	0.025 mg/l

Material and Methods

1. Effect of water temperature on the age structure of the population

a) Determination of the age structure of the population

A ligament growth curve was plotted by the method of Hendelberg (1961) as the first step in determining the age structure of the population. Large samples of living individuals (total 1100) were collected then over a 4 km part of the river on the upper boundary of distribution of the species. The length of ligament was converted to age.

b) Determination of the influence of drift on the age structure

Practical trials with labelled individuals were performed to study the effect of drift on the age structure of the population.

c) Measuring the temperature of the medium

An instrument for the daily recording of water temperature and air temperature was installed at the site of study. The Czech Weather Service's Hydrometeorological Institute in Ceské Budejovice provided data on the average monthly air temperatures since

1932; these data were converted to values corresponding to the altitude and corrected according to actual air temperature and water temperature of the site of study on the basis of data from 1986 to 1988.

For comparison data were obtained on the average monthly temperatures of water in the river Sörkedalselva in Norway, close to 60° NL, about 150 m a.s.l., which holds a reproducing population of freshwater pearl mussels (DETTMER, unpublished data).

d) Relationship between temperature and the age structure of the population

The converted average monthly temperatures were calculated for the period of glochidial development of the mussel on the host fish, i.e. August and September of the preceding year and April to July of the current year (the period from October to March was dismissed because of its negligible importance for the ripening and metamorphosis of glochidia and for difficult correction of water temperature on the basis of air temperature).

Arithmetical means of water temperature were calculated for each period of glochidial development, plotted in a diagram and compared with the age structure of the population of the freshwater pearl mussel.

2. Effect of water temperature on the glochidial development

Samples of brown trout invaded by glochidia of the freshwater pearl mussel in a seminatural rearing facility built inside the area under study were investigated for the course of development and metamorphosis of the glochidia. For comparison host fish were kept in the original medium of the river and in brooks with lower water temperature.

Host fish from the river Blanice were sampled one month resp. one week before the expected release of juvenile mussels and transferred individually to brooks at higher altitudes within the drainage area of the river. Control site A was located 850 m and control site B 950 m above sea level. The peak average temperatures in July were 13.5 °C at site A and 11.0 °C at site B.

At the same time host fish were kept in water from the river Blanice at a constant temperature (15.5 to 17.0 °C).

3. Effect of temperature on the growth of adult mussels

Adult individuals of different sizes were tagged and the length increments of their shells were measured at the end of the active season of every year. The relationship between water temperature and shell increments was evaluated.

Results

1. Effect of water temperature on the age structure of the population

Individuals living on a clean gravel and sand bottom of the site exhibit a uniform course of growth of the ligament with just minor deviations from the mean represented by the growth curve. On the other hand, individuals in old arms of the river or in places with poor water discharge and with muddy bottom show a much slower growth of the ligament and the shells. It was decided therefore, to use only the individuals from the clean gravel and sand bottom for the plotting of the growth curve.

Equation of ligament growth:

$y = 1{,}6 + 1.057x - 0.0053x^2$

$n = 80 \quad r = 0.941$

n = number of shells for the determination of the equation

r = coefficient of correlation

y = length of the ligament

x = age (years)

Fig. 1 represents the distribution of age classes of the freshwater pearl mussel along a 4 km part of the locality, as depending on the fall and the nature of

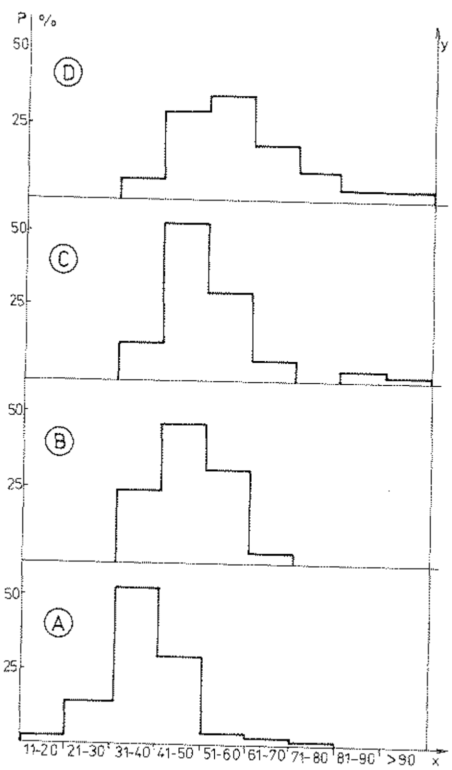


Fig. 1. Distribution of the age classes of the freshwater pearl mussel according to the length of the water course and its relative fall. (A – 1st km, sporadic meanders, relative fall 0.55 %; B – 2nd km, sporadic meanders, relative fall 0.6 %; C – 3rd km, medium-meandering course, relative fall 0.6 %; D – 4th km, frequent meanders, relative fall 0.3 %; y – direction of flow; x – age classes; P – percentual proportions of age classes in the population).

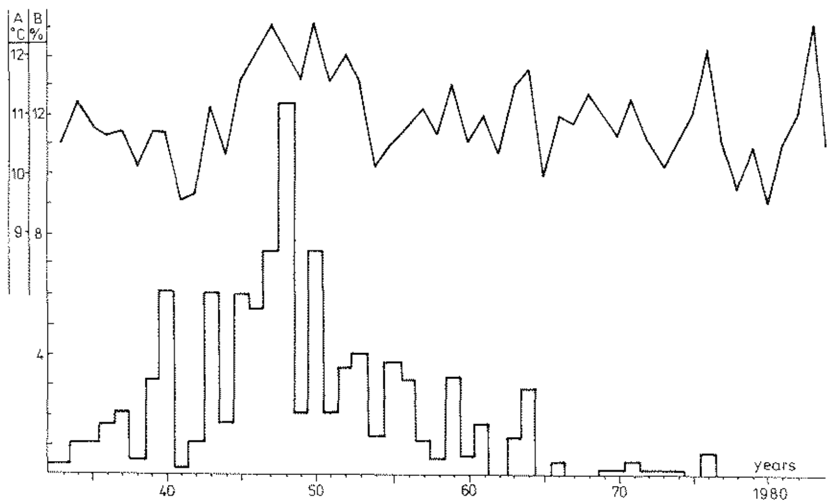


Fig. 2. Comparison of water temperature and the age structure of the freshwater pearl mussel population. (A – average monthly temperature during the period of development of the glochidia; B – percentual proportions of different year groups of mussels in the population; x – year of release of the mussels from the host).

the river bed. Of 50 mussels experimentally tagged for drift investigation, those from sandy sediments were drifted up to 800 m downstream within one year; those anchored in gravel were able to stay at their original site.

Fig. 2 is a diagram of mean water temperatures during the periods of glochidial development from 1932 until 1986 and of the proportions of different age classes (percentages) in the freshwater pearl mussel's population in a 2 km section of the river close to the end of natural distribution in the locality.

2. Effect of water temperature on the glochidial development

Under the natural conditions of the site of study, the host fish are invaded by glochidia of the pearl mussel during the second ten-day period of August to the first ten days of September; the metamorphosed juvenile mussels leave the hosts during July of the subsequent year. These dates refer to the years 1986 to 1988. There is so far no information on the course of the cycle in years with large temperature deviations.

Host fish that had been transferred to control sites A and B one month before the expected release of juvenile mussels showed different patterns in the glochidial development. At control site A about 30 % of the young freshwater pearl mussels left their hosts between the 40th and 60th day after the transfer of the fish. The other glochidia stayed on their hosts for another 100 days until the investigation had to be terminated because of freezing of the water. At site B none of the mussels left the fish even after 160 days of the trial.

Transferred on the fish to the control sites one week before the expected release of juvenile mussels, the development of the mussels was finished and the juvenile freshwater pearl mussels left the gills of the fish within 14 days at both sites A and B with no difference.

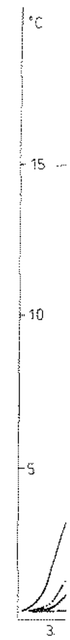
The viability of the juveniles released was not investigated – this will be done during further research work.

At the same time, a series of trials with trout invaded with glochidia of the freshwater pearl mussel were conducted, the fish being kept at a constant range of water temperatures. If water is kept within a daily range of 15.5 – 17.0 °C, the glochidia develop continuously under artificial conditions and their metamorphosis takes place, leading to the release of juvenile mussels after 84 ± 4 days. This clearly differs from the natural environment where the development lasts about 11 months.

If the length of time needed to finish the glochidial metamorphosis is calculated as the sum of average daily water temperatures (day degrees), 1300 to 1430 day degrees are derived. However, some juvenile mussels may leave the host much sooner, but these individuals are much smaller and their growth potential is limited. Their mortality within 60 days is up to 90 %. The glochidia which stay on the hosts for more than 1300 day degrees are as large, viable and active as are the individuals which leave the host under natural conditions. An attempt to accelerate the metamorphosis of glochidia was conducted successively in different stages of maturation in the gill tissue of the host. The results are shown in Table 1. Under natural conditions of the locality under study, the number of day degrees needed to finish the metamorphosis of glochidia is much higher than 1300 day degrees, amounting 1760 to 1820 day degrees in 1987 and 1818 to 1860 day degrees in 1988. As observed in both years, juvenile mussels were released from the host only after a stabilized period of 14 to 16 days with average water temperatures reaching or exceeding 15 °C. For compa-

Table 1. Trials to accelerate the growth and metamorphosis of glochidia. (A – number of day degrees for the development of glochidia on the host under natural conditions, before the beginning of the trial; B – number of day degrees during the trial until the release of the first juvenile mussels; C – total sum of day degrees until the time of release of the first juvenile mussels; D – number of day degrees needed during the trial for spontaneous release of the juvenile pearl mussels; E – total number of day degrees needed for spontaneous release of the juvenile pearl mussels).

Date	A	B	C	D	E
20. 08. 1988	0	1118	1118	1397	1397
24. 03. 1988	789	320	1109	544	1333
18. 11. 1988	846	263	1109	510	1356
02. 01. 1989	858	258	1116	528	1386
05. 05. 1988	954	188	1142	387	1341
20. 06. 1988	1478	68	1546	255	1733



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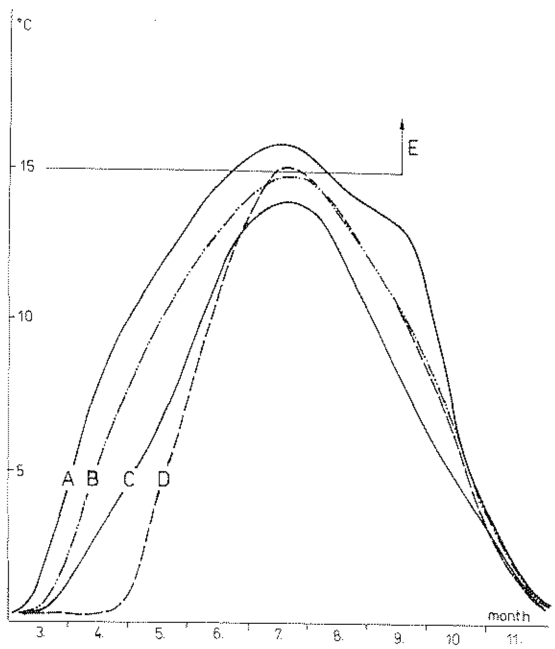

Fig. 3. The patterns of average monthly water temperatures. (A – Blanice, extraordinarily warm year 1947; B – Blanice, extraordinarily cold year 1941; C – Blanice, average temperature for 1932–1986; D – Sörkedalselva (Norway), average temperatures for 1981–1986; E – boundary of temperature curve for the reproduction of the freshwater pearl mussel).

rison Fig. 3 shows the average monthly water temperatures in the river Blanice and in the Norwegian river Sörkedalselva.

3. Effect of temperature on the growth of adult mussels

During the period of 1985 to 1987 the length increment of the shells of pearl mussels of different sizes was measured, the shells being specially labelled with a numerical code. Table 2 shows the different length increments and their annual averages (percentages) in comparison with average water temperature for April to September of every given year.

Discussion

The differences in the distribution of age classes, as illustrated in Fig. 1, are very likely caused by the gradually forced drift of the adult mussels during floods and movement of ice, which raises parts of colonies from the bottom and scatteres them along the river bed, or covers mussels with layers of sand,

Table 2. Increment of adult pearl mussels in dependence on water temperature. (A – Code denoting the mussels; B – length increment in mm; % – percentual length increment; T – average water temperature (°C) from April to September.

A	1984	1985	B	1986	B	1987	B	% 85	% 86	% 87
1	55.1	56.0	0.9	59.2	3.2	60.6	1.4	1.63	5.70	2.36
2	61.0	62.2	1.2	65.5	3.3	67.3	1.8	1.97	5.31	2.75
4	42.5	42.8	0.3	46.0	3.5	46.9	0.9	0.71	8.20	1.96
8	62.3	62.5	0.2	65.8	3.3	67.6	1.8	0.32	5.28	2.74
12	49.5	50.0	0.5	53.0	3.0	54.4	1.4	1.01	6.00	2.64
23	95.2	95.2	0.0	95.2	0.0	96.3	1.1	0.00	0.00	1.16
29	96.8	97.0	0.2	97.3	0.3	98.4	1.1	0.21	0.31	1.13
30	97.8	97.8	0.0	98.0	0.2	98.5	0.5	0.00	0.20	0.51
33	56.0	57.2	1.2	61.5	4.3	62.5	1.0	2.14	7.52	1.63
34	70.5	71.0	0.5	73.0	2.0	74.4	1.4	0.71	2.82	1.89
36	82.9	82.9	0.0	83.5	0.6	84.0	0.5	0.00	0.72	0.59
%								0.79	3.82	1.76
T								10.80	11.15	11.05

forcing them to leave their location in the firm gravel bottom and thus becoming subjected to downstream transport.

This suggests that drift may influence the age structure of the population in some parts of areas investigated. However, this is immaterial with respect to the purpose of this study: the downstream drift of the older individuals only explains their low proportion in the population but does not affect the significance of the effect of temperature on the success of reproduction.

At the upper boundary of natural distribution of the freshwater pearl mussel in South Bohemia (800 m above sea level), the age structure of the population follows the fluctuations of the average monthly temperatures (Fig. 2). The age group most amply represented in the present population of pearl mussels is that coming from the extraordinarily warm years 1946–1948. In spite of the stagnation of further reproduction caused by worsening of the biotopes, significant increases where observed in 1963 and 1964, and later in 1976. There are good reasons to believe that reproduction was also very successful in 1976. The young mussels of this year, however, stay in the interstitial zone of the bottom where they spend the first period of their life and where they are hard to reach.

If the relationship mentioned above holds generally, increased reproduction may also be expected to have taken place in these years in other European populations whose biotopes are still clean enough at least in the upper parts of the watersheds. The mechanisms by which the reproductive success of a population of freshwater pearl mussels is correlated to the temperature of the water during the period of glochidial development will be discussed as follows:

The data from Table 1 suggest that water temperature is related to the development and metamorphosis of the glochidia of the freshwater pearl mussel.

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1.97	5.31	2.75
0.71	8.20	1.96
0.32	5.28	2.74
1.01	6.00	2.64
0.00	0.00	1.16
0.21	0.31	1.13
0.00	0.20	0.51
2.14	7.52	1.63
0.71	2.82	1.89
0.00	0.72	0.59
0.79	3.82	1.76
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In an artificial environment with constant water temperature 1300 to 1430 day degrees were needed to complete the metamorphosis, (except for the one trial performed in June, which will be discussed below). It is concluded that the development of glochidia on the hosts can be controlled by water temperature from the very moment of invasion.

Under natural conditions the development and metamorphosis of the glochidia required 1760 to 1860 day degrees, but in addition, during the final 14 to 16 days the average water temperature had to be at or above 15 °C, i.e. about 225 day degrees. This finding may explain the retarded release of juvenile mussels in the above mentioned trial conducted in an artificial environment in June (Table 1).

Comparison of the final stage of metamorphosis of glochidia appears to confirm the assumption that the development of the glochidia is continuous at the beginning, but later, towards the end of the period, which could be characterized by reaching the value of about 1100 day degrees, the development slows down as if the glochidia were waiting for a longer period during which the average water temperature would remain at or above 15 °C. If the host gets into colder water before the glochidia have finished their metamorphosis, their development slows down or stops. However, if the environment becomes colder at the onset of the release of juvenile mussels from the cysts, the development is not longer retarded; but it has not yet been demonstrated for sure that juvenile mussels are viable in cold water.

This mechanisms probably allow the juvenile mussels to choose a good locality and optimum time to leave the host and start living independently:

a) in the mid section of the trout zones where the water courses mostly have uniform currents with only a low erosion of the bottom, and where the output of plankton and detritus is high enough to support the mussel and low enough not to deteriorate the conditions in the interstitial zone of the bottom;

b) in a period of minimum water flow rate when the mussels can find optimum positions in the interstitial parts of bottom, free from the danger of downstream drift to muddy sites;

c) in a period of peak development of nanoplankton in summer, providing food for the mussels.

The comparatively wide ranges of times for glochidial development on the hosts are due to the fact that under natural conditions the glochidia invade the fish for several days and that the development of the glochidia is strongly influenced by the properties of the host. The host fish may aquire temporary immunity, being able to suppress or eliminate the development of the glochidia in their gill tissue (Bauer, Vogel 1987). In practical protection, seminatural or artificial rearing of the freshwater pearl mussel and its introduction in new localities, all these facts imply a limitation of choice of suitable localities. The flowing waters, where optimum localities can be found, should have good chemical properties (BAUER, THOMAS 1980, BAUER 1988) and a suitable porous structure of the bottom; however, they should also be able to reach a temperature exceeding 1300 day degrees over a period necessary for the development and metamorphosis of glochidia, with a peak of the daily average temperature at or above 15 °C for at least 14 days in summer.

In the cold areas of North Europe this is probably realized in the oligotrophic lakes on the upper reaches of the rivers where heat accumulation occurs.

To a considerable extent, water temperature in brooks and rivers is affected by the management of the drainage area. Landscapes without forests and with regularily cut alluvial meadows, with shrubs growing along the banks of the brook, are favourable because the soil of the meadow can be well heated and the shrubs shade only the water surface, preventing algae from overgrowing the bottom. If the grass is not harvested the meadow is overgrown with tall hard grasses and the warming of the stream is reduced. When the brook flows through a forest, its water is cold. Undrained forests with plenty of moss are more favourable for keeping a good water temperature then forests from which the water flows too quickly, sometimes with an artificial draining system.

Nowadays there is a tendency to either plant forests in the alluvial areas along brooks and rivers or to build draining systems for intensive farming with the use of mineral fertilizers and pesticides. All this is harmful to freshwater pearl mussels: a forest reduces water temperature, thus lowering the boundary of the possible vertical distribution of the species; intensive farming changes water chemistry and destroys the mussels' biotope.

Summary

The last fragments of the formerly large area of occurrence of the freshwater pearl mussel (*Margaritifera margaritifera* L.) have remained in the upper reaches of rivers where the degree of eutrophication is low. However, success of reproduction in these areas is limited by the water temperature which must be high enough to allow for 1300 day degrees (sum of average daily water temperatures) during the period of development of glochidia on the host fish, the peak of the average temperature curve for the summer season being above 15 °C for at least 14 days. In an artificial environment, temperature can be used to control the development of glochidia from the very moment of invasion of the host. At a constant distribution of the average daily water temperatures within the range from 15.5 to 17.0 °C, metamorphosis and the release of juvenile mussels from the hosts occur within 84 ± 4 days. Water temperature also influences the growth of adult pearl mussels. These findings can be used in conservation practices, in seminatural and artificial rearing of the mussel, and in their possible introduction in new localities.

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BAUER, G. & THOMAS, V
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BAUER, G. (1983): Age
freshwater pearl n
– (1986): The status
the south of its Eu
– (1988): Threats to
Central Europe. -
BAUER, G. & VOGEL, C.
– Arch. Hydrobi
DETTMER, R. (1982): Ur
im Vergleich mit
Tierärztliche Hoc
DYK, V. (1974): The pea
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Veterinaria **43:** 28
HENDELBERG, J. (1961):
Rep. Inst. Freshw
WÄCHTLER, K. (1986): Z
– Naturwissensch
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References

Bauer, G. & Thomas, W. (1980): Die Ursachen für den Rückgang der Flußperlmuschel im Fichtelgebirge und Maßnahmen für ihren Schutz. – Natur und Landschaft **3:** 100–103.

Bauer, G. (1983): Age structure, age specific mortality rates, population trend of the freshwater pearl mussel in North Bavaria. – Arch. Hydrobiol. **98:** 523–532.

– (1986): The status of the freshwater pearl mussel *Margaritifera margaritifera* L. in the south of its European range. – Biological Conservation **39:** 1–9.

– (1988): Threats to the freshwater pearl mussel *Margaritifera margaritifera* L. in Central Europe. – Biological Conservation **45:** 239–253.

Bauer, G. & Vogel, C. (1987): The parasitic stage of the freshwater pearl mussel I.–III. – Arch. Hydrobiol. Suppl. **76:** 393–423.

Dettmer, R. (1982): Untersuchungen zur Ökologie der Flußperlmuschel in der Lutter im Vergleich mit bayerischen und schottischen Vorkommen. – Diplomarbeit, Tierärztliche Hochschule Hannover.

Dyk, V. (1974): The pearl oyster, a neglected indicator of the pollution of mountain and submontane water flows of the crystalline region in Czechoslovakia. – Acta Veterinaria **43:** 287–304.

Hendelberg, J. (1961): The freshwater pearl mussel, *Margaritifera margaritifera* L. – Rep. Inst. Freshwater Res. Drottningholm **41:** 149–171.

Wächtler, K. (1986): Zur Biologie der Flußperlmuschel *Margaritifera margaritifera* L. – Naturwissenschaften **73:** 225–233.

Young, M. & Williams, J. (1984): The reproductive biology of the freshwater pearl mussel *Margaritifera margaritifera* L. in Scotland. – Arch. Hydrobiol. **99:** 405–422, **100:** 29–43.

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