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Rediscovery of Southern Populations of *Margaritifera margaritifera* (L.) in Russia as a Model of Conservation Research

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Preface

Theodosius Dobzhansky once famously remarked that nothing in biology made sense except in the light of evolution. These words often came to my mind as I was doing research on various biological objects, but with time a different wording began to suggest itself. Again and again I saw that while scientists were delving deep into the taxonomy, physiology or, for that matter, evolution of a species, its numbers were decreasing so dramatically as to render its study meaningless. Even sampling may negatively affect a species, while non-action or delay on conservation may cause irreparable harm. I am now firmly convinced that nothing in biology makes sense except in the light of nature conservation.

Surprisingly, this simple idea has been slow to settle in the scientific community. I used to hear that nature conservation was 'unscientific', the province of journalists and public figures, and that 'true' scientists dealt with more 'serious' issues. It seemed to me that the only way to fight this approach was putting conservation on a solid basis through scientific publications, and I endeavoured to compose as many as possible. Over time, they formed the basis for this book. Devoted to the current state of the southern populations of freshwater pearl mussel *Margaritifera margaritifera* in Russia, it addresses various issues from ecology to history, evolution and research on ageing. All these aspects, however, gravitate towards the central axis: providing a scientific rationale for the conservation of this vulnerable organism and proposing a generally applicable model of conservation research. Indeed, after most of the book has been written, the approaches and methods developed in it have been successfully applied to several other species such as polar bears, sea otters and crayfish.

The initial stage of the research that resulted in this book was funded by the Rufford small Grants Foundation in 2008–2011. I am grateful to the Swedish branch of WWF and in particular its officer Lennart Henrikson for the provision of aquascopes and other useful things in 2010. The research in some parts of the study area was supported by the Directorate of Protected Areas of St Petersburg, the Directorate of Protected areas of Veliky Novgorod and Valdaysky National Park in 2010–2013. The chapters on ageing were encouraged and supported by Vladimir

Anisimov, President of Gerontological Society of the Russian Academy of Sciences, and by Petrov Research Institute of Oncology. The bulk of book is based on the research that I performed at the Department of Applied Ecology of the St Petersburg State University.

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Contents

About the Author

Igor Popov was born in Leningrad (now St Petersburg), Russia, in 1971. He studied biology at Leningrad State University in 1988–1993. Afterwards he worked in the Institute for the History of Science of the Russian Academy of Sciences (St Petersburg Branch), Institute for Fisheries, Directorate of Protected Areas of St Petersburg, Konrad Lorenz Institute (Austria), University of Paris 7 Denis Diderot (France) (post-doctoral fellowship supported by *Fondation La maison des sciences de l'homme*) and N. N. Petrov Research Institute of Oncology. He is currently a researcher at the Department for Applied Ecology (Faculty of Biology, St Petersburg State University). Popov's main research objects were salmonid fishes, bats, marine mammals, freshwater bivalves and crayfish. His fields of interest include ecology, evolution, history of science, paleontology, zoology and gerontology as well as various aspects of conservation biology.

Chapter 1
Introduction

> "The man, because of his egoism too little enlightened in regard of his own interests, because of his propensity to extract pleasure from everything that is at his disposal, in a word, because of his carefree attitude to the future and his fellow-men, seems to be working on the annihilation of the means of his own preservation and indeed the destruction of his own species. Destroying everywhere the large plants that protect the soil, for the sake of objects that satisfy his greed of the moment, he quickly makes barren the very soil he inhabits, allows the drying up of the water sources, drives away the animals that subsisted on them, and transforms large areas of land, once very fertile and densely populated in all respects, into naked, barren and uninhabitable deserts. [...] It seems as though the man is destined to destroy himself after having made the globe uninhabitable" (Lamarck 1820, p. 154).

Anthropogenic pressure on the environment is steadily growing, and increasingly more animal species are declining and facing extinction. The study of this process is important for providing a scientific rationale for the sustainable use of animals and the protection of rare and endangered species. Vertebrates and macroinvertebrates are especially interesting in this respect as they usually need more life space and are therefore more threatened than smaller species. While studies of such animals tend to focus on exotic or flagship species, no one would argue that less conspicuous animals deserve less attention.

This book presents the results of the research initially conceived during biodiversity observations in Northwest Russia. The idea was to perform a model study of a rare animal in the part of its distribution area where it is least studied and most threatened in order to highlight the importance of conservation research for animal protection.

The freshwater pearl mussel *Margaritifera margaritifera* (L.) was perfectly suited for such a study. The numbers of these molluscs have reduced by 95% over the last decades, and a considerable decline was also noted previously (Araujo and Ramos 2001). In such a situation, it is important to obtain information about the distribution and numbers of the surviving populations, the previous distribution of extinct populations and the prospects of their recovery.

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The research focussed on the southern populations of the pearl mussel in Russia (to the south of Karelia) for several reasons. Firstly, they are basically unexplored, with just a few anecdotal reports being available. At the same time, there is evidence that they were quite numerous in the past. Secondly, the southern populations are more exposed to anthropogenic pressure than the northern ones, and prevention of their extinction is a pressing matter. Thirdly, these populations are especially demonstrative in the context of the study of extinction and its causes. Sound scientific information about their extinction and possible conservation measures can be used throughout the distribution area of pearl mussels. Anthropogenic pressure increases steadily everywhere, and even populations that currently seem to be in good condition might be threatened in the future.

The study of *M. margaritifera* is important for characterizing the state of the environment of an area. They are good indicators of the condition of a number of ecosystems since their larvae parasitize salmonid fishes such as the Atlantic salmon *Salmo salar* and the brown trout *Salmo trutta*, which require very specific habitats.

The rapid decline of the pearl mussel indicates that it is becoming extinct, at least in much of its distribution area. The study of this species might shed light on the process of extinction in general, with possible implications for palaeontology and evolution. In addition, the extinction of the southern populations might be interesting in the context of the possible role of climate warming in the transformation of the fauna.

Finally, the study of the southern populations of pearl mussels in Russia is interesting from the viewpoint of biological methodology. They remained unexplored for a long time in spite of the proximity of St. Petersburg, a large research centre. The same is true of several other threatened species. The development of robust research models would make it possible to eliminate such paradoxes.

Inventories of pearl mussels have recently been carried out in many European countries (Gumpinger et al. 2002; Reis 2003; Cochet 2004; Larsen 2010; Moorkens et al. 2007; Araujo 2012; Cosgrove et al. 2012; Pasco and Heshard 2015; Simon et al. 2015; Olofsson 2017; Denic and Geist 2017; Oulasvirta et al. 2017 etc.) but the causes of their decline are still uncertain. Evidence points to anthropogenic pressure as the main cause but it is a multifaceted process and it is often unclear which of its numerous aspects affects pearl mussels especially strongly. Climate change might also affect pearl mussels and bring about their decline (Hastie et al. 2003).

Studies of pearl mussels in Russia has mostly been carried out on the more numerous northern populations in the rivers of the White Sea basin. The southern populations—that is, those in the rivers of the Baltic Sea basin (Leningradskaya Oblast, Novgorodskaya Oblast, Pskovskaya Oblast and Vologodskaya Oblast)—have remained almost unexplored until the present study.

The aims of this study were to characterize the current state of the southern populations of *M. margaritifera* in Russia, to provide a scientific rationale for their conservation and to propose a model of conservation research based on the obtained results and potentially applicable to other objects and areas.

The initial objectives of this research were:

1. To describe the distribution and the numbers of populations of *M. margaritifera* in the southern part of its distribution area in Russia.
2. To reveal tendencies in the state of the southern populations of *M. margaritifera* and, in particular, to assess the results of recent conservation activities.
3. To identify negative impacts on the southern populations of *M. margaritifera* and to reveal the most important (limiting) factor determining their current condition.
4. To develop conservation measures for *M. margaritifera* in terms of both practical conservation activities and the methodology of underlying scientific research.
5. To analyze the desirability of similar studies on other objects and to describe the principles and methods of the present study in general terms so that they could be broadly applicable.

   While this study was carried out, several papers on related topics were published (Zyuganov 2005a, b; Sergeeva et al. 2008; Bogatov 2009). Based on information available in them, two new objectives were set:
6. To critically assess the claim that there are three species of European freshwater pearl mussel (Bogatov et al. 2003) rather than just one (*M. margaritifera*) as commonly thought.
7. To critically assess the claim that pearl mussels are non-ageing organisms and that their larvae "cancel" the ageing of the Atlantic salmon making it stay longer in rivers (Zyuganov 2005a, b)

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Part I
European Pearl Mussel *Margaritifera margaritifera*: Background Information and Literature Review

Chapter 2
Biology, Distribution and Numbers of the European Freshwater Pearl Mussel *Margaritifera margaritifera*

Pearl mussels inhabit riffles of clean small rivers. These molluscs usually occur in shallow waters, not deeper than 2 m (Bjork 1962; Hastie et al. 2000). Very rarely they are found at a depth of 3 m or even 5 m (Hendelberg 1960; Oulasvirta 2010). In such instances, the molluscs have probably been washed away into the deep river areas by floods and survived there, or else some specific conditions suitable for them have formed in relatively deep rivers. The stream velocity in the pearl mussel habitats is 0.25–0.75 m/s, and the ground is represented by small gravel and sand.

Pearl mussels prefer soft water (Hendelberg 1960; Geist 2005). Only a few populations inhabit the rivers with water containing high concentrations of calcium and pH more than 7.5 (Lucey 1993, 2006). In pearl mussel streams of Norway, pH varies from 6.5 to 7.7. They can survive acidification down to pH 5 for a short time (Henrikson 1996).

Pearl mussel reproduces in summer. In July–August, males produce spermia (Hastie et al. 2003) flowing passively downstream. Fertilization occurs if they enter the siphon of the female. The embryos develop for 4 weeks and transform into glochidia larvae, which are about 0.07 mm in size (Hruska 2001). In late summer, glochidia leave the mollusc and try to attach to the gills of fish. The fecundity of pearl mussels is very high: each female can produce several millions of glochidia per season, up to 4,000,000 (Gum and Geist 2009).

Two fish species can be the hosts for pearl mussel larvae, the Atlantic salmon and the brown trout. Reports of other host species are unconfirmed. Glochidia can attach to the gills of other fish such as the perch *Perca fluviatilis* (Vlastov 1934) but cannot develop there normally. Pearl mussels have never been reported from rivers where salmon or trout are absent. It cannot be ruled out that two other European salmonids, the Arctic char *Salvelinus alpinus* and the taimen *Hucho hucho*, may serve as hosts for pearl mussels but the overlap of the habitats of these fishes and the pearl mussel is very small. Pearl mussels mainly infect juvenile fish, which survive after infection and acquire immunity. Repeated infection occurs rarely, if at all. Juvenile fishes are probably more suitable for the larvae because of their thinner gills (Bauer 1987b).

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The duration of various stages of the pearl mussel life cycle varies depending on the climatic conditions. Glochidia usually develop on fish gills for 2–3 months. After that their development stops for the winter, when their size does not change and accelerates again in spring. Late in spring or early in summer, the larvae transform into young molluscs, which leave the fish hosts and fall down to the bottom. If they find a suitable place there, they continue to develop. Young pearl mussels live for 5–10 years burrowing into the ground in a *hyporheic* zone, that is, the zone between the surface stream and groundwater (Orghidan 1959). They are sensitive to the condition of this zone. To ensure the existence of pearl mussels, this zone should be well washed and aerated and should consist of coarse sand and gravel. The availability of a suitable hyporheic zone is an essential prerequisite for the formation of the pearl mussel habitat. It is considered that this zone is formed especially successfully if the bottom is composed of objects of various sizes such as boulders, stones, sand and deadwood. Habitats of young mussels are easily formed between boulders or fallen tree trunks. Too much of small sediment particles are harmful for them. Pearl mussel juveniles can survive if the particles less than 1 mm in diameter make up less than 25% of the sediment (Hastie et al. 2000, 2001, 2003; Österling 2006; Geist and Auerswald 2007). The life in the hyporheic zone is considered to be adaptive: in other places, young molluscs are likely to be washed downstream to unsuitable places or eaten by predators. The juveniles attach to the substrate with the help of byssus. After reaching the size of 3–7 cm, pearl mussels become more resistant to these factors and move to the bottom surface. Adult mussels have a well-developed foot and use it for attachment in the stream. Having chosen a suitable place in a stable part of the stream, adult pearl mussels can live there for a long time, moving very rarely. Some adults continue to live in the hyporheic zone. Up to 34% of the population may remain under the bottom surface (Larsen et al. 2007).

Pearl mussels probably have few natural enemies. Though some carnivores and water birds may occasionally eat bivalves, they rarely eat pearl mussels. The sturgeon is probably the only European fish that can feed on large bivalves, but it inhabits larger rivers than those where pearl mussel live. Pearl mussels used to be very numerous in some rivers in the past, sometimes covering the bottom in several layers (Israel 1913) but these rich foraging resources were not used by any animal.

Freshwater pearl mussels inhabit only a minor part of the rivers, in which salmon and trout reproduce. Distribution areas of these three species overlap but do not coincide. Brown trout is distributed over almost all Western Europe, Asian Near East, Northern Africa, Caucasus, Eastern Europe and Western Russia. The eastern borderline passes at the upper reaches of the Volga and the Severnaya Dvina but in the north brown trout inhabits some small rivers flowing into the Barents and the White Sea eastwards from the Severnaya Dvina. Atlantic salmon mainly inhabits more northern rivers than brown trout. The southern borderline of its distribution area passes through Portugal, France and Germany; eastwards Atlantic salmon is distributed up to the Urals (Makhrov and Bolotov 2006; Snoj et al. 2011). Pearl mussels occur in the western and the north-western part of this territory. The southern borderline of their distribution area passes through Portugal, the central part of France, the southern part of Germany, Austria, the Czech Republic, Baltic

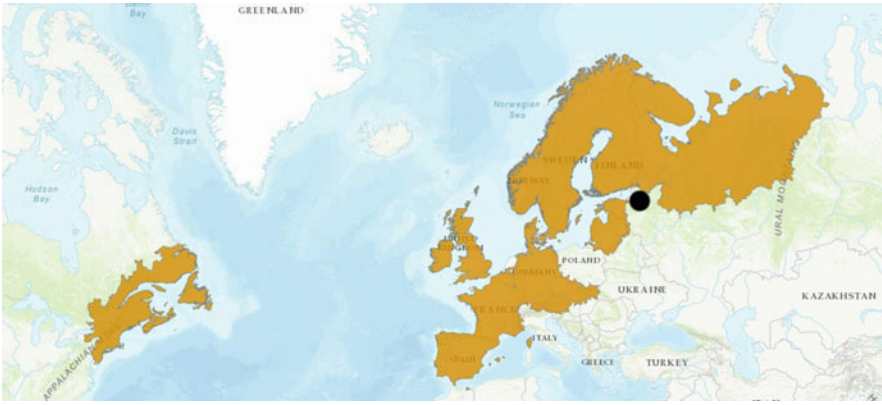

Fig. 2.1 Pearl mussel distribution according to the IUCN red list (Moorkens et al. 2018) and the location of the study area (●). (background map taken from iucnredlist.org with permission)

states and Northwest Russia (Degerman et al. 2009). The distribution pattern is a series of islets. In addition, *M. margaritifera* inhabit the rivers of North America flowing into the Atlantic Ocean. The Atlantic salmon inhabits them too but brown trout is absent there. Similar freshwater mussels belonging to other species occur in the basin of the Pacific Ocean.

The north-eastern part of the pearl mussel distribution is studied insufficiently. Some authors think that it covers a large territory up to the Urals (Moorkens et al. 2018; Welter-Schultes 2012) but this information is unconfirmed. Noteworthy, the study area of this work (or most of it) is not included in the distribution area of the pearl mussel (Fig. 2.1).

The host fishes of pearl mussels are similar in many respects. Both salmon and brown trout reproduce in the riffles of rivers. The females deposit eggs into redds (hollows they make in the bottom) and cover them with small stones after fertilization. This usually happens at the end of autumn. The fries hatch in spring, leave the redd and distribute over the riffle, where they live for a year or more. Juveniles (smolts) migrate downstream to a sea or lake during spring floods but afterwards return to the river to spawn. The details of migration and the duration of various stages of lifecycle vary depending on numerous conditions such as the river length, climate, area of lake or sea, etc. (Kazakov 1998). Unlike salmon, brown trout often spends the entire life in the river. If there is an obstacle for downstream migration such as a dam or a waterfall, a resident population may originate (*Salmo trutta* morpha *fario*). The same may happen in cold mountain rivers flowing into a warm sea, which is unsuitable for the brown trout. The southern populations of the brown trout are mainly represented by resident forms. As for the Atlantic salmon, only its males can usually live in the river permanently. Resident fluvial forms are an exception. Atlantic salmon is a more marine and northern species than the brown trout. Having left the river, it adapts easily to marine conditions and can migrate in the sea for long distances. Brown trout are slow to adapt to salty water and usually do not migrate far from the river mouths. In places where these two species coexist, the

Atlantic salmon is usually bigger than the brown trout. In the Caspian Sea and the Black Sea, where the Atlantic salmon is absent, the brown trout may become quite large (weight more than 30 kg) and similar to salmon. There is an opinion that the Atlantic salmon originated directly from the brown trout and that it happened relatively recently (Makhrov 2005).

Nowadays two-thirds of the European pearl mussel populations are associated with Sweden and Norway. There are 551 populations in Sweden and 350–400 populations in Norway (Degerman et al. 2009). In Scotland, which is rich in pearl mussel streams, 73 populations have been recorded (Cosgrove et al. 2016). However, the number of pearl mussel individuals is not known with certainty either in Scandinavia or in Scotland. There are probably still several million pearl mussels there though many populations have declined or become extinct. (There used to be 155 rivers with pearl mussels in Scotland.) Only 18 Scottish populations are currently considered as stable, and the juveniles occur only in 52. There are no corresponding numbers for Scandinavia but the situation there is likely to be similar to that in Scotland. In Russia, pearl mussels are mostly concentrated in one river, the Varzuga, in the southern part of the Kola Peninsula. There are about 144 million individuals there (Henrikson and Söderberg 2010). Most of the other pearl mussel populations in Russia remain unexplored.

Some pearl mussel populations exist owing to the brown trout, while others are associated with the Atlantic salmon. The "trout" populations are more numerous. In rivers where salmon and trout co-occur, there are two forms of mussels, the "salmon" form and the "trout" form. In such cases, salmon and trout usually occupy different river sections, with salmon keeping to more full-flowing sections with larger gravel at the bottom. Pearl mussel forms reflect these differences both in their own distribution and the reproductive season. "Trout" populations of the pearl mussel reproduce earlier (Larsen 2002; Salonen et al. 2017). In this way, two forms of the pearl mussel become reproductively isolated. Such differences are usually not reflected in the taxonomy in the English-language literature, while Russian ichthyologists traditionally use for such cases the category of the "morph" (Semyonov-Tyan-Shanskij 1910; Berg 1910), that is, a kind of variability occurring in different parts of the distribution area of the species. The pearl mussel may be said to be represented by the "salmon" morph and the trout "morph".

The populations of the Atlantic salmon and the brown trout differ in many respects such as migration routes, typical size, typical age, etc. Sensitivity to parasites is one such difference, the best-known case being the infection of salmon with the monogenean *Gyrodactylus salaris*. The Baltic populations are natural hosts of this parasite, and Baltic salmons do not die after infection, while the penetration of *G. salaris* into northern rivers may cause mass salmon mortality (Artamonova et al. 2011). Salmonid populations may also differ in the sensitivity to pearl mussel infection. It is considered that the infection is especially successful in native populations; in other words, pearl mussels infect fish from other rivers less successfully, as shown for some populations in Germany (Buddensiek 1995; Altmüller and Dettmer 2000, 2006) and Sweden (Söderberg et al. 2008). However, there is little information on this topic.

The lifecycle of freshwater pearl mussels is long. They start to reproduce at an age of 10–20 years and may live more than 100 years, though it is unclear how much more. There have been reports of 215-year-old (Zyuganov 2004) and even 280-year-old pearl mussels (Degerman et al. 2009). According to a review compiled by Austrian scientists, there is a reliable record of a 116-year-old shell found in Sweden, while records of 200 years and more are likely to result from erroneous methods of age estimation. In the Austrian rivers, pearl mussels live for 50–70 years (Moog et al. 1993).

The age of pearl mussels is usually determined by counting year rings of the shell surface. However, exact counts are problematic because the central part of the shell is often eroded and the rings are indiscernible there. The last rings on the edge of the shell are also poorly visible because they become progressively shorter with age. Another technique of age determination is based on counting stripes in the ligament joining the two valves. It is more accurate but can be used only on recently dead mussels. At present, a shell from Finland with 162 rings seems to be a record. A detailed description of this specimen is available and, taking into account the eroded part of the shell, its age was estimated as exceeding 180 years (Helama and Valovirta 2008). There are no detailed descriptions of shells aged more than 200 years (noteworthy, most of such exceedingly old shells have been reported by a single author, V. Zyuganov) (Popov 2009; Makhrov and Bolotov 2010).

It is thought that pearl mussels reach sexual maturity by the age of 20 years and that after that they continue to reproduce until they die (Bauer 1987a). At the same time, cases are known when the oldest individuals do not reproduce (Bauer 1987a). One may come across claims, especially in the context of studies dealing with ageing (see below), that the fecundity of pearl mussels increases with age. For some populations, however, no correlation between fecundity and age was revealed (Moog et al. 1993) but individual differences were found: females make yearly pauses in the reproduction. Only two-third of females (or even fewer) may reproduce simultaneously in some populations (Moog et al. 1993). A larger share of reproducing females, 80–100%, was also reported (Degerman et al. 2009).

Most of the data on pearl mussels was obtained in Western European countries. In Russia, the studies on them were scarce. For a long time, these molluscs were only mentioned briefly in the context of pearl fishing. Some northern populations of Russian pearl mussels were observed in the 1930s (Vlastov 1934; Makarov 1934; Graevskij and Baranov 1949). These studies were mainly related with attempts to organize the collection of raw materials for jewellery but some studies of pearl mussel biology were also carried out. Boris V. Vlastov (1934) conducted experiments on fish infection by glochidia showing that glochidia could attach to almost any fish except the pike (*Esox lucius*). Since observations were short (several days), the real host of the pearl mussel was not revealed. There were also experiments on pearl mussel acclimatization, with mussels being introduced into some brooks of Karelia (Makarov 1934) and into the Valdayka River of Novgorodskaya Oblast (Sal'dau 1940). The results were not monitored but they were likely to be negative since there are no salmonids in these steams.

After that, the studies on pearl mussels in Russia almost stopped. A new surge of activity occurred in the 1970s, when some studies on pearl mussels were initiated by B. F. Golubev, who worked in the Institute for Jewellery. The aim was to estimate the suitability of pearl mussels as a source of raw materials for jewellery (Golubev and Esipov 1973). Some pearl and mother-of-pearl were collected. Jewellers explored these materials carefully, regretting that the place of collection remained unknown because the collectors kept this information hidden. These studies resulted in a book on pearl structure (Korago 1981).

In the 1980s–1990s the physiology and the growth of pearl mussels were studied, and shell measurements were made (Alimov 1981). These studies were related to the so-called "comparatory method" of bivalve taxonomy (Logvinenko and Starobogatov 1971). Its advocates split the bivalve species based on the measurements of shell convexity. As a result of the application of this method, three species of the European pearl mussel instead of one were described: *Margaritifera elongata* (Lamarck 1819) ("elongated pearl mussel"), *Margaritifera borealis* (Westerlund 1871) ("north-European pearl mussel") and *Margaritifera margaritifera* (Linnaeus 1758) ("pearl-producing pearl mussel") (Bogatov et al. 2003; Starobogatov et al. 2004). At the same time, pearl mussels in the natural environment remained almost unstudied. Only one population was described in detail, the one in the Varzuga River in the Kola Peninsula. This river, famous for an exceptional abundance of Atlantic salmon, attracted the attention of fishery experts, and at some moment they also paid attention to the pearl mussels, which were also abundant there (Kazakov et al. 1992). Afterwards, the pearl mussels of the Varzuga and some neighbouring rivers came into the focus of studies by V. V. Zyuganov (Zyuganov et al. 1994). He authored the idea that the pearl mussel and the salmon live in symbiosis: salmon helps the pearl mussel to reproduce, while pearl mussels purify water in its spawning grounds. Another aspect of this symbiosis was, according to Zyuganov, the "abolition of ageing" of salmon by pearl mussel: infected salmons do not die after the spawning but survive owing to the substances coming from glochidia.[1]

Zyuganov repeatedly made the following claims: (1) Pearl mussels do not age at all but live up to 200–300 years. (2) When they die, they do so not because of ageing but because of excessive growth. At some moment the shell becomes too large, and the mollusc cannot keep it vertically in a stream; it falls on one side, cannot feed normally and dies. (3) Pearl mussels possess unique capacities for regeneration, regenerating after damage even when very old. They can be used as a source of drugs

[1] "Here we postulate that there is a wonderful case, when biochemical program of accelerated ageing and post-spawning suicide of the another species of salmon, namely, Atlantic salmon *Salmo salar* can be switched off due to the impact of a symbiotic organism, larvae of the freshwater pearl mussel *Margaritifera margaritifera*, which occasionally parasitize salmon gills" (Zyuganov 2005a, p. 435). "Pearl mussel concerns about the fact that the salmon host (adult fish or parr juvenile), which received portion of larvae in autumn, would not die, but would live in healthy condition as long as possible, at least up to the next summer, to provide the possibility for the small mollusc to complete its long metamorphosis in the gills of fish, leave the host and start free life on the river bottom" (Zyuganov 2005a, p. 437).

for the abolition of ageing in humans and for curing diseases and injuries such as cancer and hip fracture. Zyuganov started to produce an Elixir Arctica+, consisting of cognac, sticklebacks and gills of salmon infected by pearl mussels. This elixir is still being sold (www.arctic-plus.ru). Claims about abolition of ageing and symbiosis were published in the journals of the Russian Academy of Sciences (Zyuganov 2005a, b), have become known and are still being discussed (Taeubert and Geist 2017).

As the present study was carried out, I published a criticism of Zyuganov's ideas (Popov 2009). Two other authors joined the discussion focussing on the claim that the pearl mussel influenced the life cycle of the Atlantic salmon (Makhrov and Bolotov 2010). In short, no evidence of any such influence was found. In addition, there are indications that Zyuganov misrepresented some data. The main arguments against Zyuganov's ideas are as follows (Popov 2009, Makhrov and Bolotov 2010):

1. The Atlantic salmon and the brown trout are more widely distributed than pearl mussels. In most habitats of salmonids in Europe, pearl mussels have never been recorded and are absent now.
2. Pearl mussels infect mainly juveniles and do not "need" to "delay" adult salmons in the river by cancelling their ageing.
3. Survival or death of the Atlantic salmon depends on numerous other factors, e.g. the length of the river. In short rives, such as the Neva and the Vuoksa, salmons survive fairly often while in larger rivers this happens more rarely. In hatcheries salmons (uninfected with pearl mussels) can be kept for a long time (12 years and more) to be used annually for reproduction.
4. Zyuganov cited a paper by J. Flemming (1998) to support his claim that the Atlantic salmon spawns up to six times if infected with pearl mussels. That paper, however, reports a single case of such repeated spawning and does not mention pearl mussels at all (Flemming 1998).
5. Zyuganov misrepresented his own data. It is unclear why pearl mussel should "try to delay" salmon for several months in the river if glochidia parasite its gills only for 18 days (Zotin and Zyuganov 1994). To prove the positive influence of infection on salmon survival, Zyuganov (2005a, b) kept adult salmons in cages and tried to demonstrate that uninfected salmons died more rapidly. According to his data, after 5 days and 25 days of keeping in cages under stress the number of surviving infected salmons was greater than that of surviving non-infected ones: in two series of 60 individuals after 5 days all non-infected salmons died, but 32 infected salmons survived in one series, 8 infected salmons survived in the other one; in the other case after 25 days 60 non-infected salmons survived and 12 ones died, 70 infected salmon survived and 2 died. However, these experiments were designed without taking into account many important characteristics of salmonids. The presence or absence of glochidia was certainly not the only difference between the fish in the experiments. Numerous factors affect the survival of salmons under such conditions: size (large fish die faster than small ones), physiological condition, injuries during catching, duration and conditions of transportation, season, water temperature (salmons do not tolerate prolonged

exposure to hot water) as well as position and construction of the cages. In Zyuganov's experiments, salmons were caught from June to November in the course of 16 years in several rivers and kept in different devices (cages of two kinds or in blocked river sections). With this kind of experimental variability, no meaningful connection between salmon survival and mussel infection can be made. The story about the anti-ageing elixir is even less convincing. While cognac may have some effect on human health, there is no evidence that the addition of salmon gills alters it in any way.

The claim that pearl mussels do not age might seem acceptable in the context of a similar interpretation of age-related changes in other animals. Leonard Hayflick, a famous researcher of ageing, coined the phrase "Some animals age, others may not" (Hayflick 1996), which became very popular. An idea of "negligible senescence" is being developed: some animals age, but do so "negligibly" (Finch 1990, 1999, 2009). These ideas are used to substantiate projects aimed at the search of drugs prolonging life and preserving good health indefinitely (e.g. https://www.sens.org/, http://www.agelessanimals.org/https://www.skq-cosmetic.ru etc.). It is thought that if "negligibly ageing" animals do die, they do so not of age but of other causes. "The pearl mussel, which grows throughout its lifetime, perishes because the weight of the shell valve becomes too large for the muscle keeping the organism vertically at the river bottom. The muscle also grows with age but not fast enough to keep up with the shell growth. Giant turtles, which also grow throughout their lifetime and finally lose mobility, may die for a similar reason (disproportionate growth of the shell and the limb muscles). Both these species live for more than two centuries without showing any senile features. Bowhead whale can compete with them in respect of the lifespan. The reason of its death is unknown but we know that at a time scale of two centuries spontaneous L-D isomerisation of amino acids in the proteins of the crystalline lens must exceed 20%, which would be critical for the sight of an animal. It is known that crystallins are not replaced in an animal's lifetime. This means that isomerisation of amino acids may cause the disruption of the protein structure and the loss of transparency of the crystalline lens" (Skulachyov 2009, p. 128). (The fact that whales have a highly developed echolocation system suitable for navigation in the total darkness of the ocean depths is overlooked.) Lists of "non-ageing" animal species are being compiled. AnAge database compiled by a large team within the framework of a large-scale international project *Human Ageing Genomic Resources* (HAGR) (de Magalhaes et al. 2009) contains seven such species: olm (*Proteus anguinus*), Blanding's turtle (*Emydoidea blandingii*), Eastern box turtle (*Terrapene carolina*), Rougheye rockfish (*Sebastes aleutianus*), Red sea urchin (*Strongylocentrotus franciscanus*), Ocean quahog clam (*Arctica islandica*), Great Basin bristlecone pine (*Pinus longaeva*). The addition of one more species to this list owing to the activity of some enthusiasts is unsurprising.

It is difficult to check the ideas about negligible senescence because their authors often speculate on untestable phenomena. Ageing can be characterized using Gompertz–Makeham law, postulating that the probability of death increases with age, but it is difficult to assess the changes of this probability in nature. One gets an impression that lists of non-ageing animals are deliberately made in such a way as to preclude studies of their mortality. It is difficult indeed to assess the probability of death of rockfish or whales in the depths of the ocean. Pearl mussels seem to be an exception because they do offer a possibility of such study. Dead pearl mussels often remain in the same habitats as living ones, and the age at which they died can be estimated. The habitats of pearl mussels are compact (in comparison with those of whales) and may be studied. Finally, the pearl mussels are not exterminated by predators. Proceeding from these ideas, a study aimed at assessing the ageing or non-ageing of pearl mussels was carried out within the framework of the present research (Popov and Ostrovsky 2011). It seems important for the evaluation of the reasons for pearl mussel decline: if the pearl mussels can live forever, the processes associated with the decline or restoration should apparently unfold differently in their populations than in those of "usual" animals.

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