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Differences in the Lifespan of the Freshwater Pearl Mussel *Margaritifera margaritifera* as Evidence for the Infeasibility of Negligible Senescence (Based on Data for St. Petersburg and Leningrad Oblast)

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Abstract—It is considered that the main specific feature of organisms with negligible senescence is that the probability of adult individuals dying does not change with their age. However, there are almost no direct observations that could either confirm or refute this statement; moreover, such data are unobtainable for many species. From this standpoint, we have studied the freshwater pearl mussel, a species displaying signs of negligible senescence (continuous growth, long maximal lifespan, and the ability to reproduce during its entire life). Examination of individuals that have died in a natural environment suggests that the probability of their death increases with age, i.e., this species is subject to aging. This fact, as well as the gaps in substantiation of the concept of "negligible senescence", shows that the concept in question is erroneous.

Keywords: "negligible senescence", freshwater pearl mussel, longevity, lifespan
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The concept of "negligible senescence" has become an integral component of biogerontology [12]. It is believed that some organisms are not subject to aging; therefore, studies of these organisms can provide data on how to control the negative manifestations of human senescence. This has spawned large-scale research projects, for example, a project involving rockfish (genus *Sebastes*), performed by 12 American and 2 European universities [15]. An even more ambitious foundation—"Strategies for Engineered Negligible Senescence" [28]—was organized under the slogan of "negligible senescence". The creators of the foundation believe that the human aging can be reduced to negligibly small levels and the human lifespan can be increased in the near future. In addition to rockfish, some sturgeon, turtle, and bivalve mollusk species are considered to be nonaging organisms. The following features are regarded as characteristic of organisms displaying "negligible senescence": they live for a long time, they continue growing during their entire lives, and their probability of dying does not change with age, i.e., their aging approaches zero. However, factual justification of the "negligible senescence" concept has some gaps. There are no units for measuring senescence similar to units of length or weight; therefore, the claim of "zero" senescence is insufficiently grounded. There are also no data demonstrating that nonaging organisms actually never meet a natural death but are rather killed by predators, pathogens, or some other external forces. The belief that the probability of dying does not change with age is based on examination of individuals who have lived a long time that displayed no distinctions from young individuals in their state of health; however, there are no data on the probabilities of their dying under natural conditions, as well as on changes in this parameter with age. Such data are completely unobtainable for many species. First, this is because some of these animals live in the ocean and, in addition, at a depth of several kilometers, which hinders their being observed. Second, humans consume these species a great deal, which prevents determination of their lifespan. However, such information is important for estimating the actuality of nonaging: if nonaging organisms can meet a natural death, if they have a mean and maximum lifespan, and if the probability of living to the maximum age differs for individual members of population, then their aging is not "zero", but rather somewhat slow as compared with other organisms.

The data of this kind can be obtained by studying the European freshwater pearl mussel *Margaritifera margaritifera* (L.). This species completely meets the above definition of "nonaging" organisms and is sometimes included in the corresponding lists [8, 25]: pearl mussels live over 100 years without losing the ability to reproduce, grow during their entire lives, and the individuals of advanced age display no noticeable distinctions in viability from young individuals.

Fig. 1. A studied colony of freshwater pearl mussels.

Unlike the populations of the above-mentioned animals, pearl mussel colonies are frequently rather compact, located on certain river sites [24]. The shells of dead individuals lie near living individuals, and their ages and circumstances of death can be determined; in addition, predators barely feed on freshwater pearl mussels. The goal of this work was to determine the death age of freshwater pearl mussels and their probability of dying at a young age. Based on these data, we estimate the viability of negligible senescence.

MATERIALS AND METHODS

This study was performed on the territory of Leningrad oblast. Rivers with a high likelihood of finding freshwater pearl mussels were selected based on museum lists, archive materials [3], questionnaire data, and varying indirect evidence. In the chosen rivers, sites with an area of 500 m^2 suitable for pearl mussel habitats (with swift flow and a clean nonsilted bottom) were examined with the help of an aquascope. When pearl mussels were found, the density of mollusks was determined, the environmental state was assessed, and the sources of adverse effects were detected. One of the rivers presenting special interest from the standpoint of the stated problem was studied in a more comprehensive manner, namely, all the mollusks were counted and the entire river bed was examined.

To estimate the lifespan, the shells of the dead mollusks were collected and measured. The age was determined according to the conventional method by counting the annual growth rings of the shell [7, 19]. To calculate the mollusk's age, the maximal number of the rings on both valves was added to the age determined for the central eroded region of the shell, where growth lines were not preserved. For this purpose, the length of the eroded area was compared with the shell size of six-year-old live mollusks with well-distinguishable annual rings. Counting of the annual lines on the ligament (an elastic cord connecting the valves) was used as a control for the data obtained by counting the annual rings on the shell. Nonetheless, use of the ligament was limited, since only a small fragment of it remained in the majority of the examined shells (over 20 years old).

RESULTS AND DISCUSSION

In total, eight rivers inhabited by freshwater pearl mussels were found. The density of pearl mussels in seven of the rivers was low, and they were localized in individual rapids. Dead pearl mussels there were very few in number because of the small population sizes and shift of the shells by flow to deep regions. The conditions for study were very favorable in only one river of the eight: this river is rather shallow (usually 20–60 cm) and has a small width (3–5 m), clear water, predominantly sandy bottom, and relatively slow flow (about 0.3 m/s); it lacks any pronounced rapids; and the pearl mussel population is very high (about 40000 individuals). In some sites, the mollusk density reached 1000 individuals per square meter (Fig. 1). The recorded density and population suggest very favorable conditions for pearl mussels (for comparison, Austria has over 20 rivers inhabited by this species, and the total pearl mussel population there is about 70000 [16]). As for the density, we have not found in the current literature any information on analogous colonies. In Western Europe, such colonies were observed only several hundred years ago [10, 20, 21]. The dead shells were located immediately near the living individuals. They were not carried away, but were gradually covered with sand and dissolved in water. All the dead shells suitable for determining age were collected at a site with a length of 100 m containing about 10000 mollusks. In total, there were 127 shells. Age determination demonstrated that the larger part of the mollusks died at the age of 30–50 years (58%); 27% of the individuals reached 30 years and 9% lived to the age of 60 years. Those who had lived a long time were extremely rare: only one individual 95 years old was found (Fig. 2)

As was expected, the mollusks grew at different rates: the shell sizes of 30- and 50-year-old mollusks were similar, and the 95-year-old individual was not the largest representative. The differences between the sizes of the dead shells display a distribution close to the normal one (table, Fig. 3).

These data show that the probability of pearl mussels dying changes with age: the probability of living to an age of 100 years is smaller than to the age of 50. Quite likely, if samples of a larger volume were collected, it would be possible to distinctly trace a Hompertz–Makeham distribution. This means that the aging process takes place in this species: either the ability to withstand negative external impacts decreases or some processes in the body are impaired, making impossible further existence. The rate of this

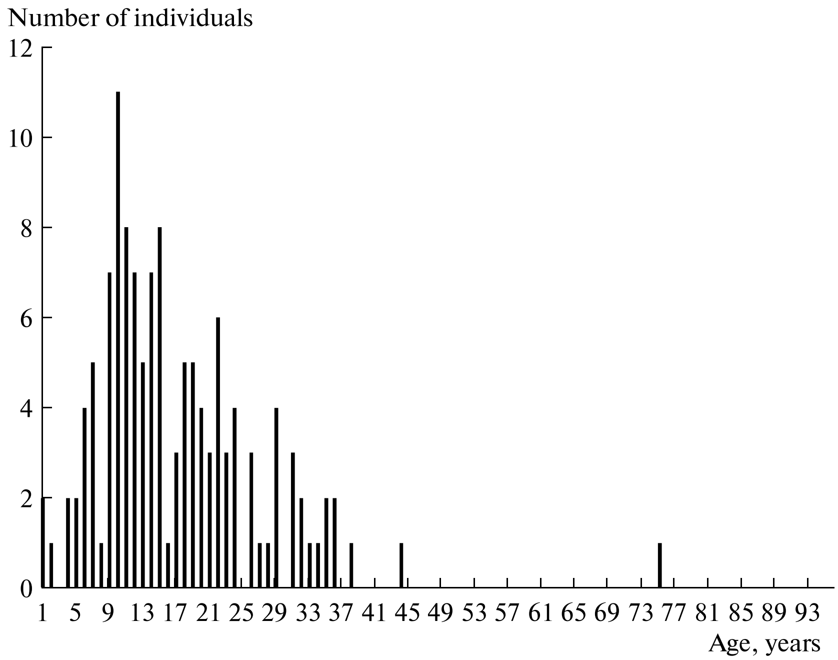

Fig. 2. Differences in the age of dead pearl mussels.

process is not negligibly small, but rather similar to that in humans.

Analogous data are also known for other populations studied earlier by various researchers. According to Hastie [17], the number of dead shells of each age cohort approximately corresponds to the number of live mollusks in this cohort (with certain corrections for shells carried away by water flow and dissolved), i.e., pearl mussels die at various ages. For example, pearl mussels in Austria usually live for 50–70 years [23]. Longevity extremes are different in different areas: pearl mussels older than 65 years have not been found in the southern (Spain) [26], whereas they live longer in the north.

There are some data on record lifespans of 190, 200, or more years [29]. However, some authors believe that such estimates are erroneous [23]. A precise age estimation of such aged individuals is impossible, because the central part of their shell is damaged and the latest annual rings are hardly distinguishable. It is likely that the only reliable record at the moment is a dead pearl mussel found in the north of Finland with 162 annual growth rings. Based on the calculations and measurements of the shell region with damaged rings, its age was approximately determined as exceeding 180 years [18].

Thus, pearl mussels can live 180 years under conditions favorable for longevity—in an oligotrophic river with a low water temperature [24] providing for a low metabolic rate; however, no one has yet found, for example, a 300-year-old pearl mussel. This means that age-related changes leading to death take place in organisms of pearl mussels similar to the other animals. For example, if a common long-living hedgehog succeeds in living to the age of 11.2 years [27], it is improbable that there will be a hedgehog that will live for 50 years. It is impossible to prove that it is impossible to exceed the highest recorded age; however, it is similarly impossible to prove that a hedgehog can live for 50 years. Thus, it is reasonable to consider that the maximum lifespan of a hedgehog is about 11–12 years and that hedgehogs cannot live longer even under favorable conditions because aging processes take place in their organisms. Therefore, let us assume that the maximum lifespan of the pearl mussel is 180 years, while it also has a mean lifespan, which is considerably shorter. There are no grounds to consider that aging is absent in pearl mussels. If this aging does not manifest itself as does aging in mammals, this is connected with the large number of differences in the structure and physiology of these animals.

It is important to pay attention to that fact that, if researchers came across only 100-year-old pearl mussels, then the characterization of their aging would not differ at all from the characterizations of the above-mentioned negligibly aging organisms that actually figure in gerontology due to such fragmentary data. Thus, the resulting set of species is rather strange. For example, the list of negligibly senescing species includes two species of American turtles (*Emydoidea blandingii* and *Chrysemys picta*), although it is unclear what their principal difference is from other turtles [13]. The fact is that the "nonaging" turtles were for many years observed in a reserve, where it was noticed that they lived for a long time and continued to lay eggs. The researcher who studied these turtles retired, Size and age of the studied shells

Age, years	Number of shells	Shell length, mm
21	2	69, 78
22	1	92
24	2	82, 100
25	2	99, 110
26	4	74, 94, 97, 103
27	5	95, 97, 99, 104, 116
28	1	96
29	7	88, 91, 93, 95, 96, 100, 100
30	11	85, 91, 98, 100, 101, 103, 103, 103, 105, 105, 115
31	8	94, 102, 104, 105, 105, 107, 110, 117
32	7	95, 97, 101, 102, 105, 112, 117
33	5	90, 93, 95, 96, 100
34	7	95, 106, 107, 108, 108,114, 115
35	8	91, 93, 101, 102, 103, 109, 110, 118
36	1	96
37	3	100, 101,112
38	5	99, 101, 109, 116, 121
39	5	90, 92, 102, 103, 110
40	4	99, 107, 107, 112
41	3	98, 120, 125
42	6	96, 106, 109, 110, 120, 125
43	3	104, 130, 130
44	4	110, 114, 115, 120
46	3	102, 116, 119
47	1	107
48	1	110
49	4	103, 124, 125, 132
51	3	121, 125, 128
52	2	95, 123
53	1	126
54	1	121
55	2	120, 123
56	2	120, 134
58	1	125
64	1	113
95	1	130

the observations were not continued, and data on how the probability of their dying changed with age are absent [13]. The rockfish appeared in the list of nonaging species in a similar manner. An expert in managing research projects read the well-known book by Hayflick and noticed the phrase stating that some organisms age, whereas others do not. Correspondingly, the expert turned to the problem of aging and selected an object that attracted attention by virtue of the data on its great age and appeared convenient for several reasons, while no comprehensive analysis of the animal world's diversity and data on other animals was performed [15]. However, some other fish species could be taken as such an object. For example, the common cod could also be included into the list on nonaging species. This fish has been harvested intensely for several centuries and for a long time has had almost no possibility of living to the maximum age. However, such cases may have taken place in the past: 100–200 years ago, considerably larger individuals were caught than we can imagine now. For example, a cod with a weight of 211 pounds was caught in 1895, whereas 50-pound fish today are regarded as large and a 100-pound cod individual is exceedingly rare [11].

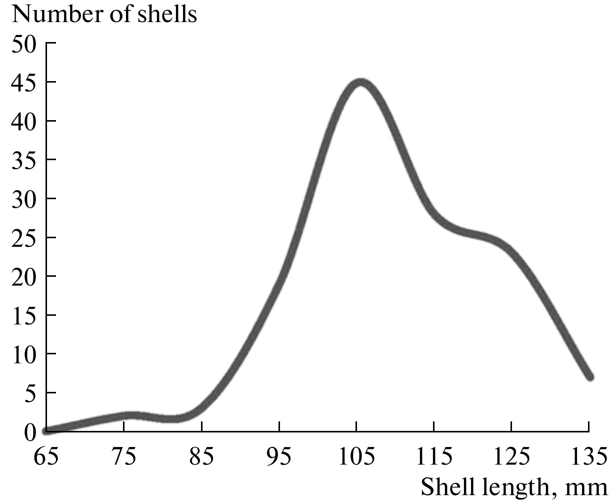

Fig. 3. Differences in the sizes of studied dead shells (n = 127).

Recently, depletion of biological resources has led to commercial catching of fish species previously fished very rarely that have had the possibility of living for a long time. Their specific biological features are regarded as exotic and requiring special attention, although there are no grounds to consider that their aging mechanisms fundamentally differ from the aging mechanisms of many other fish species: there are only differences in the growth and development rates connected with the differences in the temperature and feeding resources of the corresponding biotopes. Moreover, the tissue samples of "nonaging" fish brought by fishermen were mainly studied, while there are no data on the natural mortality of these fish. Since changes in the probability of natural death with age were not observed, the main principle for determination of nonaging animals cannot be implemented. It is substituted for by other characteristics, such as long maximum lifespan, retention of ability to reproduce, and good health at an advanced age. However, these principles are insufficient. First, if the maximum lifespan of a species is longer than that of other species, this does not mean that senescence is absent and that representatives of this species can live forever. Second, a decrease in the ability to reproduce and cessation of growth are only signs of age-related changes in some species, for example, in humans. As for the other "nonaging" species, they considerably differ from both humans and all other mammals. In other words, it is inappropriate to evaluate turtles and mollusks using the standards applicable to mammals. Third, preservation of sound health in some individuals at an advanced age in no way proves that senescence is absent in all the remaining representatives of this species, all the more so as the corresponding tests are considerably incomplete.

The belief in the existence of nonaging animals has so strongly entered the minds of gerontologists that several examples are referred to without indicating the corresponding sources or cited in an incorrect manner. Consequently, what we observe is an amplification of errors. For example, the bowhead whale is frequently mentioned in this connection, since it lives for over 200 years and does not appear to age [8]. Indeed, the age of one whale was estimated as 211 years old [14]; however, there are almost no data on senescence manifestations or their absence in this individual. The age was estimated based on examination of eye tissue specimens brought by a hunter (the hunter believed that this whale was old, because its meat and fat were tough). The fact of "recognition" of the potential immortality of the hydra [1] is mentioned in an analogous manner. The hydra's body has a zone of cells that constantly divide and gradually restore worn and lost cells. However, the fact of immortality cannot be regarded as proved, with which the author of the cited paper partially agreed [22]. The hydras were observed for four years, and some age-related changes were nonetheless recorded, although mortality remained insignificant. The author gave indirect evidence that presupposed certain grounds to assume that the hydra is potentially immortal.

As for freshwater pearl mussels, incorrect information about them has been reported in detail; in particular, a fantastic picture of their death is given—as they growth, the shell increases until the mollusk lacks sufficient muscle strength to keep it in a vertical position, so that the mollusk falls and dies [8]. This hypothesis has no real confirmation, since pearl mussels usually dig into the bottom so that only a small part of the shell remains above and lives in the part of the river bed where the medium is especially stable; thus, they do not require exertion to keep the shell in the same place, and, moreover, in addition, the shell is not overly heavy. According to our data, pearl mussels usually die when their shell has not yet reached the maximally possible size (see Fig. 3). In addition, those who hold the opinion that nonaging organisms (not only pearl mussels, but also whales and turtles) are killed by their growth fail to take into account the fact that, if these species have anything that can be considered negligible, it is increase in size in an advanced age. This increase becomes ever smaller with time, and the body size almost does not change. In adult pearl mussels, the annual increase in size amounts to fractions of millimeters.

"Nonaging" organisms are used to a certain degree when grounding various concepts associated with senescence [1, 2, 4, 5, 8, 9]. When such examples are excluded, many ideas, if not all, appear either incorrect or incomplete. However, these concepts are not just theoretical constructs divorced from practice, but are directly connected with the development of drugs and programs for controlling the negative manifestations of senescence. Here one can come across numerous careless statements. For example, the documents of the "Strategies for Engineered Negligible Senescence" foundation contain assurances that human senescence will be almost eradicated and any person will be able to live for 150 years or more while retaining sound health—the only thing they need being the necessary funding for the foundation. Such declarations contradict the common opinion that absolutely everything in nature changes, ages, and ceases to exist. Not only living objects, but also inorganic ones, are subject to change; mountains gradually fall, waterfalls–become lower, rivers become shallow and slow their flow, lakes also become shallow and transform into bogs, and so on. Living organisms change considerably more quickly; their senescence manifests itself more obviously; and, therefore, it is difficult to believe that this process can be canceled. One might think that the time of searching for Philosopher's Stones and elixirs of perpetual youth would have long ago passed. Yet such quests are take place now with all the characteristics of the scientific community [6]. On the other hand, outside the scientific community, numerous suspicious drugs against senescence, the action of which cannot be verified, are produced. Even scientific papers frequently affirm the possibility of a complete absence of senescence, encouraging these activities, declaring that all-mighty human intelligence can arrest the universal laws of nature, such as the inevitability of changes in living objects and their aging. However, declarations of success in the near future should have more solid grounds than fragmentary data on a few animals that can live for a long time.

It is appropriate to note here that the detection of "nonaging" organisms not only leads to useless wasting of funds and effort, but also can cause significant damage to nature. For example, there has existed and, perhaps, still exists production of powder of dried shark cartilages proposed for treating cancer. Experts believe that this is as useful as swallowing of sequoia sawdust to grow taller; however, the unverified data on the absence of cancer in sharks (which was later refuted) induced the corresponding business. As a result, thousands of sharks were annually killed. Along with the demand for shark fins as a gourmet item, this led to considerable damage to the shark population, and now sharks are passing from a commercial to a protected and endangered species [11]. Attention attracted to turtles, rockfish, and pearl mussels may have the same consequences.

CONCLUSIONS

Despite freshwater pearl mussels have several specific features regarded as indications of "negligible senescence", the probability of these mollusks dying does change with their age—namely, it increases—i.e., the studies of the model object do not confirm, but rather refute, the concept of negligible senescence. Since no other data are available on age-related change in the probability of "negligibly senescing" organisms dying, the currently available information once more favors the conventional opinion on senescence: senescence is inevitable and cannot be completely avoided, while "negligible senescence" is a myth and, moreover, a harmful one, as it misinforms the public and discredits the scientific community.

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