Catastrophic senescence of the Pacific salmon without mutation-accumulation

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Abstract

We derive catastrophic senescence of the Pacific salmon from an aging model which was recently proposed by Stauffer. The model is based on the postulates of a minimum reproduction age and a maximal genetic lifespan. It allows for self-organization of a typical age of first reproduction and a typical age of death. Our Monte Carlo simulations of the population dynamics show that the model leads to catastrophic senescence for semelparous reproduction as it occurs in the case of salmon, but to a more gradually increase of senescence for iteroparous reproduction.

Keywords: population dynamics, aging, Stauffer model, Monte Carlo

1 Introduction

According to the evolutionary theory of aging senescence is ultimately caused by a declining pressure of natural selection as one gets older and older [1]. One manifestation of senescence (which can be most easily handled on the computer) is an increase of mortality with age or, more precisely, a decrease of survivors at age \( a \), from an initial population of newly born offspring at time 0. Senescence is attributed to several factors like environment, metabolism, and, most important, by several genetic mechanisms. Two major genetic mechanisms, which are under discussion and need not necessarily exclude each other, are antagonistic pleitropy and mutation-accumulation. Based on the latter mechanism, i.e. on the hypothesis of an increase of deleterious mutations with age, Penna et al. (1995) proposed a bit-string model [2], which nowadays is widely used for Monte Carlo simulations of aging, because it predicts many experimentally observed features of senescence (for a recent review...
see [3]). One of the successful predictions is the catastrophic senescence for the Pacific salmon.

Pacific salmon show the most dramatic manifestation of aging. As semelparous individuals they breed only once in their life, all at the same age, with plenty of offspring, and die a few weeks later. In contrast to salmon, iteroparous individuals breed repeatedly and age more gradually.

2 The model

Recently Stauffer has proposed a model which is based on the postulate of a minimum reproduction age and a maximal genetic lifespan [4]. Only these two numbers are transmitted from generation to generation, with certain mutations, by asexual reproduction. The population consists of $N$ individuals $i$ ($i \in 1, ..., N$) initially. Each individual is characterized by three integers: its age $a(i)$, its minimum reproduction age $a_m(i)$ and its maximal genetic lifespan $a_d(i)$ with $0 \leq a_m(i) < a_d(i) \leq 32$. The maximal lifetime is restricted to 32 time units (called years), the minimum reproduction age may be chosen between zero and $a_d(i) - 1$. Within these constraints the values of $a_m(i)$ and $a_d(i)$ are randomly mutated for an offspring by $\pm 1$, away from the maternal values, and for each child separately. These mutations realize some kind of antagonistic pleiotropy in the sense that a shorter lifespan or a later reproduction age increase the birth rate. (“Parents die to make place for their children.”) After an individual has reached its minimum reproduction age, it gives birth to one offspring with probability $b$, chosen as $(1 + \epsilon)/(a_d(i) - a_m(i) + \epsilon)$ with $\epsilon = 0.08$ for convenience. Independently of the genetic death, which happens automatically and unavoidably if $a(i) = a_d(i)$, at each time interval an individual can also die “accidentally”, with the Verhulst probability $N/N_{max}$. $N_{max}$ is called the carrying capacity to account for the fact that any given environment can only support populations up to some maximal size $N_{max}$. Otherwise the individuals die because of food and space limitations. Stauffer’s model shows the basic features required for senescence. The age distribution shows an increase of mortality with age. Moreover, a self-organization of a typical age of first reproduction and of death is observed, similarly to Ito’s self-organization of a minimum reproduction age in the framework of the Penna model [3].

In this paper we apply Stauffer’s model to the population dynamics of Pacific salmon and check whether the model is able to reproduce the qualitative features of catastrophic senescence. For a given value of $N_{max}$ and an initial population of $N$ individuals we specify $a_m(i) = 1$ and $a_d(i) = 16$ for all $i = 1, ..., N$ as initial values. One Monte Carlo iteration then consists of the following three steps that we call “deaths”, “births” and “aging”.

• In the first loop of “deaths” over all individuals, each individual dies either with the Verhulst probability $N/N_{max}$, or, if it survives space and food limitations,
because it has reached its maximal genetically allowed age $a_d(i)$. Otherwise it survives. The initial population of size $N$ gets reduced this way.

- In the second loop of “births” over all individuals, each individual gives birth to $n_b \geq 1$ offspring with probability $b = 1.08/(a_d(i) - a_m(i) + 0.08)$, provided the maternal age is not below the minimum reproduction age and equals a fixed given integer $a_0$ with $0 \leq a_m(i) \leq a_0 < a_d(i) \leq 32$ and $a_0(i) = a_0$ is chosen the same for all individuals. The latter condition obviously accounts for the specific features of salmon which breed only once and all at the same age. It turns out that the choice of the number of offspring $n_b$ is not arbitrary, because the second condition is so restrictive that the population only survives for sufficiently large $n_b$. Now the values of $a_m$ and $a_d$ for the offspring are mutated away from the maternal values, again at each time interval by $\pm 1$ for each child separately as in Stauffer’s model, but with probability $p_s < 1$. This way the mutations become suppressed with probability $1 - p_s$, to account for the experimental fact that the time interval for reproduction of salmon is rather narrow for any generation. Unless mutations are suppressed, they have the tendency of spreading the first reproduction age within a broader time interval. On the histograms of aging this has a similar effect as iteroparous reproduction. The question is whether the minimum reproduction age adjusts itself to a value which is self-consistent with the prescribed fixed reproduction age $a_0$. The remaining mutations should drive the initial values for $a_m(i)$ towards $a_0$.

- In the third step of a single iteration, the population which remains from the first two steps ages by one time unit, $(a(i) \rightarrow a(i) + 1)$. The population size and averages over the individual minimum reproduction ages and the maximal lifespans are stored. From a certain number of iterations on also the individual ages $a(i)$, $a_m(i)$ and $a_d(i)$ are stored in histograms as a function of the time interval $j$, $j \in (1, ..., 32)$.

Now the iterations are repeated a number of $t$ times until the population dynamics has stabilized and the fluctuations in average values are negligibly small.

3 Results

Figs.1 and 2 show various histograms of ages $a_d$ for genetic death which were obtained for the following choice of parameters. In Fig.1 the carrying capacity $N_{max}$ is chosen as $2 \cdot 10^5$, $N$ initially as $N_{max}/2$. The number of iterations $t$ is $2 \cdot 10^4$. The actual reproduction age $a_0$ is fixed to 6, and the number of births $n_b$ which an individual can give to offspring at the age of 6 is 12. Mutations of the minimum reproduction age of offspring are suppressed by $80%(+)$, $95%(x)$ and $99%(\star)$, respectively. The histograms show a clear self-organized maximum of genetic death at an age of 7. In discrete time units this means that death occurs most likely
directly after reproduction. The peaks are the sharper the stronger the suppression of mutations. The qualitative shape of the histograms stays the same when \( N_{\text{max}} \) is varied over several orders of magnitude. Already after \( \approx 100 \) iterations the population dynamics stabilizes in the sense that the population size oscillates regularly between stable minimum and maximum values. These regular oscillations build up randomly during the first 100 iterations and then are reproduced with the period \( a_0 = 6 \). The value of \( n_b = 12 \) is the minimal integer so that the population with 95\% suppression of mutations survives as a whole. For smaller \( n_b \) it dies out after a few iterations. This feature is in qualitative agreement with nature. Pacific salmon produce plenty offspring once they breed to compensate for the restrictive conditions on \( a_m \) and \( a_0 \) independent of \( i \). The maximum of the histogram of ages for the minimal reproduction age lies at an age of 6, consistent with the prescribed value \( a_0 \).

In Fig.2 we compare histograms of ages for genetic death between iteroparous (full line) and semelparous (dashed line) reproduction. The dashed curve was obtained for \( N_{\text{max}} = 2 \cdot 10^5 \), \( t = 2 \cdot 10^4 \), \( a_0 = 6 \), \( n_b = 12 \), \( 1 - p_s = 99\% \). Again it shows a sharp peak at the age of 7. The histogram for iteroparous reproduction was obtained for \( N_{\text{max}} = 2 \cdot 10^7 \), \( t = 2 \cdot 10^4 \), reproduction can happen at any age between \( a_m(i) \) and \( a_d(i) \), (i.e. \( i \)-dependent and possibly several times in one life), \( n_b = 1 \) and no suppression of mutations of \( a_m(i) \) and \( a_d(i) \) for the offspring. The hundred times larger value for \( N_{\text{max}} \) was chosen for convenience to get comparable numbers for \( a_d \) in spite of the different reproduction conditions. The maxima of both curves are self-organized, but in the iteroparous case the maximum is much broader, going along with a gradual increase of senescence with time or a less rapid aging than in the case of salmon, compatible with the Penna model [2].

4 Summary

Stauffer’s model based on the two postulates of a minimum reproduction age and a maximal genetic lifespan predicts the catastrophic senescence for the Pacific salmon in a qualitative way. The larger the suppression of mutations, the faster die the individuals after reproduction, and the larger is the number of births in one reproduction step which is necessary to sustain the species. The self-organized maximum of the histogram of ages \( a_m \) is self-consistent with the only allowed age \( a_0 \) for reproduction, a restriction that is used as an input. Stauffer’s explanation works without mutation-accumulation, whereas mutation-accumulation was an essential ingredient in the Penna model. Therefore, differently from what the success of the Penna model might have suggested, mutation-accumulation does not seem to be essential for explaining gross qualitative features of senescence.
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Figure 1: Histogram of ages for genetic death; mutation probability 20(+), 5(x) and 1(⋆) percent
Figure 2: Histogram of ages for genetic death: iteroparous (full) and semelparous (dashed) reproduction