DYNAMICS OF TRANSITION TO CHAOS IN STRUCTURED BIOLOGICAL POPULATIONS

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Abstract

This work proceeds with research series of natural evolution in biological population with marked seasonality of life-cycle. The modeling analysis of connection between ontogenesis duration and mode of dynamic behavior of biological community (the structure and dimension of chaotic attractors arising) was conducted. It is shown, that during the process of natural evolution of natural population with designated seasonality of life circle the nonrandom transition from stable regimes of populations dynamics to fluctuations and chaos (the pseudo stochastic regimes) have to occur. In case of more complicated nonlinear models of dynamics of populations with age structure the increasing of average individual fitness leads to arising of chaotic attractors which structure and dimension changes with model parameters modifications. The increasing of duration and complexity of ontogenesis in average does not increase the degree of attractors chaotization. The resonant values of reproductive potential for long ontogenesis have been found, and these values give the windows of regularization in chaotic dynamics.

Key words

Age structure, attractor, equilibrium, evolution, population size, stability

1 Introduction

The life cycles of many biological species have pronounced temporal periodicity which is as a rule associated with the seasonal periodicity of Earth climate. The main majority of such species has well-defined (quite short) breeding season in which the each local population consists of discrete non-overlapping age groups (during which their local populations can be considered as a set of discrete non-overlapping age groups). In many cases the size of each of these age groups is defined basically by the sizes of previous age groups in the previous reproduction period. For annual plants, many insect species, some fish species, am-phibious and reptiles each separate population is single age class and neighboring generations of such population are non-overlapping. In the '70s detailed investigations of homogeneous models of population dynamics have appeared; these investigations were carried out by Far-Eastern researcher A.P. Shapiro [Shapiro, 1972; Shapiro and Luppov, 1983] and his American colleague R.M. May [May, 1975]. The investigation of chaotic regimes of dynamic behavior found in Mays, Rickers, Hassels etc. models [Ricker, 1954; Hassell, Lawton and May, 1976] allows us to visualize some general regularities appearing with sufficiently large values of reproductive potential and degree of ecological limitation. If this chaotic behavior begins from not great value of population size, then there will be the slow growth of population size during large number of generations; then will be a sharp rise following by considerably greater decrease of population size (to level not far from initial) in next generation. However these periodic changes do not return population precisely to initial level. So despite of evidently periodic character of number dynamics, there are not any total coincidence neither in number values nor in number of generations in phase of increase. Such not clearly periodic behavior of number is typical for many natural populations of higher organisms [Ruxton, Gurney and de Roos, 1992; Getz, 2003; Lebreton, 2006; Reluga, 2004], especially for insects (for example, locusts, grasshoppers, nightflies).

2 Dynamics of population size in age-structured species

The simplest population dynamics models consider changes of whole population number only, assuming that different generations of the population do not overlap. But such conception is not correct, when lifetime of each generation is essentially longer then time between breeding seasons is. In this case each local population consists of individuals from different age groups during breeding season. So, it is natural to consider the

number of each separated age group as a model variable. The treatment for clustering the population is defined by the characteristics of biological species.

2.1 Model of population consisting of two age-classes

Let's consider the model with age structure, which may be presented by the set of two age classes, there are junior and elder. The junior age class consists of immature individuals and reproductive part consists of individuals participating in breeding process.

Let's define X_n - the number of individuals in junior age class in n-th breeding season, and Y_n - the number of individuals in reproductive part of population. The breeding season comes to end by the appearing of newborn individuals of next generation. Let's assume that during the time between two reproductive periods the individuals from junior age class reach the age of reproductive part, and newborns (or larvae) - to junior. Also let's assume that fitness and reproductive potential of reproductive individuals are not dependent on their age. These assumptions are correct for organisms with not great lifetime consisting of two or three breeding periods; such as many insects, fishes, small mammals, biennials or triennials and others.

Let's define $a(Y)$ - the product of first-year offsprings birth rate and fitness; $f(X)$ and $g(Y)$ the fitness of immature and mature individuals respectively. Here we'll limit the consideration by the situation, when effect of limiting factors concentrates on the stage of immature age class, i.e. $a(Y) \equiv a$, $g(Y) \equiv c$. The constants a and c are positive and $c < 1$. Usually the density-dependent factors limit the population growth, so let fitness of junior age group $f(X)$ be the decreasing function (i.e. $f'(X) < 0$) and it will tending to zero when its argument indefinitely grows. So we can receive the dynamics equations which describe the numbers of discussed age classes in neighboring generations:

$$\begin{cases} X_{n+1} = aY_n \\ Y_{n+1} = X_n f(X_n) + cY_n. \end{cases} \quad (1)$$

With the assumption $f'(X) < 0$ system (1) has single nontrivial stationary solution, which is defined from equations:

$$f(\bar{X}) = (1 - c)/a, \bar{Y} = \bar{X}/a. \quad (2)$$

The condition of this solution existence is: $af(0) > 1 - c$. Its stability is defined by the eigenvalues: $\lambda^2 - c\lambda - aF'(\bar{X}) = 0$, here $F(X) = Xf(X)$.

It is easy to show that solution (2) may be unstable only with complex eigenvalues $|\lambda| > 1$. In this case, the loss of stability is accompanied by the appearance of limiting invariant curves, which upon further change in the parameters are destroyed with the formation of highly complex structures, which are called the strange attractors [Frisman, 1994].

Let's assume that limitation of junior age class number is realized by linear rule: $f(X) = 1 - X/K$ as in Verhulst model. Here K is the so-called carrying capacity (i.e., the maximum number of sustainable population). Then let's change the absolute age classes' numbers on relative (or dimensionless) ones: $x = X/K$, $y = Y/K$.

So (1) transforms to:

$$\begin{cases} x_{n+1} = ay_n \\ y_{n+1} = x_n(1 - x_n) + cy_n. \end{cases} \quad (3)$$

Detailed analysis of mechanisms of arising and evolution of model (3) complicated limit sets shows that for large area of acceptable (i.e. biologically substantial) values of parameters such limit sets are the strange attractors having enough varied and fanciful shape [Frisman, 1994].

2.2 Model of population consisting of three and more age-classes

The suggestion that time that passes between two neighboring periods of reproduction is enough for growth of junior individuals to reproductive age and larvae to junior is not true for some biological species (such as saury, cod, many sorts of salmons, muskrat, vole and other). These species have more complicated age structure than those considered in previous section and so they cannot be described by model of population with two age classes.

In the general case the age structure of majority of populations may be described by separating three age classes, they are newborn individuals (X), immatures (Z) and matures (Y). The duration of each age class, as well as the duration of life, may differ for different species. So the maturing of immature individuals to reproductive stage continues one or more than one seasons (k periods of breeding) and so the model (1) may be generalized as:

$$\begin{cases} X_{n+1} = aY_n \\ Z_{1,n+1} = X_n f(X_n) \\ Z_{2,n+1} = c_2 Z_{1,n}, ..., Z_{k,n+1} = c_2 Z_{k-1,n} \\ Y_{n+1} = c_1 Y_n + c_2 Z_{k,n}. \end{cases} \quad (4)$$

The system (4) also has single non trivial stationary solution, which is defined from equations:

$$\begin{aligned} f(\bar{X}) &= (1 - c_1)/(c_2)^k a, \quad \bar{Y} = \bar{X}/a \\ \bar{Z}_1 &= \bar{X}(1 - c_1)/(c_2)^k a \\ \bar{Z}_2 &= \bar{X}(1 - c_1)/(c_2)^{k-1}a, ..., \\ \bar{Z}_k &= \bar{X}(1 - c_1)/c_2 a. \end{aligned} \quad (5)$$

The comparison of systems (1) and (4) stationary solutions shows that appearance of additional k age classes leads to increase of youngest age group limitation in

equilibrium; and this effect is inversely as the multiplied fitness of young individuals on the next k years $(c_2)^k$.

The condition of existence for this solution as following: $(c_2)^k a f(0) > 1 - c_1$. Its stability is defined by the eigenvalues:

$$\lambda^{2+k} - c_1\lambda^{1+k} - (c_2)^k aF'(\bar{X}) = 0, \qquad (6)$$
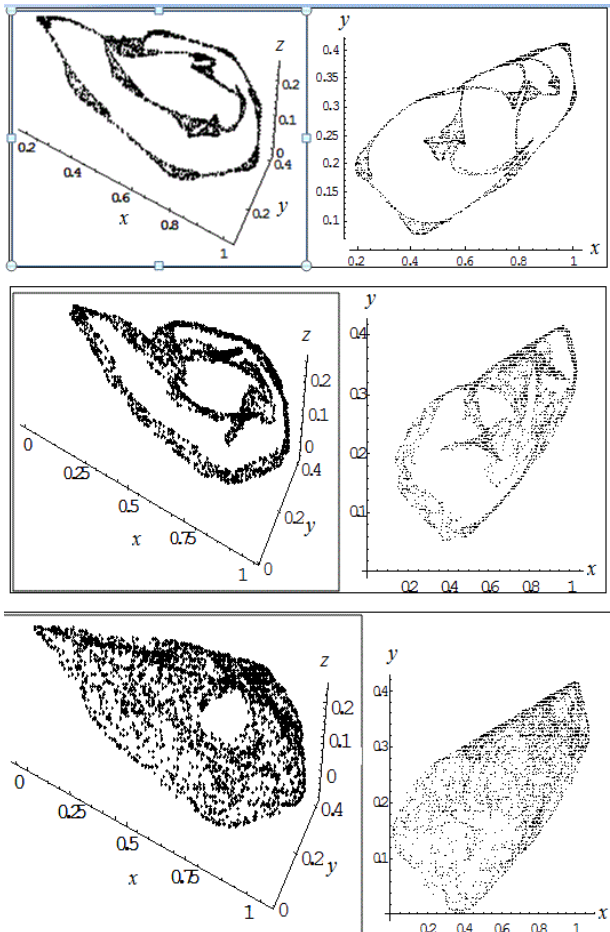
here $F(X) = Xf(X)$.

Figure 1. The limit invariant curves of system (4) in three-dimensional phase space with variables x, y and z (on the left) and in two-dimensional phase space with variables x and y (on the right). The linear function of density limitation for size growth is chosen: $f(x) = 1 - x$. The other model parameters are: $c_1 = 0.5, c_2 = 0.9$. The reproductive potential (a) increases top-down: 2.45, 2.495 and 2.57.

The numeric modeling of model dynamics for multiage population allows us to show that just like in two-age population, the model dynamics complicates and there are attractors of enough various and fanciful shape as a result of increasing of reproductive potential a and fitness c_i. Some examples of the limit

sets of three-age population model with linear limitation of yang age class number (in dimensionless variables: $x = X/K$, $z = Z/K$ and $y = Y/K$) one can see on the figure 1.
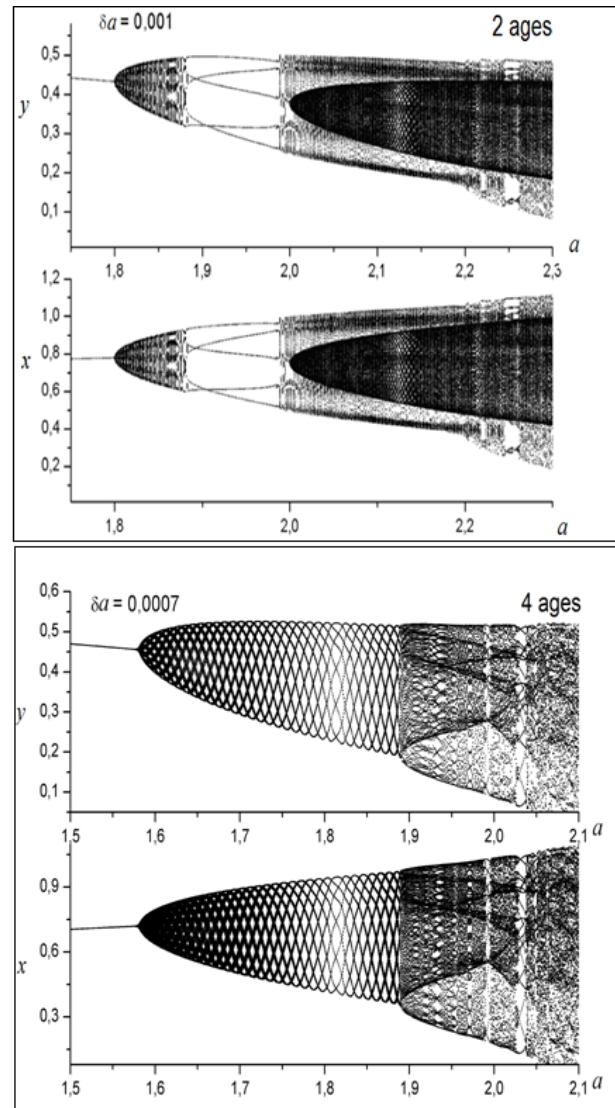

Figure 2. Number distribution of immature (x) and mature (y) age groups in limit curves (or attractors) of model with various age-groups numbers depending on value of coefficient a and step of its changing δa. Other model parameters are: $c = 0.6; c_1 = 0.6; c_2 = 0.95$.

It is easy to show that solution (5) may be unstable only with complex eigenvalues $|\lambda| > 1$ for the even number of age classes. In case when population consists of odd age classes the real values of $\lambda < 1$ may be in the model. However the loss of stability of solution (5) also occurs by the complex values of eigenvalues with $|\lambda|$ crossing unit in the three-age model with linear limitation of junior group size [Zhdanova and Frisman, 2011].
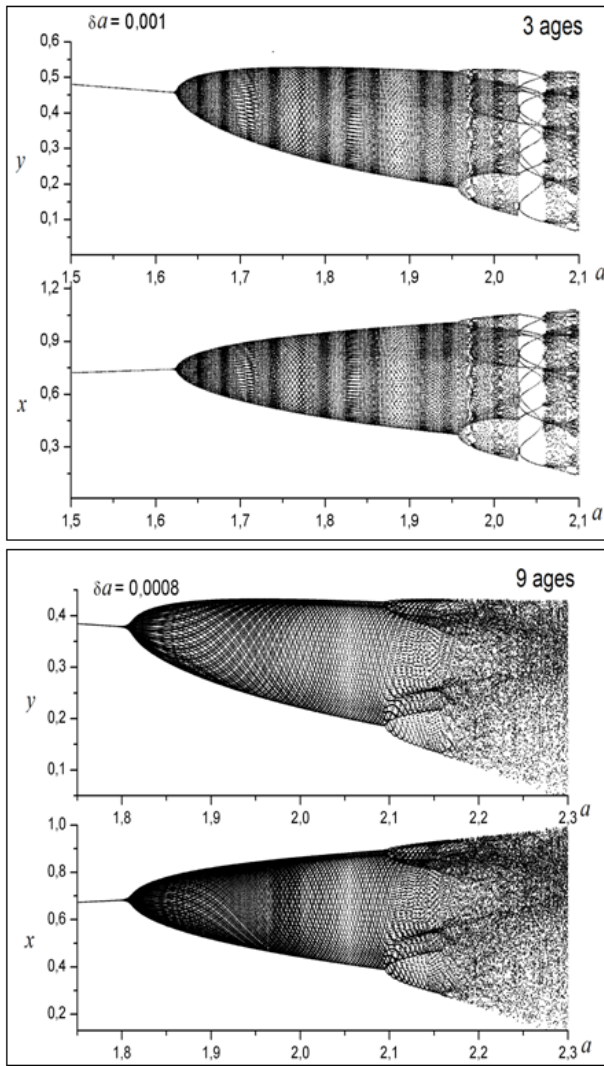
Let's consider some scenarios of stability loss by

Figure 3. Number distribution of immature (x) and mature (y) age groups in limit curves (or attractors) of model with various age-groups numbers depending on value of coefficient a and step of its changing δa. Other model parameters are: $c_1 = 0.6$; $c_2 = 0.95$.

Figure 4. Number distribution of immature age group (x) in limit curves (or attractors) of model; on the bottom part the dynamics of Lyapunov exponents (left axis) and attractors dimensions (right axis) depending on value of coefficient a.

the non trivial equilibrium of multi-aged population model with linear limitation of immature age group size: $f(x) = 1 - x$.

On the figures 2 and 3 one can see some examples of the number distribution of immature (x) and mature (y) age groups in limit curves of models of populations with various depth of age structure depending on value of reproductive potential . In spite of large values of additional age groups (z_i) fitness ($c_2 = 0.95$) the effect of age-structure complication is clearly presented. It is evident from figures that at beginning the increase of maturing duration of immature individuals is followed by the reducing of reproductive potential a values region where non trivial equilibrium remains stable; then (for populations with 4-5 age groups) this region begin grow and population with 9-10 age groups has already more extensive region with stationary number dynamics than those with two age classes. In addition the
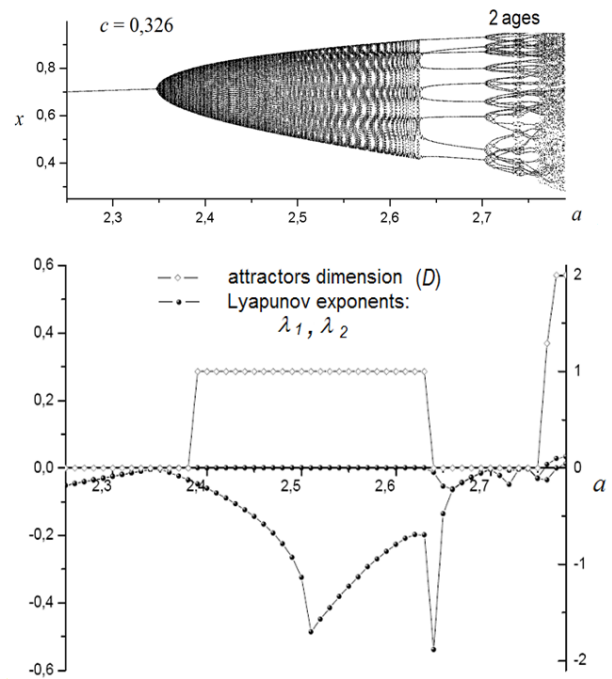
upper limit of mature and immature age classes number shifts down. There are not any clear regularities connected with age groups evenness or oddness.

Let's complete the phenomenological picture of model dynamic regimes by the dynamics of Lyapunov exponents (λ_i) and by dimensions (D) of emerging attractors.

Bennetin's algorithm [Neymark, Landa, 1987] for calculation of Lyapunov exponents was applied; and Lyapunov attractor dimension was calculated by the Kaplan-Yorke formula:

$$D = j + \sum_{i=1}^{j} \lambda_1 / |\lambda_{j+1}|, \qquad (7)$$

here $j = max\{m : \sum_{i=1}^{m} \lambda_i \geq 0\}$.

On the figures 4 - 7 one can see pairs of charts: the bifurcation diagrams on the top part of figures and on the bottom - the dynamics of Lyapunov exponents and of attractors' dimensions for 2-, 3- and 4-age populations. Results of conducted investigation show that attractors of less dimension than maximal possible one are prevalent in the large part of acceptable parametric region of reproductive potential (a) values. In addition, when in two-aged model there are some attractors of dimension 2 with extremely large value of parameter a; but in three-aged model the attractors reach dimension 3 not for all values of parameter c_1 (results not shown); extension of maturing period on next unity does not
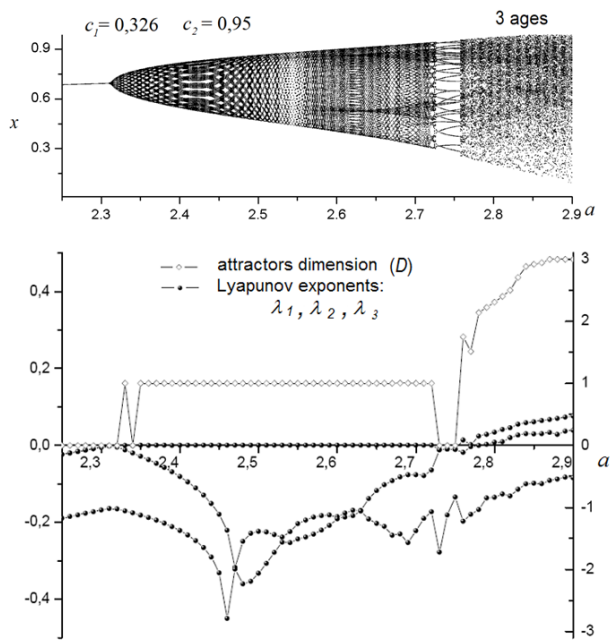
Figure 5. Number distribution of immature age group (x) in limit curves (or attractors) of model; on the bottom part the dynamics of Lyapunov (left axis) exponents and attractors dimensions (right axis) depending on value of coefficient .

Figure 6. Number distribution of immature age group (x) in limit curves (or attractors) of model; on the bottom part the dynamics of Lyapunov exponents (left axis) and attractors dimensions (right axis) depending on value of coefficient a.

lead to emerging of attractor with dimension 4 moreover, there are not even any attractors of dimension 3 in four-aged population model.

So the results of conducted numerical investigation show that although increasing of ontogenesis duration follows by growth of potential possibilities for intensification of systems dynamics chaotization but expected growth of chaotization does not occur and in average the dynamics of system with more complicated structure looks like less various then those of population with short ontogenesis. In biological aspect this fact means that population with long ontogenesis in average has more ordered dynamics and consequently it is more viable.

3   Conclusion

The model analysis of connection between ontogenesis duration and character of isolated population dynamics (the structure and dimension of emerging attractors) has conducted. In uniform population the growth of reproductive potential follows by the logical transition from stable dynamic regimes of population size to the fluctuations and chaos. For more complex non-linear dynamics models of population with age structure (with long ontogenesis) the growth of reproductive potential leads to arising of chaotic attractor, which structure and dimension changes with varying of model parameters values too. Nevertheless, growth of ontogenesis duration and complexity does not increase the power of attractors' chaotization. The most dynamic stability is presented by such factors as increas-
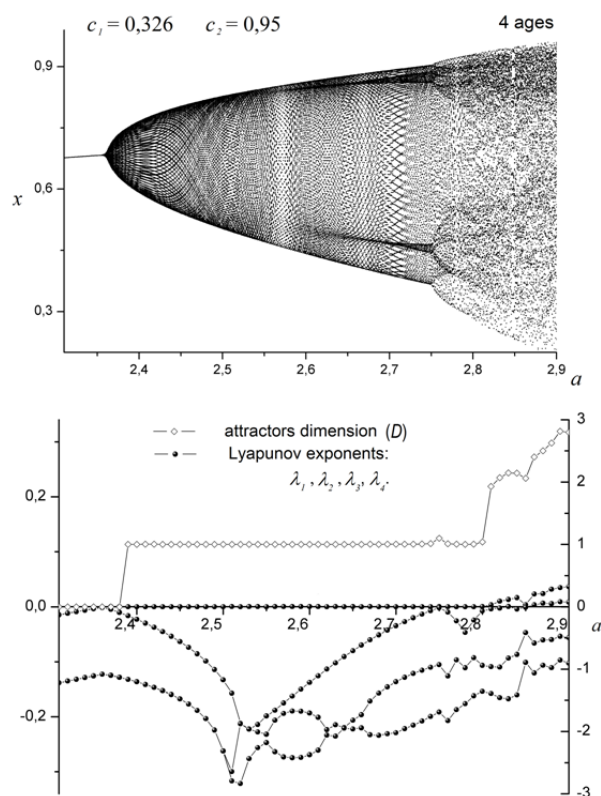
ing of reproductive potential values region with stable dynamics in multi-age populations, the restriction of fluctuation scope of population groups' sizes, and scant diversity of attractors with large dimension.

This result provides one possible explanation at the model level the fact that many natural biological population with age structure demonstrate clear stable or pseudo-cyclic dynamics [Bobyryev, Kriksunov, 1996; Clutton-Brock et al., 1997; Fewster et al., 2000; Freckleton, Watkinson, 2002; etc.], despite there are wide variety of dynamic regimes that theoretically possible for structured populations [Greenman and Benton, 2004].

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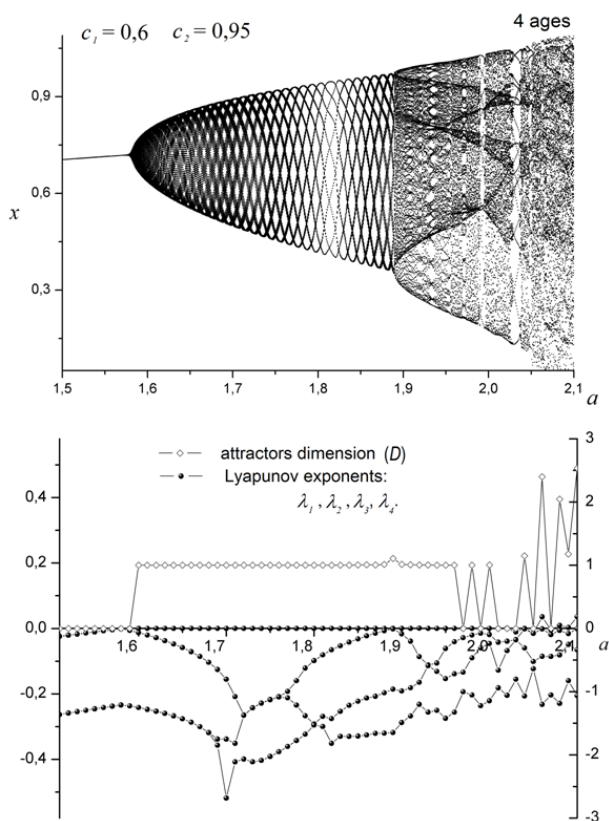
Figure 7.   Number distribution of immature age group (x) in limit curves (or attractors) of model; on the bottom part the dynamics of Lyapunov exponents (left axis) and attractors dimensions (right axis) depending on value of coefficient a.

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