

# A NONLINEAR DYNAMICS OF POPULATION SIZE: THE INFLUENCE OF AGE STRUCTURE IN POPULATION ON THE TRANSITION TO CHAOS

Efim Ya. Frisman

Far Earsten Branch of Russian Academy of Science  
Complex Analysis of Regional Problems Institute  
Russia

[frisman@mail.ru](mailto:frisman@mail.ru)

Oksana L. Zhdanova

Far Earsten Branch of Russian Academy of Science  
Institute of Automation and Control Processes  
Russia

[axanka@iacp.dvo.ru](mailto:axanka@iacp.dvo.ru)

## Abstract

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 population's 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" increases the degree of attractors' chaotization. In spite of this fact the resonant values of reproduction potential for long ontogenesis have been found, and these values give the windows of regularization in chaotic dynamics.

## Key words

Population dynamics, ontogenesis, evolution, self-organization.

## 1 Introduction

The traits of age structure define many characteristics of population. The influence of external environment factors on population with several age groups, such as those defining the success of reproduction in concrete year, has less power. Even extremely unfavorable conditions of reproduction which able to set conditions for total loss of this year offspring isn't catastrophic for population with complex age structure, as the same pair of parent take part in reproduction more than once. For example the same female of cod able to spawn every year during nine years as from six-year-old to fifty-year-old. The female of humpback salmon spawns in age of two year and immediately after

spawn will be its death. It is evident that appearance of unfavorable conditions for spawn immediately leads to considerable decrease of all population size. This occurs because the major part of population consists of young fishes of this year. Consequently, the multi-age populations are considerably less reactive on the short-term fluctuations such factors that able to affect single age groups. With it, any influence that leading to considerable change of just single age class size are remaining visible and affecting the structure of multi-age population during considerably long time.

On the other hand the influence of external environment factors on the population's number dynamics may be comparable or even less marked than influence of other factor – the intra-population mechanisms of number growth regulation. The deep understanding of activity results of intra-population self-organization mechanisms is necessary for further investigation the question: what occurs with biological population affected by changing factors of external environment? This work devoted to the modeling analysis of connection between ontogenesis duration and mode of dynamic behavior of biological community in condition that only intra-population mechanisms of number growth regulation are considered.

## 2 Number dynamics mode of population's with nonoverlapping generation

Each single population of many kinds of annuals, some fish species, amphibia and reptiles is single age class as neighboring generations of such population doesn't overlap. If the external conditions vary from one generation to another not very strong than the number of certain generation defines by only the previous one. Let's define  $N_n$  the number of  $n$ -th generation and then we can write following deterministic equation which describes the number dynamics of such single-age population:

$$N_{n+1} = F(N_n). \quad (1)$$

The simplest form of this equation is following:

$$N_{n+1} = rN_n, \quad (2)$$

here  $r$  is some constant (i.e. each individual gives  $r$  offsprings into the next generation, no matter how large the parent population is).

Equation (2) is famous as a Malthus's model. Its solution is a geometric progression with ratio  $r$  and initial term  $N_0$ , in fact this is identical to exponential growth of population number in absence of limiting factors.

It is well known that it is unreal to see in nature the sufficiently long exponential growth of number. The influence of limiting factors will have an impact sooner or later and so it appears that the coefficient  $r$  in equation (2) is a function of number. Let  $r = af(N)$ , here  $f(N)$  is function describing the limitation and  $a$  is the parameter named as reproductive potential of population and characterizing the growth of population to void (i.e.  $a$  have to be chosen so that  $f(0) = 1$ ). Now we receive following instead of (2):

$$N_{n+1} = aN_n f(N_n). \quad (3)$$

In the '70s deep investigations of number dynamics models such as (3) appeared; these investigations carried out by Far-Eastern researcher A.P. Shapiro [Shapiro, 1972; Shapiro and Luppov, 1983] and his American colleague R.M. May [May, 1975]. They showed that population number dynamics which is describing by equation (3) may be quite complex provided by the function  $F(N) = aNf(N)$  decreases sufficiently fast (for example, faster than  $1/N^2$ ).

After specifying the type of function  $f(N)$  the bifurcation diagram for equation (3) one can construct numerically. This diagram characterize the limit trajectories depending on value of coefficient  $a$ . The most investigated ones are the discrete analog of Verhulst's model with  $f(N) = 1 - kN$  (fig.1 on top) and Ricker's model with  $f(N) = \exp(-bN)$  (fig.1 on bottom) [Ricker, 1954].

Very interesting particular case that generalizing the

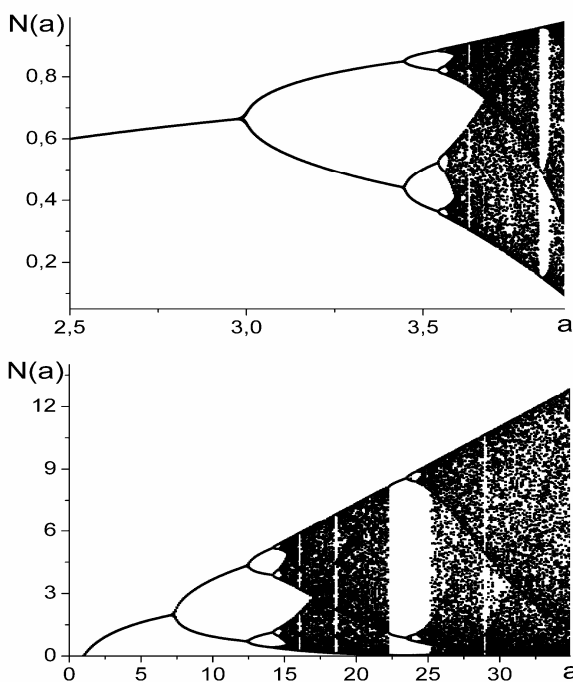


Figure 1. The number distribution in limit curves (or attractors) of model (3) depending on value of coefficient  $a$ . Lines correspond stationary points and limit circles with length 2, 4 etc. In the hatched area the points of the each limit trajectory fill some interval of number values: top) Verhulst's model -  $f(N) = 1 - kN$ ; bottom) Ricker's model -  $f(N) = \exp(-bN)$ .

equations of Verhulst and Ricker is the three-parameter Hassel's model [Hassell, Lawton, May, 1976]:

$$N_{n+1} = \frac{aN_n}{(1 + \gamma N_n)^\beta}.$$

This model allows to investigate the dynamics of population number with various intensity of ecological limitation that is characterizing by parameter  $\beta$  (its increase leads to growth of decrease rate of  $f(N) = 1/(1+N)^\beta$  for large values of  $N$ ). So when limitation is weak (small values of  $\beta$  ( $\beta < 2$ )) there aren't any un-monotonic regimes of number dynamics for any values of  $a$ . But with larger values of  $\beta$  ( $\beta > 3$ ) the monotonic increase of parameter  $a$  leads to arising of first series of bifurcation and then to the arising of chaotic regime. On the other hand when large value of parameter  $a$  is fixed ( $a = 30$  and more) the increasing of parameter  $\beta$  leads to analogous reorganizations in dynamic regime as increase of  $a$  do. The difference of it is bifurcations against the background of decrease of equilibrium number when  $\beta$  grows, as opposed to the equilibrium number increase when  $a$  grows (fig. 2).

The investigation of chaotic regimes of dynamic behavior which had been found in Ricker's, Verhulst's etc. models 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 number then there will be the slow growth of number during large number of generations, then will be a sharp boom following by considerably greater decrease of population number (to level not far from initial) in next generation. However these periodic changes don't return population precisely to initial level. So despite of evidently periodic character of number dynamics, there aren't any total coincidence of number values and even number of generations in phase of growth. Such nonstrictly periodic behavior of number is typical for many natural populations of higher organisms, especially for insects (for example, locusts, grasshoppers, night-flies).

It seems that the slow and quite inhomogeneous growth of parameter  $a$  have to occur in natural populations, because of new adaptive mutations selection setting conditions for

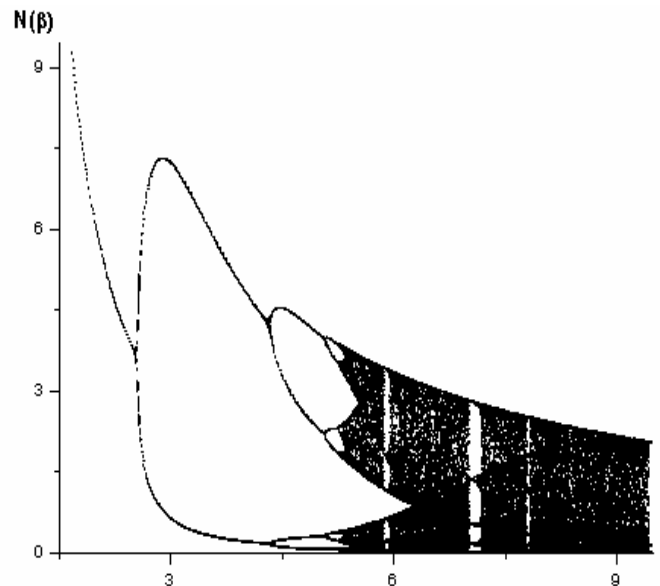


Figure 2. . The number distribution in limit curves (or attractors) of Hassel's model depending on value of coefficient  $\beta$  with  $a = 50$ .

quite not great increment of reproductive potential. Though unlimited growth of  $a$  may be tragic for population, as this may lead to sharp dynamic fluctuations and so population number may become so little that it can't ever restore.

So it is evident now that the progressive growth of average fitness may be in discordance with stability of population growth for limited populations with un-overlapped generations [Witten, 1978]. This fact is in evident conflict with intuitive understanding of population stability increasing with growth of its average fitness.

### 3 Strange attractors in the model of population consisted from two age classes

The simplest population dynamics models consider changes of whole population number only, assuming that different generations of the population don't 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 the individual from different age groups during breeding

season. So, it is natural to consider the number of each separated age group as a model's variable. The treatment for clustering the population is defined by the characteristics of biological species.

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 impuberal individuals and reproductive part consists of individuals participating in reproduction process.

Let's define  $x_n$  – the number of junior age class in  $n$ -th reproduction season, and  $y_n$  – the number of reproductive part of population. The reproductive 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 depended from their age. These assumptions are correct for organisms with not great lifetime consisting of two or three reproductive periods;

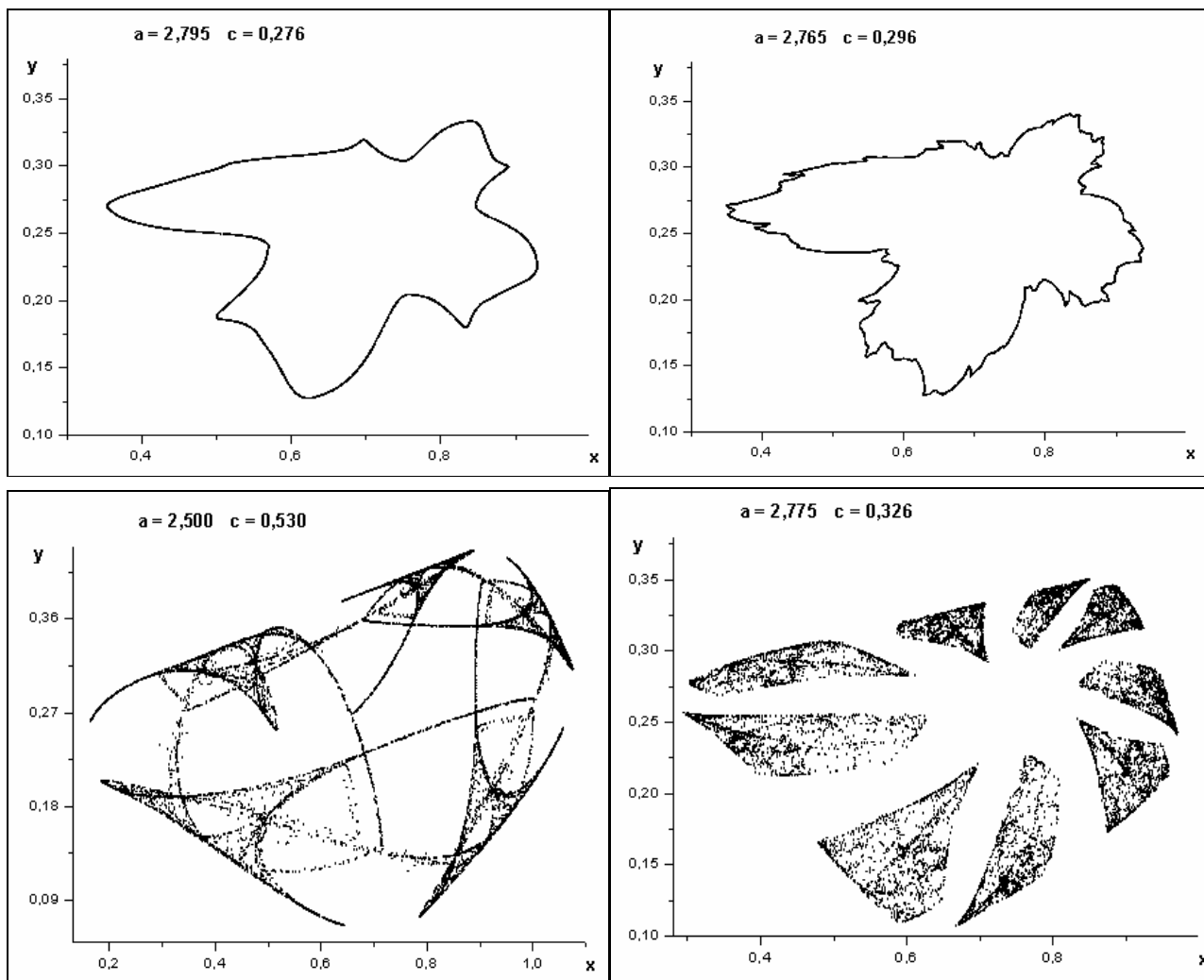


Figure 3. The limit invariant curves of system (4) with original shape: "pigeon", "maple leaf", "swallows", "pyramids".

such as many insect, fishes, small mammals, biennials or triennials and others.

Let's define  $a(y)$  – the product of first-year offspring's birth rate and fitness;  $f(x)$  and  $g(y)$  – the fitness of un-pubertal and pubertal individuals respectively. Here we'll limit the consideration of situation, when effect of limiting factors concentrates on the stage of un-pubertal 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 is 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:

$$\begin{cases} x_{n+1} = ay_n \\ y_{n+1} = x_n f(x_n) + cy_n \end{cases} \quad (4)$$

With the assumption  $f'(x) < 0$  system (4) has single nontrivial stationary solution, which defines from equations:

$$f(\bar{x}) = (1-c)/a, \quad \bar{y} = \bar{x}/a. \quad (5)$$

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

It is easily to show that solution (5) may be unstable only with complex eigenvalues  $|\lambda| > 1$ . In this case the loss of stability followed by arising of limit invariant curves which collapse and form complicated enough structures called the strange attractors when parameters change [5].

Let's assume that limitation of junior age class's number is realized by linear rule:  $f(x) = 1-x$ ; then (4) transforms to:

$$\begin{cases} x_{n+1} = ay_n \\ y_{n+1} = x_n(1-x_n) + cy_n \end{cases} \quad (6)$$

Detailed analysis of mechanisms of arising and evolution of model's (6) 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 and Zdanova, 2008]. Here we'll only make some examples of original limit trajectories (fig. 3) and then continue the consideration of more complicated models of structured populations.

#### 4 The features of dynamic behavior of population with complicated structure

The suggestion that time those pass between two neighboring periods of reproduction is enough for growth of junior individuals to pubertal age and larvae to junior isn't true for some biological species (such as saury, cod, many sorts of salmon, muskrat, vole and other). These species

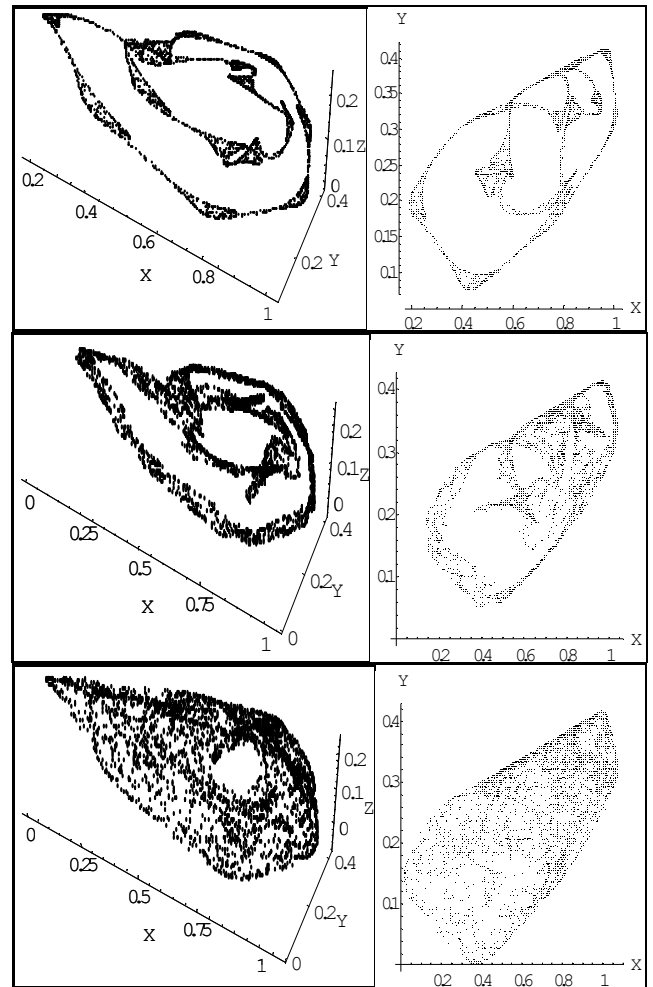


Figure 4. The limit invariant curves of system (7) in three-dimensional phase space with variables  $x, y$  and  $z$  (on the left) and in two-dimensional phase space with variables  $x$  and  $y$  (on the right). The linear function of density limitation for size growth is chosen:  $f(x) = 1-x$ . The 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.

have more complicated age structure than those considered in previous section and so they can't 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 ( $x$ ), un-pubertal ( $z$ ) and pubertal ( $y$ ). Each of these age classes duration as far as duration of whole life may grate differs for various kinds of organisms.

Let's begin from consideration of most simple case when time between two neighboring breeding periods is enough for growth of un-pubertal individuals to pubertal stage. As it is typical for grate number of species that the death rate is high only in and the surviving individuals demonstrate the low mortality in further stages, so let's suppose that density-dependent regulation of size growth realizes only in early stage of ontogenesis when larvae survives and it describes as a decreasing function  $f(x)$  (i.e.  $f'(x) < 0$ ) tending to zero when its argument indefinitely grows. For the next years the fitness of individuals remains invariable and may be

described as a constant  $c_2$  which is not far from unit. So  $(1 - c_1)$  is a natural death rate of pubertal individuals:

$$\begin{cases} x_{n+1} = ay_n \\ z_{n+1} = x_n f(x_n) \\ y_{n+1} = c_1 y_n + c_2 z_n \end{cases} \quad (7)$$

With the assumption  $f'(x) < 0$  system (7) has single nontrivial stationary solution, which defines from equations:

$$f(\bar{x}) = (1 - c_1)/c_2 a, \quad \bar{y} = \bar{x}/a, \quad \bar{z} = \bar{x} \cdot (1 - c_1)/c_2 a. \quad (8)$$

The condition of existence of this solution is:  $c_2 a f(0) > 1 - c_1$ . Its stability defines by the eigenvalues:

$$\lambda^3 - c_1 \lambda^2 - c_2 a F'(\bar{x}) = 0, \text{ here } F(x) = x f(x).$$

In general case the maturing of un-pubertal individuals to pubertal stage continues more than one season ( $k$  periods of breeding) and so the model (7) may be generalized as:

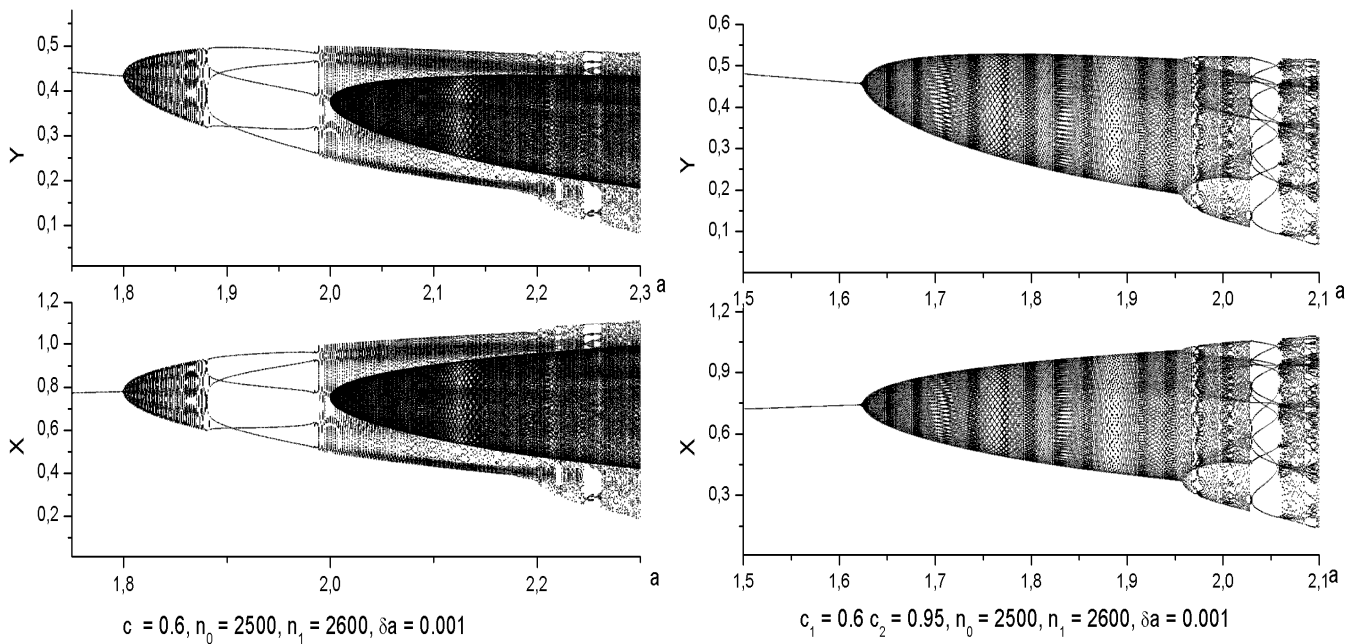


Figure 5. The number distribution of un-pubertal and pubertal age groups in limit curves (or attractors) of model of both two-age population ((6), on the left) and three-age population ((7), on the right) depending on value of coefficient  $a$ . The linear function of density limitation for size growth is chosen:  $f(x) = 1 - x$ .

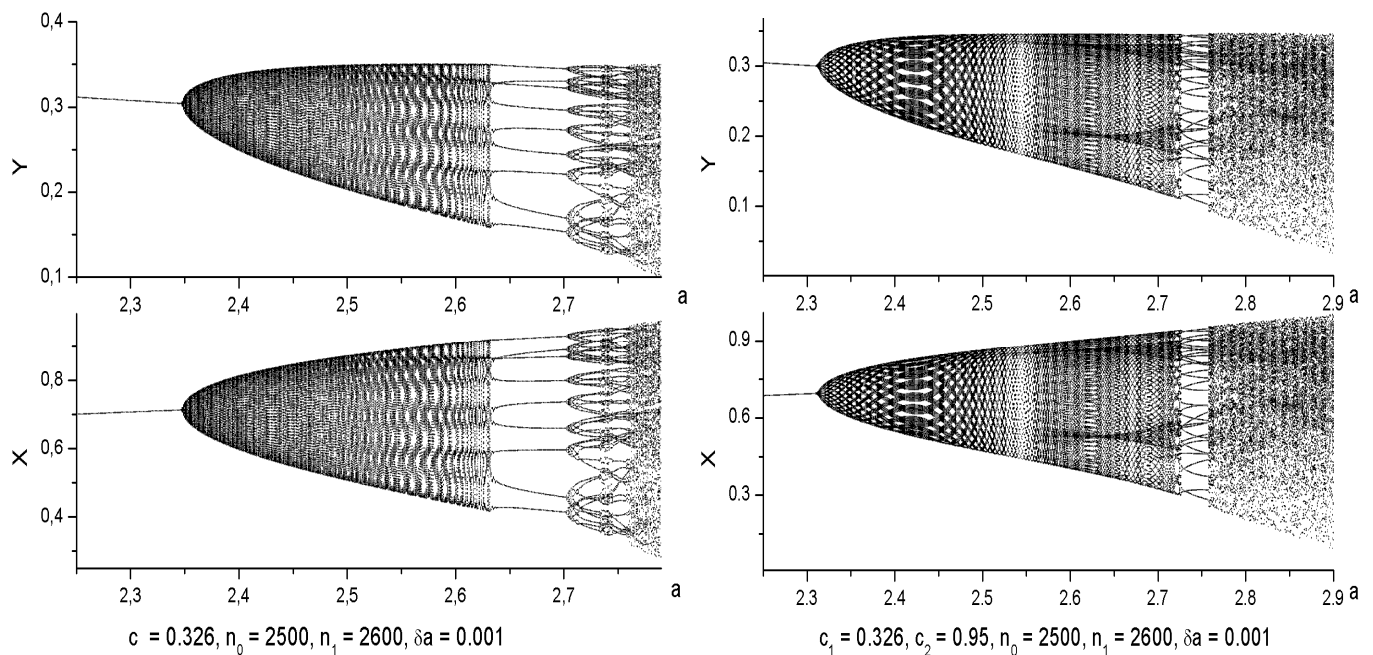


Figure 6. The number distribution of un-pubertal and pubertal age groups in limit curves (or attractors) of model of both two-age population ((6), on the left) and three-age population ((7), on the right) depending on value of coefficient  $a$ . The linear function of density limitation for size growth is chosen:  $f(x) = 1 - x$ .

$$\begin{cases} x_{n+1} = ay_n \\ z_{1,n+1} = x_n f(x_n) \\ z_{2,n+1} = c_2 z_{1,n}, \dots, z_{k,n+1} = c_2 z_{k-1,n} \\ y_{n+1} = c_1 y_n + c_2 z_{k,n} \end{cases} \quad (9)$$

The system (9) also has single nontrivial stationary solution, which defines from equations:

$$\begin{aligned} f(\bar{x}) &= (1 - c_1)/(c_2)^k a, \quad \bar{y} = \bar{x}/a, \\ \bar{z}_1 &= \bar{x} \cdot (1 - c_1)/(c_2)^k a, \\ (10) \end{aligned}$$

$$\bar{z}_2 = \bar{x} \cdot (1 - c_1)/(c_2)^{k-1} a, \dots, \bar{z}_k = \bar{x} \cdot (1 - c_1)/c_2 a.$$

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

$$\lambda^{2+k} - c_1 \lambda^{1+k} - (c_2)^k a F'(\bar{x}) = 0, \quad (11)$$

here  $F(x) = x f(x)$ .

The numeric modeling of model dynamics for multi-age population allows us to show that just like in two-age population, the model dynamics complicates and attractor of enough various and fanciful shape arising as a result of increasing of reproductive potential  $a$  and fitness  $c_i$ . Some examples of the limit sets of tree-age population model with linear limitation of yang age class number one can see on the figure 4.

Let's consider also numerically question about nature of stability loss of sole non-trivial equilibrium in multi-age population model as complexity of equation (11) doesn't allow us to make any qualitative summary even about eigenvalues  $\lambda_i$ .

On the figures 5 and 6 one can see some examples of the number distribution of un-pubertal ( $x$ ) and pubertal ( $y$ ) age groups in limit curves (or attractors) of model of both two-age population (4) and three-age population (7) depending on value of coefficient  $a$ . Here we chosen the linear function of density limitation for size growth:  $f(x) = 1 - x$ . In spite of the value of additional age class ( $z$ ) fitness was fixed on the enough high level ( $c_2 = 0.95$ ), the effect of equilibrium number decreasing in un-pubertal and pubertal age classes ( $x$  and  $y$ ) and also the decrease of region with reproductive potential ( $a$ ) values where the non-trivial equilibrium remains stable and respectively the dynamics of the system is stationary are visible. On the other hand there are some large "resonant" values of reproductive potential with those the windows of regularization in chaotic dynamics arises exactly in tree-age population.

## 5 Conclusion

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 population's dynamics to fluctuations and chaos (the pseudo stochastic regimes) have to occur, i.e. the transition from equilibrium regimes of dynamics to non-equilibrium one. 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" increases the degree of attractors' chaotization. In spite of this fact the resonant values of reproduction potential for long ontogenesis have been found, and these values give the windows of regularization in chaotic dynamics. It may be concluded that prolongation and complication of ontogenesis increasing chaotization "in average" is able eventually to ensure the transition "from chaos to order" and even it able to lead to stable dynamic regimes.

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## References

- Frisman, E.Ya., Zdanova, O.L. (2008) Strange attractors in simplest models of the biological populations number dynamics. *Proc. "ENOC'2008"* pp. 1667 – 1671.
- Hassell, M.P., Lawton, J.N., May, R.M. (1976) Patterns of dynamical behavior in single species populations. *J. Anim. Ecol.* 45(2). pp. 471 - 486.
- May, R.M. (1975) Biological population obeying difference equations: stable points, stable cycles, and chaos. *J. Theor. Biol.* 51(2). pp.511 - 524.
- Richer, W.E. (1954) Stock and recruit. *Theor. J. Fish. Res. Bard. Can.* 11(5). pp.559-623.
- Shapiro, A.P. (1972) To the quest. about circl. in the recurrent seq. *Cont. and Information.* (3). pp. 96 – 118.
- Shapiro, A.P., Luppov, S.P. (1983) Recurrent equations in the population biology theory. M: Nauka.
- Witten, M. (1978) Fitness and survival in logistic models. *J. Theor. Biol.* 74 (1). pp. 23 - 32.