COMPARISON FOR TWO REGULATION TYPES OF GROWTH OF A SIMPLE AGE STRUCTURE POPULATION

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Abstract

The effects of the following modes of density-dependent control of population growth: density-dependent adult survival rate, juvenile survival rate are compared based on the mathematical model of population dynamics. It is shown that the most efficient mechanisms limiting population size are the decreasing survival rate of the offspring with the increase in their number. However, these same mechanisms are responsible for oscillations of the population size and its chaotic change. The density-dependence of the adult survival rate is not efficient in constraining the population growth, but it can substantially limit the magnitude of oscillations of the population size.

Key words

Population model, discrete-time model, age structure, density-dependent factors, stability, bifurcations.

1 Introduction

Here we consider evolutionary scenarios of the origination of oscillatory and chaotic population dynamics in the species with the simple age structure. We compare the two possible mechanisms of density-dependent population growth: density-dependent adult survival rate, juvenile survival rate. The relative efficiency of these mechanisms is discussed. Moreover, the suggested model allows one to consider compensatory mechanisms stabilizing the populations that approach the "May threshold" and are responsible for the allometric effect [Ginzburg and etc.,2010].

The dynamic equations for a simple age-structured model are as follows [Frisman, Skaletskaya,1994]:

$$\begin{cases} x_{n+1} = a \cdot y_n \\ y_{n+1} = s(x_n, y_n) \cdot x_n + v(x_n, y_n) \cdot y_n \end{cases}, \quad (1)$$

where x is a number of juveniles, y is a number of adults, n is a reproductive season number, a is the birth rate, and $s(x, y)$ and $v(x, y)$ are the survival rates of juveniles and adults respectively. Functions: $s(x, y)$, $v(x, y)$ monotonously decrease as their arguments increase.

We consider the special versions of the model (1), when one of its parameters is an exponential function selected following Ricker's model [Ricker,1954], and the two others are constants.

Small mammals (murine rodents, squirrels, etc.), fast maturing fish (as navaga, smelt, etc.), many insects, and biennial and triennial plants may serve as example [Frisman, Skaletskaya,1994; Frisman and etc.,1988; Ferriere, Gatto, 1993]. It is these groups of species that have complex oscillating dynamics and are the most common objects of experimental research and examples in the theoretical population biology.

2 Model with density-dependent juvenile survival rate

The substitutions $s(x, y) = \exp(-\alpha x - \beta y)$, $v(x, y) = v$ and $\alpha x \to x$, and $\alpha y \to y$ transform (1) into

$$\begin{cases} x_{n+1} = a \cdot y_n \\ y_{n+1} = x_n \cdot \exp(-x_n - \rho \cdot y_n) + v \cdot y_n \end{cases}, \quad (2)$$

where α and β are the intensities of the birth rate decline because of the growth of juvenile and adult numbers respectively $\rho = \beta/\alpha$ is a parameter which characterizes the ratio of intensity of the limitation of juvenile survival rate due to the number of adults and the self-limitation. Analysis of this system becomes simpler if we also introduce new parameters $c = \rho/a$; $\rho = ac$. The only non-trivial stationary solution of (2) is
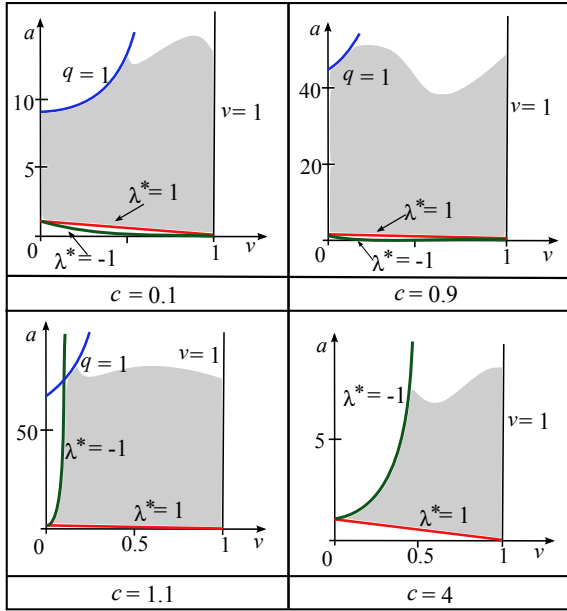
Figure 1. The stability domain of a non-zero solution for the system (2) with selected values of the parameter c.
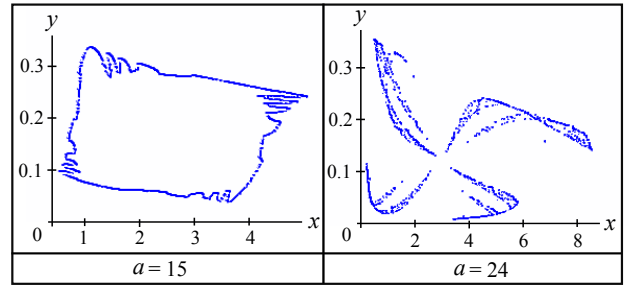

Figure 2. The "portraits" of attractors dependent on the parameter a at $c = 0.1$ and $v = 0.05$.

$q = 1$:

$$a = a_3 = (1 - v) \exp \frac{(2 - v)(1 + c)}{1 - v}. \quad (5)$$

Note that the line $a = 1 - v$ is also a line of the system bifurcation. If $a = v < 1$ (3) has a unique zero equilibrium point which is globally stable (i.e., population degenerates). If parameters change, and the line $a + v = 1$ is crossed over (already when $a - v < 1$) the trivial (zero) solution loses its stability, and a new stable non-zero (non-trivial) solution (3) appears.

Coordinates $(v; a)$ allow one to easily trace the change of the stability domain of this solution with the change of the parameter c (fig. 1).

Depending on the mode of stability loss by the non-zero solution for the system (2), we can identify the following intervals for the values of parameter c:

1. $0 < c \leq 1$

In this case, the stability domain is bound by one curve (5) and considerably expands with the increase of the parameter c. Loss of stability may happen only if the solutions for the characteristic equation are conjugate at $|\lambda| = 1$ transition through 1.

It has been previously shown that the decline of the juvenile survival rate with the growth of the number of juveniles only ($\beta = 0, c = 0$) may lead to fairly complex oscillations of the population size [Frisman, Skaletskaya,1994]. It is now clear that if the juvenile survival rate does not only depend on the group's own number but also modestly on that of the adults, not only does the equilibrium population size decrease, but its stability domain significantly expands (fig.1, upper row).

The population equilibrium loses its stability with the growth of parameter a. The smaller the parameter c is, the sooner the loss of stability happens. It is followed by a series of bifurcations, an emergence of the invariant curve and complex attractors(fig.2).

Also, the system has attractors of fractional dimension for small values of adult survival and at very high values of birth rate (fig. 3).

2. $1 < c < 3$.

Within this range of parameter c, decline of the juvenile survival rate related to the number of adults leads
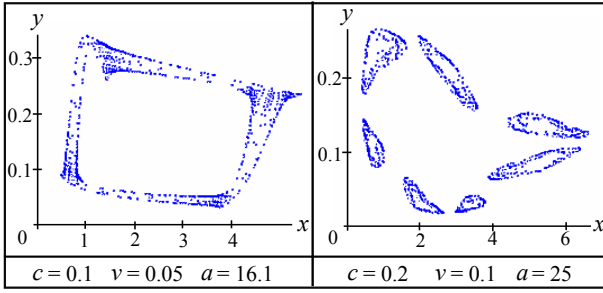
$$\overline{x} = \frac{1}{1 + c} \ln \frac{a}{1 - v}, \overline{y} = \frac{1}{a(1 + c)} \ln \frac{a}{1 - v} \quad (3)$$

and it exists if $a \geq 1 - v$ and $0 \leq v < 1$.

The standard method of finding the stability domain is based on the following theorem:

Solutions of the equation $\lambda^2 + p\lambda + q = 0$ belong to the circle $|\lambda| < 1$ if and only if $|p| - 1 < q < 1$ [Shapiro,Luppov, 1983].

In our case

$$p = -\left(\frac{c \cdot (1 - v)}{1 + c} \ln \frac{1 - v}{a} + v \right),$$

$$q = -(1 - v)\left(1 + \frac{1}{1 + c} \ln \frac{1 - v}{a} \right).$$

And therefore the boundaries of the stability domain for the equilibrium point (3) are as follows:

$\lambda^* = 1$:

$$a = a_1 = 1 - v,$$

$\lambda^* = -1$:

$$a = a_2 = (1 - v) \exp \frac{2v \cdot (1 + c)}{(c - 1)(1 - v)}, \quad (4)$$

Figure 3. The "portraits" for attractors of fractional dimension at $0 < c \leq 1$.

Figure 4. Bifurcation diagram with the "portrait" of attractor and graphs for the 1st Lyapunov coefficient (λ) and the dimension (D) of the attractor versus the value of the parameter a.

now to noticeable contraction of the stability domain of population equilibrium size. In this case, there are two possible scenarios of stability loss: the emergence of 2-cycle when v is small and the emergence and destruction of the invariant curve when v is large.

3. $c \geq 3$.

With further growth of the parameter c, loss of the equilibrium stability may happen only with the transition of one of the eigenvalues through -1 and is accompanied by a cascade of period-doubling bifurcations. In this case, further contraction of the stability domain is observed, and self-limiting of the juvenile group becomes irrelevant.

Fig.4 shows a bifurcation diagram, demonstrating progressive complication of the population dynamics through the cascade of period-doubling bifurcations at $c \geq 3$.

The diagram is followed by the graphs for the 1st Lyapunov coefficient and the attractor's dimension. Benettin's algorithm has been used for the Lyapunov coefficient calculation, and the attractor's dimension has been calculated using Kaplan-Yorke's formula [Kaplan, Yorke,1979]. The chaotic structures that emerge in this case have a dimension of a little bit greater than one. The dimension is slowly growing with the increase of the parameter a. The fig.3 also shows the most common type of attractor in this case. It has a large distance between the extreme points and resembles the Henon's attractor [Henon,1976].

3 Model with Density-dependent limitation of the adult survival rate

The substitutions $\beta x \rightarrow x$, $\beta y \rightarrow y$ and $s(x, y) = s$, $v(x, y) = \exp(-\alpha x - \beta y)$ transform (1) into the system

$$\begin{cases} x_{n+1} = a \cdot y_n \\ y_{n+1} = s \cdot x_n + \exp(-\gamma \cdot x_n - y_n) \cdot y_n \end{cases}, \quad (6)$$

where $\gamma = \alpha/\beta$.

$h = a\gamma = a\alpha/\beta$ is a convenient parameter for the analysis of a non-zero equilibrium existence and stability for the system (6).
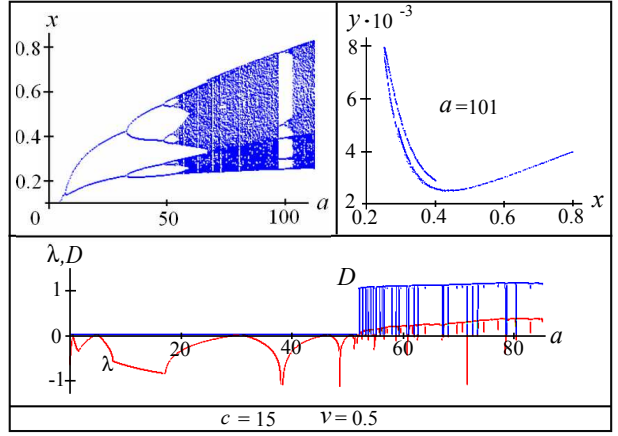
The system (6) has unique non-zero stationary solution:

$$\overline{x} = \frac{a}{1+h} \ln \frac{1}{1-as}, \quad \overline{y} = \frac{1}{1+h} \ln \frac{1}{1-as}. \quad (7)$$

Inequality $as < 1$ is necessary for its existence.

Boundaries of the stability domain for the non-zero stationary solution are defined by the following conditions:

$\lambda^* = 1$:

$$a = 1/s, \quad (8)$$

$\lambda^* = -1$:

$$a = \frac{1}{s} \cdot \left(1 - \exp\left(2\frac{h+1}{h-1}\right)\right), \quad (9)$$

$q = 1$:

$$-as - \frac{h(1-as)}{h+1} \ln(1-as) = 1. \quad (10)$$

The stability domain for the non-zero equilibrium (7) is formed by the curves (8) and (9). The curve (10) does not intersect with the domain of existence of the stationary point and, therefore, does not restrict its stability domain.

At $h < 1$ the curve (8) is above the curve (9). The closer h is to 1, the smaller the distance between the curves (8) and (9) is. Loss of stability of the equilibrium (7) happens with the growth of either birth rate a or the juvenile survival rate s while crossing over the curve (9). It is accompanied by one of the eigenvalues
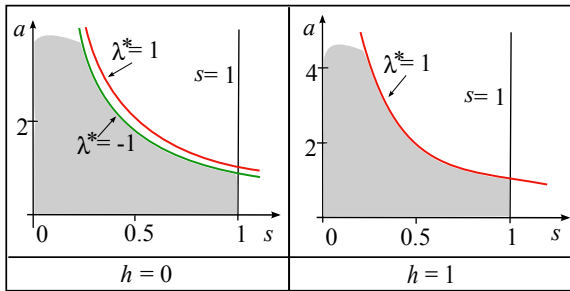
Figure 5. Stability domain of the non-zero equilibrium for the system (6).

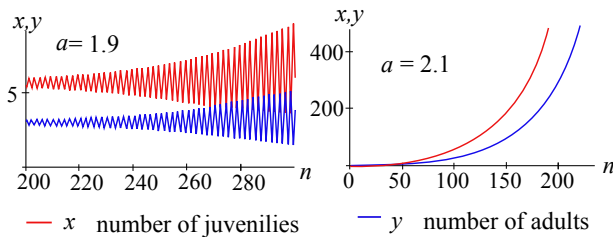— x number of juvenilies   — y number of adults

Figure 6. Trajectories of the system (6) at $h = 0, s = 0.5$, for the different values of the reproductive potential of the population.

transition through -1 and the 2-cycle emergence. However, the parameter domain supporting the periodic dynamics is small (it achieves the maximum size at $h = 0$ which corresponds to the limiting version of the model (6) at $\gamma = 0$, fig.5). Further increase of the parameters and crossing over the bifurcation boundary $as = 1$ leads to the unlimited growth of the population.

Fig.6 shows the behavior of the trajectories of the system (6) depending on the values of the reproductive potential at $h = 0$.

At $h \geq 1$ the curve (9) is outside the domain of positive parameter values; therefore, we do not observe any stable cycles. Non-zero equilibrium (7) is stable over the entire domain. Loss of stability happens with the crossing over the bifurcation boundary $as = 1$ and is accompanied by unrestricted population growth.

4 Conclusion

The offspring survival decrease, which is directly or indirectly related to its number growth, is also common among mammals, small and large. However, we find that just this mechanism of population growth control can lead to complex population oscillations if reproductive potential increases. We are just beginning to appreciate the possibilities of evolutionary behavior of the ecologically limited populations with age structure [Ginzburg and etc.,2010; Ferriere, Gatto, 1993; Charlesworth,1993; Frisman, Zhdanova,2009]. Scenarios of their genetic and dynamic development are very impressive and are by far not fully understood and described.

The parametric stability domain of the population

grows if the juvenile survival rate depends not only on their number, but also modestly depends on the number of adults. Moreover, the regulation of the juvenile survival rate mostly by the number of adults appears to be inefficient; the stability domain substantially contracts, and leaving the domain leads to the oscillations of a large magnitude.

Thus, adding the restricting power of the juvenile number to the model increases the stability domain of the population and eventually makes the oscillatory dynamics impossible. However, stability domain is still rather small, so we can assume that the decrease in the adult survival rate with the population growth cannot efficiently control the population size. However, limiting of the adult survival rate by the numbers of both age groups may be able to considerably weaken intensity and magnitude of population oscillations.

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