

Continuous-discrete model of predator-prey system dynamics with satiation effect

Utyupin Yu.V.¹, Utyupina S.P.¹, Nedorezov L.V.²

¹Siberian Research Institute of Geology, Geophysics and Mineral Resources

E-mail: yuraut@yandex.ru

²University of Nova Gorica, Slovenia

E-mail l.v.nedorezov@gmail.com

Abstract. Model of predator-prey system dynamics with satiation effect is considered. Within the framework of model it is assumed that appearance of new individuals of both populations is considered at fixed time moments. Death processes of individuals have continuous nature. Obtained dynamic regimes are discussed.

Description of model

In our previous publication (Utyupin, Nedorezov, 2014) continuous-discrete model of predator-prey system dynamics was considered. Analyzed model had three variables: $x(t)$ is number of preys at moment t , $z(t)$ is number of predators, and $W(t)$ which is equal to total sum of food in digestive system of all predators at time moment t . In current publication we consider modification of this model when $W(t)$ isn't a total sum of food in digestive system of all predators but sum of food in digestive system (DS) of one predator.

It leads to necessity of modification of all equations of model (Utyupin, Nedorezov, 2014). Moreover, model can be simplified: we'll assume that variable $W(t)$ is fast with respect to two other variables $x(t)$ and $z(t)$. One more simplification is following: we'll assume that there are no self-regulative mechanisms in predator population, and respectively number of preys (food conditions) is unique regulator of number of predators. These simplifications allow giving deeper analysis of model of predator-prey system dynamics than we could provide for previous model.

Let's assume that on every time interval $[t_k, t_{k+1})$ dynamics of considering system is described by the following equations (Isaev et al., 1984, 2001):

$$\frac{dx}{dt} = -a_1x - b_1x^2 - c_1 \frac{xz}{x + A},$$

$$\frac{dz}{dt} = -a_2 z - b_2 \frac{z}{x + A}, \quad (1)$$

In system (1) parameter a_1 is intensity of natural death rate of preys; b_1 is coefficient of self-regulation in population of preys; coefficient c_1 is maximum of intensity of predation (when number of preys is rather big, $x \gg A$), and c_1/A is minimum of intensity of predation (when number of preys is rather small, $x \ll A$). Parameter a_2 is intensity of natural death rate of predators; parameter b_2 is an intensity of additional death process which determines by the existence of food conditions: it decreases at increase of number of preys, and it increases with increase of number of predators. All parameters in model (1) are non-negative.

At time moments t_{k+1} of appearance of individuals of new generation the following relations are truthful (Nedorezov, Utyupin, 2011; Nedorezov, 2012):

$$\begin{aligned} x(t_{k+1}) &= Y_1 x(t_{k+1} - 0), \\ z(t_{k+1}) &= f(\theta) z(t_{k+1} - 0). \end{aligned} \quad (2)$$

In (2) Y_1 is productivity of preys survived to time t_{k+1} ; function θ describes food conditions for predators during certain time period $[t_{k+1} - \tau, t_{k+1})$:

$$\theta = \frac{1}{h} \int_{t_{k+1} - \tau}^{t_{k+1} - 0} \frac{x(u)}{x(u) + A} du.$$

Non-negative function $f(\theta)$ has following properties:

$$f(\theta) \in C, \quad f(0) = 0, \quad \frac{df}{d\theta} > 0.$$

Making situation simpler we'll assume that $\tau = 0$ and $f(\theta) = Y_2 \theta$. After this simplification conditions (2) will have the following forms:

$$\begin{aligned} x(t_{k+1}) &= Y_1 x(t_{k+1} - 0), \\ z(t_{k+1}) &= \frac{Y_2 x(t_{k+1} - 0) z(t_{k+1} - 0)}{x(t_{k+1} - 0) + A}. \end{aligned} \quad (3)$$

Without losing generality we can put that $h = b_1 = c_1 = 1$ (it can be provided with simple transformation of variables). System (1) will have the form:

$$\begin{aligned} \frac{dx}{dt} &= -a_1 x - x^2 - \frac{xz}{x + A}, \\ \frac{dz}{dt} &= -a_2 z - b_2 \frac{z}{x + A}. \end{aligned} \quad (4)$$

Properties of model (3)-(4)

Model (3)-(4) has following obvious properties:

1. Solutions of model with non-negative initial values will be non-negative for all $t > 0$.
2. There exists value $x = \bar{x}$ and all trajectories with non-zero initial values come into the strip $0 < x \leq \bar{x}$. If $z(0) = 0$ model (3)-(4) transforms into the following system of equations:

$$\frac{dx}{dt} = -a_1x - x^2,$$

$$x(t_{k+1}) = Y_1x(t_{k+1} - 0).$$

Solution of this system gives the following recurrence equation:

$$x(t_{k+1}) = \frac{Y_1a_1x(t_k)}{(e^{a_1} - 1)x(t_k) + a_1e^{a_1}}.$$

This equation is well-known Kostitzin model (Kostitzin, 1937) which has one non-zero global stable equilibrium:

$$\bar{x} = \frac{a_1(Y_1 - e^{a_1})}{e^{a_1} - 1}.$$

This equilibrium exists if and only if the following inequality is truthful:

$$Y_1 > e^{a_1}. \tag{5}$$

If condition (5) isn't truthful origin is global stable equilibrium. Thus, below we'll assume that condition (5) is truthful for model parameters.

3. Let's consider an image of half-line $x = \bar{x}$, $0 \leq z < \infty$ which can be obtained after one iteration determined by the model (3)-(4). It is important to note that transformation determined by equations (3)-(4) is continuous because equations for "jumps" of trajectories (3) are determined by continuous functions, and for system (4) conditions of theorem about continuous dependence on parameters are realized. Thus, considering half-line transforms into continuous line after iteration. Note that stationary state $(\bar{x}, 0)$ transforms into itself.

It is possible to prove that image of point (\bar{x}, z) when $z \rightarrow \infty$, converges to origin. Let $x(t)$ and $z(t)$ be solutions of system (4) with initial point (\bar{x}, z_0) . Taking into account that inequalities $z_1(t) < z(t) < z_2(t)$ are truthful where $z_1(t)$ is solution of equation

$$\frac{dz_1}{dt} = -a_2z_1 - b_2 \frac{z_1}{A}, \tag{6}$$

and $z_2(t)$ is solution of equation

$$\frac{dz_2}{dt} = -a_2z_2 - b_2 \frac{z_2}{\bar{x} + A}, \tag{7}$$

with initial values $z_i(t_0) = z_0$, $i = 1, 2$, we can show that $x(t) < x_1(t)$ where $x_1(t)$ is solution of equation

$$\frac{dx_1}{dt} = -\frac{x_1 z_1}{x_1 + A}, \quad (8)$$

with initial values $x_1(t_0) = \bar{x}$. Thus, the following inequality is truthful:

$$z(t_0 + 1) = Y_2 \frac{x(t_0 + 1 - 0)z(t_0 + 1 - 0)}{x(t_0 + 1 - 0) + A} < Y_2 \frac{x_1(t_0 + 1 - 0)z_2(t_0 + 1 - 0)}{x_1(t_0 + 1 - 0) + A}.$$

Solutions of equations (6)-(8) give us following relations:

$$z_2(t_0 + 1 - 0) = z_0 e^{-C_2},$$

$$x_1(t_0 + 1 - 0) + \ln(x_1(t_0 + 1 - 0)) = \bar{x} + \ln \bar{x} - \frac{z_0}{C_1} (1 - e^{-C_1}),$$

where

$$C_1 = a_2 + \frac{b_2}{A}, \quad C_2 = a_2 + \frac{b_2}{\bar{x} + A}.$$

When $z_0 \rightarrow \infty$ we have

$$x_1(t_0 + 1 - 0) \rightarrow \exp\left(\bar{x} + \ln \bar{x} - \frac{z_0}{C_1} (1 - e^{-C_1})\right).$$

Thus the following inequality is truthful at $z_0 \rightarrow \infty$:

$$z(t_0 + 1) \leq \exp\left(\bar{x} + \ln \bar{x} - \frac{z_0}{C_1} (1 - e^{-C_1})\right) z_0 e^{C_2}.$$

This inequality allows us concluding that at $z_0 \rightarrow \infty$ image of point (\bar{x}, z_0) converges to origin. In other words, strip $(0, \bar{x}) \times (0, \infty)$ transforms into closed limited domain D . Respectively, we obtain that second variable is limited too.

4. Let's analyze conditions of stability of point $(\bar{x}, 0)$. Note that within the limits of rather small domain near this point system (4) has the following form:

$$\begin{aligned} \frac{dx}{dt} &= -a_1 x - x^2, \\ \frac{dz}{dt} &= -a_2 z - b_2 \frac{z}{x + A}, \end{aligned} \quad (9)$$

Let's find solutions of system (9) with initial values $x(0) = x_0$, $z(0) = z_0$. From the first equation of system (9) we have the following function:

$$x(t) = \frac{a_1 x_0}{a_1 e^{a_1 t} + x_0 (e^{a_1 t} - 1)}. \quad (10)$$

This function we have to put into second equation of system (9):

$$\frac{dz}{dt} = -z \left(a_2 + b_2 \frac{e^{a_1 t} (a_1 + x_0) - x_0}{x_0 (a_1 - A) + A e^{a_1 t} (a_1 + x_0)} \right).$$

Solution of this equation gives the next result:

$$z(t) = z_0 e^{-a_2 t + \frac{b_2 t}{a_1 - A} \left(\frac{e^{a_1 t} A (a_1 + x_0) + x_0 (a_1 - A)}{a_1 (A + x_0)} \right)^{\frac{b_2}{A(a_1 - A)}}}.$$

At time moment $t=1$ numbers of individuals survived to this moment, are determined by the relations:

$$x(1-0) = \frac{a_1 x_0}{a_1 e^{a_1} + x_0 (e^{a_1} - 1)},$$

$$z(1-0) = z_0 e^{-a_2 + \frac{b_2}{a_1 - A} \left(\frac{e^{a_1} A (a_1 + x_0) + x_0 (a_1 - A)}{a_1 (A + x_0)} \right)^{\frac{b_2}{A(a_1 - A)}}}.$$

Finally, we get the following transformation of first quota of the plane into itself:

$$x(1) = Y_1 x(1-0),$$

$$z(1) = \frac{Y_2 x(1-0) z(1-0)}{x(1-0) + A}.$$

After finding of eigenvalues of Jacobi matrix of this transformation of plane we obtain the following condition of local stability of point $(\bar{x}, 0)$:

$$Y_2 e^{-a_2 + \frac{b_2}{a_1 - A} \frac{a_1 x_0 (a_1 (A + x_0))^{\frac{b_2}{A(a_1 - A)}}}{(x_0 (a_1 + A(e^{a_1} - 1)) + A a_1 e^{a_1})^{\frac{b_2}{A(a_1 - A)}}}} \leq 1.$$

Numerical analysis of model (3)-(4)

Numerical analysis of model was provided in the following manner. All parameters of model were fixed, and Y_2 was used as bifurcation parameter. Changing of structures of phase space was considered at increasing of parameter Y_2 .

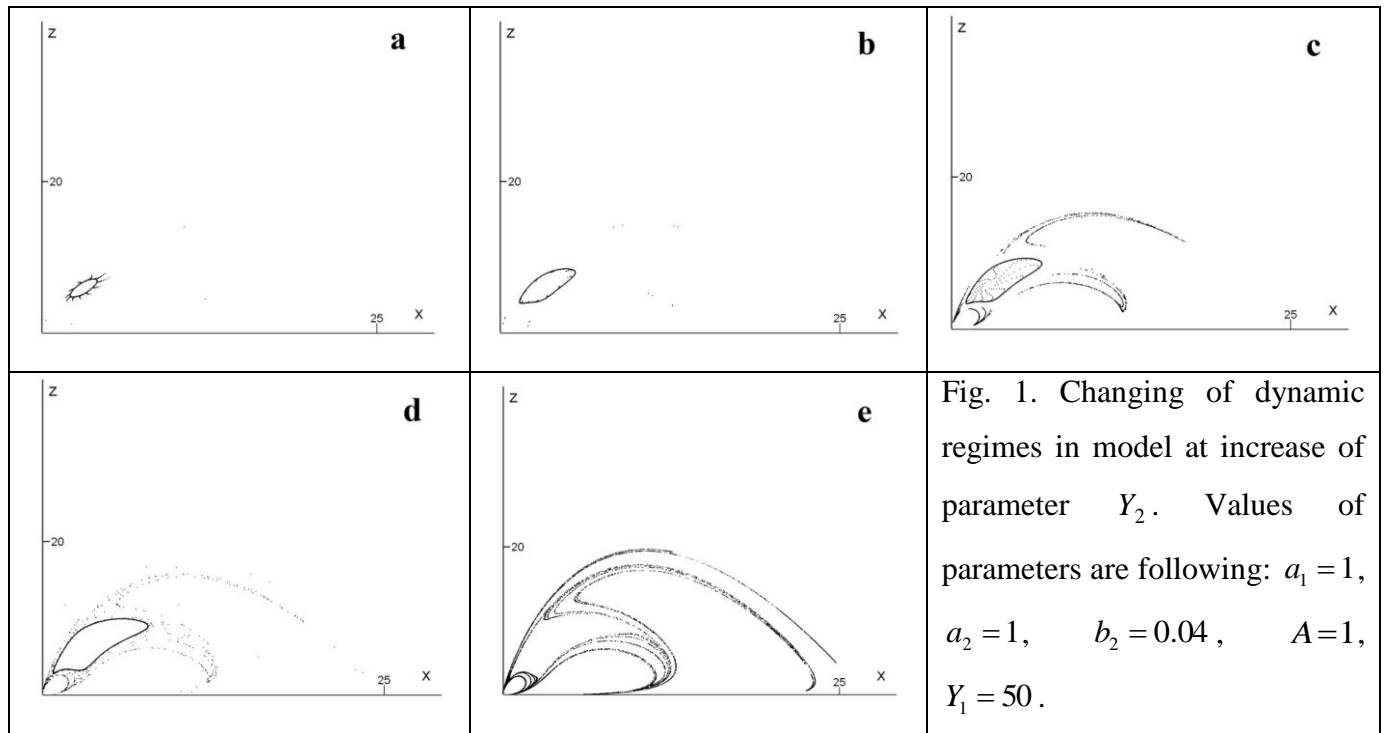
It is obvious, if Y_2 is rather small point $(\bar{x}, 0)$ is global stable equilibrium of system. Predators extinct for all initial values of population sizes. Increase of Y_2 leads to the situation when stationary state $(\bar{x}, 0)$ becomes unstable. This bifurcation leads to appearance of non-trivial stable stationary state.

Note, that it is possible to show that isocline of horizontal inclines (this is a curve which contains points with the following property: images of these points have the same ordinates) intersects

line x and has horizontal asymptote. Isocline of vertical inclines intersects axis z and contains point $(\bar{x}, 0)$. It is also obvious that isocline of horizontal inclines increases strongly in R_+^2 .

When parameter Y_2 increases isocline of horizontal inclines doesn't change, and point of intersection of isocline of vertical inclines with axis x moves left. Thus, non-trivial stationary state moves left along the isocline of vertical inclines when Y_2 increases. Further pictures of bifurcations depend on values of other parameters and can be qualitatively different.

On figure 1 there is one of possible lines of bifurcations of trajectories on phase plane (x, z) . When parameter Y_2 is rather small non-trivial stationary state is global stable equilibrium. Increasing of parameter can lead to situation when non-trivial stationary state continues to be stable but concentration of trajectories leads to appearance of cycles on the plane. At further increase of parameter stationary state becomes unstable, and closed invariant curve appearance on plane (fig. 1a). In a result of bifurcations of duplication of cycle cycles of various lengths can be observed (fig. 1b: there is 16-cycle). Further bifurcations of duplication lead to appearance of stable chaotic attractor (fig. 1c).



At increase of parameter Y_2 chaotic attractor can loose its stability. In this case all trajectories converge to invariant curve (fig. 1d). After a certain number of bifurcations which lead to loosing of stability of attractor and its further restoration, attractor becomes bigger up to its biggest size (fig. 1e). At this situation there are no other stable attractors on the plane.

Thus, analysis of rather simple mathematical model shows that at certain conditions difficult dynamic regimes can be observed on phase plane. At present time there are no possibilities to establish correspondence between model dynamic regimes and regimes observed in natural conditions.

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