ABOUT A CONTINUOUS-DISCRETE MODEL
OF PREDATOR-PREY SYSTEM DYNAMICS

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Abstract. In current publication mathematical model of predator-prey system dynamics is considered. It is assumed that death process in populations has a continuous nature, and appearance of individuals of new generations is realized at fixed time moments. Dynamics regimes of model are analyzed.

1. Introduction

Models of predator-prey system dynamics of Volterra type (Volterra, 1931; Lotka, 1920, 1925; Goel, Maitra, Montroll, 1971; Pielou, 1977; Maynard Smith, 1968, 1974; Nedorezov, Utyupin, 2011 and many others) have one common problem. The same problem is typical for models of Kolmogorov type (Kolmogoroff, 1936; Rescigno, Richardson, 1967; Rosenzweig, 1969; Isaev et al., 1984, 2001; Nedorezov, 1997, 2012 and others): in both cases we talk about process of transformation of biomass of consumed preys into predators. For example, within the framework of Lotka − Volterra model (Volterra, 1931; Lotka, 1920, 1925) it is assumed that time of process of this transformation is equal to zero:

$$\frac{dx}{dt} = ax - bx^2 - cxz, \quad \frac{dz}{dt} = exz - fz - gz^2. \tag{1}$$

In model (1) $x(t)$ is prey population size at moment t; $z(t)$ is number of predators at the same time moment; a is an intensity of birth process of preys; b and g, $b, g = const \geq 0$, are coefficients of self-regulation; cxz is speed of consumption of preys by predators at moment t and, respectively, exz is a speed of increase of number of predators at the same time moment, $c, e = const > 0$, $c > e$; f is intensity of natural death rate of predators, $f = const > 0$. Inequality $c > e$ is based on assumption

that model (1) is balanced: increase of number of predators cannot be bigger than number of consumed preys.

It is obvious that this assumption about zero transformation time preys into predators has no relation to reality (and doesn't correspond to idea about of a balance of biomass transformation; thus, all models of (1) type are non-balanced models). Serious problem of correct modification of model (1) is following: processes of consumption of preys and appearance of new predators are combined together, and described by one and the same function. Respectively, when we try to modify this function, additional natural questions can arise. For example, when we want to take into account the effect of saturation of predators we use the following expression which describes the process of interaction between species and at the same time the process of increase of number of predators:

$$\frac{hxz}{1+mx}. \tag{2}$$

In expression (2) $h, m = const \geq 0$. This expression looks rather natural: for fixed value z unlimited increase of preys x leads to situation when predators have their maximum value of reproduction, and consumption of preys is determined by number of predators only. On the other hand, for every fixed value x we have to have the respective behavior of expression (2). It is obvious that for every fixed value x and rather small value of predators z reproduction coefficient of predators must have its maximum value. When value of predators z is rather big and continues to increase reproduction coefficient must go to zero: it must be observed as a result of intra-population competition for food. But intra-population competition (gz^2) has no influence on reproduction, and reproduction coefficient of predators is equal to constant for every fixed value x. Thus, it allows concluding that model (1) and expression (2) don't correspond to rather obvious assumptions about interaction between species and their self-regulation.

We cannot obtain better situation after incorporation into model a fixed time lag. In such a situation effect of "double law" can appear in model: individuals live with two or more different laws of population size changing (Nedorezov, 2012, 2013).

In a case when models are systems of recurrence equations we haven't problems of that type. In these models (see, for example, Beddington, Free, Lawton, 1975; Berryman, Turchin, 2001; Maynard Smith, 1968, 1974; Nedorezov, Utyupin, 2011) process of interaction between species, processes of population sizes increasing are described by generalized functions. Thus, in these models it is impossible to divide processes of interaction, self-regulations, and birth-death processes.

In most cases these generalized functions are rather simple. Respectively, these models can be effectively analyzed with the help of computer. At the same time analytical investigations of such models can meet with serious problems.

In current publication we'll analyze continuous-discrete model of predator-prey model dynamics which is really balanced. Within the framework of model processes of consumption and reproduction are divided. This model doesn't look like models of Volterra type (1), and analysis of this model meets with serious problems even in most primitive cases.

2. Model

Let's assume that we have fixed time moments t_k, $t_{k+1} - t_k = h = \text{const} > 0$, of appearance of individuals of new generations of both populations. Let $x(t)$ be a number of preys at moment t, $z(t)$ be a number of predators at the same time moment. Within the framework of model we'll assume that t is continuous variable. Between fixed time moments t_k we observe monotonic decreasing of numbers of both species in result of natural death, self-regulation, and interaction between predators and preys.

Let's note that in general cases changing of population sizes are realized at different time moments. Moreover, during a certain time interval one of populations may have several generations, and, respectively, its number plays a role of fast variable with respect to another one. It leads to appearance of so-called "narrow phase portraits" (Nedorezov, Khlebopros, 1985; Isaev, Nedorezov, Khlebopros, 1995; Isaev et al., 2001).

Let $x_k = x(t_k), z_k = z(t_k)$ be population sizes of preys and predators after appearance of individuals of new generations; $x(t_k - 0)$ and $z(t_k - 0)$ are the numbers of survived individuals to moment t_k, i.e. numbers of individuals which can produce new individuals. On every time interval $[t_k, t_{k+1})$ dynamics of preys we'll describe as first equation of system (1):

$$\frac{dx}{dt} = -a_1 x - b_1 x^2 - cxz. \tag{3}$$

In equation (3) parameter a_1 is intensity of natural death rate of preys (part of parameter a in equation (1)); b_1 is coefficient of self-regulation in population of preys; c is coefficient of consumption of preys: its amount depends on a level of saturation of predators. It is obvious that $a_1, b_1 = const > 0$.

Let's introduce into considering model one more variable $W(t)$ which is equal to total sum of food in digestive system of all predators at time moment t. Let W_0 be a maximum volume of one predator. If so, for every time moment t the following inequality must be truthful:

$$W(t) \leq W_0 z(t).$$

If expression cxz describes the speed of consumption of preys by predators then expression $kcxz$ describes the speed of food flow into digestive system of predators, $k = const$, $0 < k < 1$. Coefficient k is equal to quota of loss of biomass. Maximum volume of biomass in digestive system

of predators is equal to $W_0 z(t)$ at moment t. Thus, the level of satiety of predators can be estimated with following expression:

$$\theta = W_0 z(t) - W(t).$$

It is naturally to assume that increase of amount θ leads to increase of speed of consumption of preys; respectively, $c(0)$ is a minimum value of this function (and this minimum can be equal to zero):

$$\forall\, \theta \quad c(\theta) \geq c(0) \geq 0, \quad \frac{dc}{d\theta} \geq 0.$$

Numerical investigation of model was provided for $c(\theta) = c_1 \theta$, $c_1 = const > 0$.

Dynamics of predators on time interval $[t_k, t_{k+1})$ we'll describe as following:

$$\frac{dz}{dt} = -a_2 z - b_2 z^2. \tag{4}$$

In (4) coefficient a_2 is intensity of natural death rate of predators; b_2 is coefficient of self-regulation. Note, that in general case amounts of these coefficients are not constants and depend on values of variable θ: intensity of death rate of hungry predators is bigger than intensity of death rate of replete of food predators. For fixed number of predators we may have rather small number of preys, and it can lead to increase of additional death rate which is determined by self-regulative intra-population mechanisms. Thus, for functions a_2 and b_2 the following conditions must be truthful:

$$a_2(0) > 0, \quad \frac{da_2}{d\theta} \geq 0; \quad b_2(0) \geq 0, \quad \frac{db_2}{d\theta} \geq 0. \tag{5}$$

Note, that conditions (5) for function b_2 are rather natural and we can assume that such dependence on θ can be observed in nature; at the same time dependence of function a_2 on θ may have more complicated nature. Intensity of death rate a_2 of predators may depend not on current value of level of fullness of digestive system but on integral of θ for certain time interval. Numerical investigations of model were provided with $b_2 = const > 0$, $a_2(\theta) = a_2^0 + a_2^1 \theta$ where $a_2^0, a_2^1 = const > 0$.

Dynamics of fullness of digestive system is determined by influence of three following processes: inflow of food (in a result of consumption of preys), natural outflow from this system, and outflow which depends on death of predators. As it was pointed out above increase of value of variable $W(t)$ is realized with speed $kcxz$. For the first time a speed of natural outflow from digestive system can be assumed to be proportional to $W(t)$ with constant coefficient q.

For time interval $\Delta t \to 0$ population of predators can be decreased on $(a_2 z + b_2 z^2)\Delta t$ individuals. Respectively, with every dead individual system loses $W(t)/z(t)$ of food. Thus, total decreases of food is equal to $(a_2 + b_2 z)W\Delta t$. Finally, dynamics of variable $W(t)$ can be described with following equation:

$$\frac{dW}{dt} = kcxz - qW - (a_2 + b_2 z)W. \tag{6}$$

Combining all equations (3)-(6) we obtain the model of predator-prey system dynamics on time interval $[t_k, t_{k+1})$. Let Y_1 and Y_2 be amounts of productivities of preys and predators respectively. These amounts are equal to averages of offspring of preys and predators survived to fixed time moment. If volume of food for preys is rather big we can assume that Y_1 is constant. But in general case amount of Y_1 depends on food conditions for preys during a certain time interval. Numerical investigation of model was provided for $Y_1 = const > 1$. For this condition and $z_0 = 0$, $x_0 > 0$ population size of preys is stabilized at unique global non-trivial stationary state (Nedorezov, Nedorezova, 1995). Taking into account all notifications introduced above we can conclude that changing of number of preys at fixed time moments is determined by the following expression:

$$x_{k+1} = x(t_{k+1}) = Y_1 x(t_{k+1} - 0).$$

For preys we can point out conditions when their productivity can be assumed to be a constant. But for predators such assumption is unrealistic. Their productivity depends on food conditions: in other words, it depends on average of θ on certain time interval. Decreasing of this average leads to the respective (monotonic) decrease of productivity of predators. Moreover, productivity of predators must depend on speed of inflow of food into digestive system: increasing of this speed (it is obvious, that amount of this speed characterizes food conditions for predators) leads to increasing of productivity. Let $\bar{v}$ be an average of food flow into digestive system, and $\bar{\theta}$ be an average of function θ on the same time interval:

$$\bar{v} = \int_{t_k}^{t_{k+1}} c(u)x(u)z(u)\,du, \quad \bar{\theta} = \frac{1}{h}\int_{t_k}^{t_{k+1}} \theta(u)\,du.$$

Thus, we have $Y_2 = Y_2(\bar{\theta}, \bar{v})$. Changing of number of predators at fixed time moments is determined by the following expression:

$$z_{k+1} = z(t_{k+1}) = Y_2 z(t_{k+1} - 0).$$

For numerical analysis it was assumed that

$$Y_2 = Y_2(\bar{\theta}) = Y_2^0 e^{-s\bar{\theta}} \int_{t_k}^{t_{k+1}} c(u)x(u)z(u)\,du.$$

Parameter Y_2^0 is positive coefficient. Parameter s corresponds to sensitivity of predator's productivity to food conditions.

Question about changing of variable $W(t)$ isn't clear. In most primitive case we can assume that the following relation is truthful:

$$W(t_{k+1}) = pW(t_{k+1} - 0).$$

Parameter p is constant, $p = \mathrm{const}$, and $0 < p < 1$.

Model (3)-(6) described above has following obvious properties. For non-negative and finite initial values of variables solutions of model are non-negative and bounded. There exists stable invariant compact (which contains origin) in non-negative part of phase space of system. If $Y_1 < \exp(a_1 h)$ origin is global stable state of system: both populations eliminate asymptotically. If $Y_2(0) < 1$ predators extinct for all initial values of population size; if, additionally, inequality $Y_1 > \exp(a_1 h)$ is truthful size of population of preys stabilizes at unique positive stationary state (for pointed out conditions this stationary state is global stable attractor).
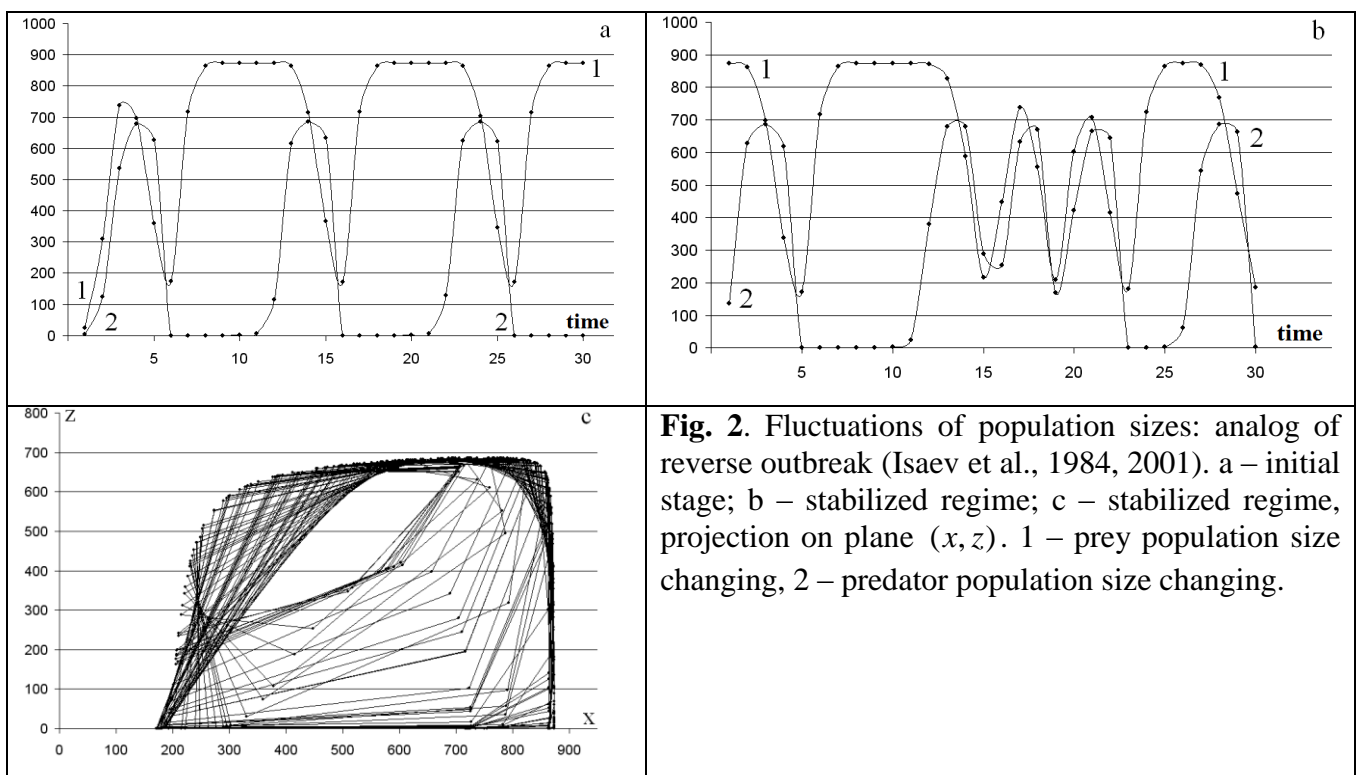
3. Numerical analysis

On figure 1a there is the dynamic regime obtained for the following model parameters:
$a_1 = 0.07$, $b_1 = 0.020918$, $c_1 = 1.2$, $W_0 = 1$, $k = 0.7$, $a_2^0 = 0.002$, $a_2^1 = 300$, $b_2 = 0.15$, $q = 0.0023$, $Y_1 = 20$, $Y_2^0 = 5 \cdot 10^8$, $s = 0.0001$, $p = 0.9$.
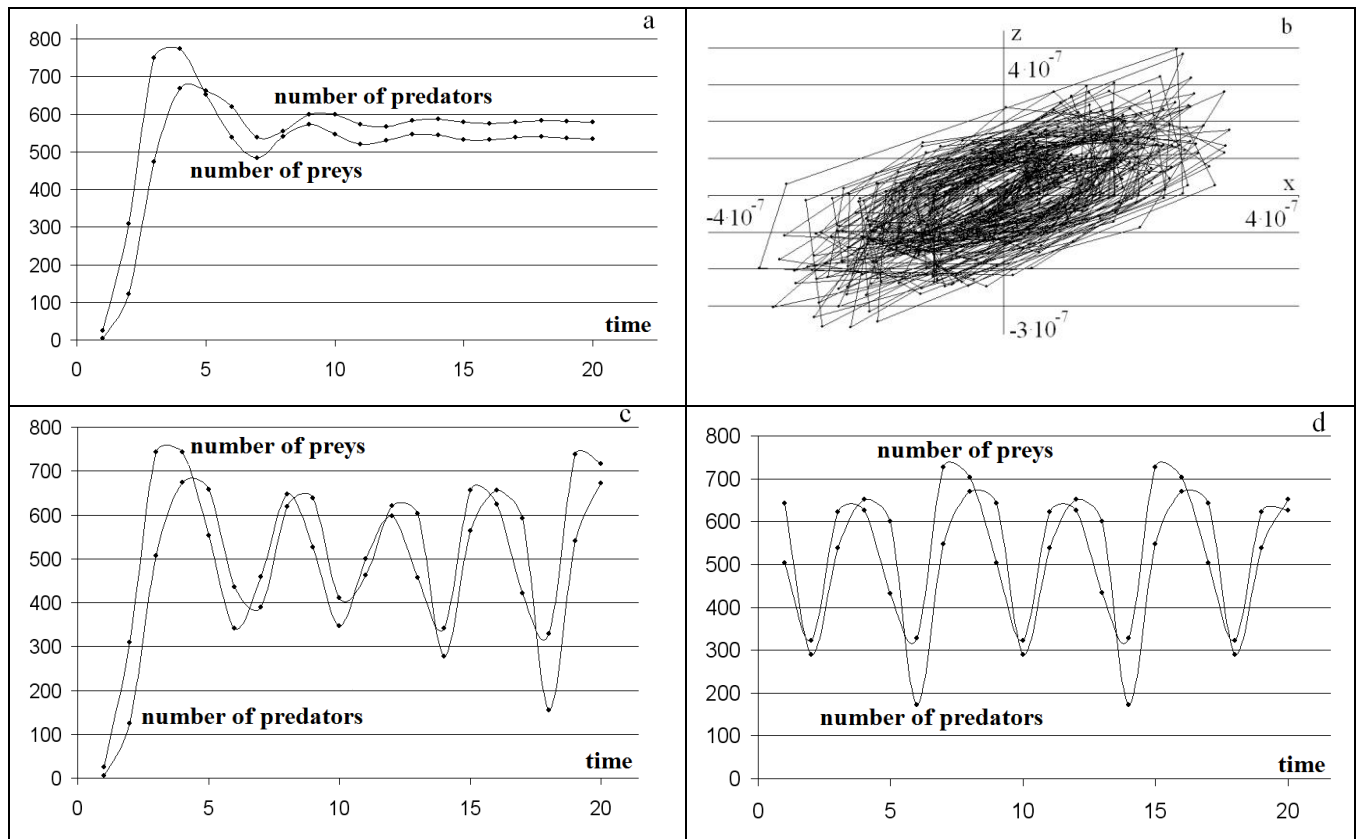
Fig. 1. Selected dynamic regimes of model (3)-(6). a – regime of small fluctuations near positive values (initial stage of regime); b – the same regime, fluctuations of population sizes on the plane (x, z) in stationary (stabilized) regime; c – cyclic fluctuations (initial stage of regime); d – the same regime, stabilized regime.

On fig. 1 there is a dynamic regime which looks like the regime of fading fluctuations near positive levels. But in reality this is non-fading fluctuations (stationary regime of population sizes behavior) near averages $\bar{x} \approx 537.1762$ and $\bar{z} \approx 579.8717$ with rather small amplitude of deviations (deviations belong to set $[-4 \cdot 10^{-7}, 4 \cdot 10^{-7}] \times [-4 \cdot 10^{-7}, 4 \cdot 10^{-7}]$, fig. 1b). If this regime is cyclic it has length which is more than 1000.

On figures 1c and 1d regime of periodic fluctuations (initial stage and regime under stabilized conditions) of population sizes is presented. This regime was found for $c_1 = 1.4$ when predators have more strong influence on preys than in previous case. Other parameters have the same values. Note, that presented cycle is also fuzzy.

Fig. 2. Fluctuations of population sizes: analog of reverse outbreak (Isaev et al., 1984, 2001). a – initial stage; b – stabilized regime; c – stabilized regime, projection on plane (x, z). 1 – prey population size changing, 2 – predator population size changing.

Further increasing of this parameter, $c_1 = 1.65$, leads to realization of very interesting dynamic regime (fig. 2) which looks like a regime of reverse outbreak analyzed in our previous publications (Isaev et al., 1984, 2001). Basic regime of reverse outbreak is characterized by the following features: under normal conditions population density of preys is rather big; influence of unfavorable weather conditions and decreasing of density to certain threshold lead to situation when density continuous to go down under favorable conditions. Later density returns back to previous amounts.

On fig. 2a we can observe the similar situation. During rather long time period (6 time steps) population size continuous to be rather gig (it is about 900). After that it decreases (to a certain minimum value) with further stabilization on previous high level.

Note, that analog of reverse outbreak within the limits of model (3)-(6) is observed under stabilized conditions. Thus, we can point out basic differences between original dynamic regime and its analog: in last case we didn't talk about unfavorable influence of weather conditions. As we can see on fig. 2c this regime is periodic, and its correspondence with reverse outbreak regime can be explained as non-homogenous moving of system along the cycle. It is interesting to note: prey population size changing looks like a reverse outbreak (fig. 2) but at the same time predator population size changing looks like an outbreak proper (Isaev et al., 1984, 2001).

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