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Continuous-discrete model of population dynamics with time lag in a reaction of intra-population self-regulative mechanisms

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Abstract

Continuous-discrete model of population dynamics is considered in current publication. It is assumed that death process of individuals has a continuous nature, and appearences of individuals of new generations are observed at fixed time moments. It is also assumed that population has non-overlapping generations, and for every generation self-regulative mechanisms have distributed time lag in reaction on population size changing. For particular case when death rate of individuals between fixed time moments corresponds to Verhulst's law, it was obtained that various cyclic regimes can be observed in phase space. For various values of model parameters the structure of domain in space of parameters, where chaotic dynamic regimes can be realized, is described.

Keywords population dynamics; mathematical model; broken trajectories; time lag; reaction; self-regulative mechanisms.

1 Introduction

It is possible to point out several main goals of the development of theory of continuous-discrete models of population dynamics (differential equations with impulses; Poulsen, 1979; Aagard-Hansen, Yeo, 1984; Nedorezov, 1986, 1997; Nedorezov and Nedorezova, 1994, 1995; Il'ichev, 2004; Kulik and Tisdell, 2008; Mailleret and Lemesle, 2009; Nedorezov et al., 2010; Nedorezov and Utyupin, 2011, and others). First of all, it gives a background for using discrete mathematical models (maps, models with discrete time) for fitting empirical datasets, for new and qualitative (from biological point of view) interpretations of discrete model parameters (Tonnang et al., 2009, 2010; Nedorezov and Sadykova, 2008, 2010; Nedorezova and Nedorezov, 2012). It is well-known that discrete models play very important role in description of dynamics of various populations and in development of methods of optimal management (Ricker, 1954; Vorontsov, 1978; Isaev et al., 2009; Sharma and Raborn, 2011; Griebeler, 2011; Nedorezov, 2012, and others).

The second, it allows obtaining new discrete models of population dynamics which cannot be obtained using traditional ways for discrete models development (Nedorezov and Utyupin, 2011). The third, continuous-discrete models give more realistic description of population processes in various cases. For example, within the limits of this approach we can get more realistic models for population dynamics in boreal zone, for management process of exploited populations etc.

Time lag in a reaction of regulative mechanisms onto population size changing is one of the basic properties of natural regulators. In some ecological theories time lag is marked as main property of population

regulators, and pointed out that interaction of population with regulator with respective time lag can lead to realization of outbreak regimes (Isaev et al., 1984, 2001, 2009; Berryman, 1981). Our previous publications (Nedorezov and Nazarov, 1998, 2000; Nedorezov et al., 1998) were devoted to constructing and analyses of continuous-discrete models when population dynamics in current vegetation season depends on averages of population sizes in some previous vegetation periods. Current publication is devoted to constructing and analysis of model of population dynamics when intra-population regulative mechanisms have time lag within the vegetation time interval, and have influence on dynamics of one generation only.

2 Model Description

Let's assume that at fixed time moments t_k, $t_{k+1} - t_k = const = h > 0$, $k = 0,1,2...$, there are the appearance of individuals of new generations and death of all individuals of previous generation. It means that in considering situation there is non-overlapping generations. Let $x(t)$ be the population size at time moment t, and $x(t_k - 0)$ be the number of individuals survived to moment t_k. If Y is average productivity of individuals then changing of population size at fixed moments t_k can be described with the following equation

$$x_k = x(t_k) = Yx(t_k - 0).$$ (1)

Below it is assumed that $Y = const > 0$. But in general case it isn't true, and productivity depends on food conditions for individuals during the vegetation period (or part of this period). In particular, it can lead to the dependence of productivity of individuals of current generation on food conditions in previous vegetation periods (Nedorezov, Nazarov, 1998, 2000).

On every time interval $[t_{k-1}, t_k)$ population dynamics will be described with following differential equation

$$\frac{dx}{dt} = -xR(\theta).$$ (2)

In equation (2) $R(\theta)$ is the intensity of death rate of individuals, θ is an average of individuals of current generation on time interval $[t_{k-1}, t)$:

$$\theta = \frac{1}{t - t_k} \int_{t_{k-1}}^{t} x(s)ds.$$

In biggest part of mathematical models of isolated population dynamics it is assumed (Verhulst, 1838; Volterra, 1931; Smith, 1974; Nedorezov, 1986, 1997 and many others) that function R satisfies the following relations

$$R(0) > 0, \ \frac{dR}{d\theta} > 0, \ R(+\infty) = +\infty.$$ (3)

In (3) $R(0)$ is Malthusian parameter (in considering situation $R(0)$ is intensity of death rate when population size is rather small). Increasing of value of function R with increasing of amount of θ correlates with strengthening of influence of intra-population self-regulative mechanisms on population dynamics. Population size changing is graphically presented on Fig. 1.
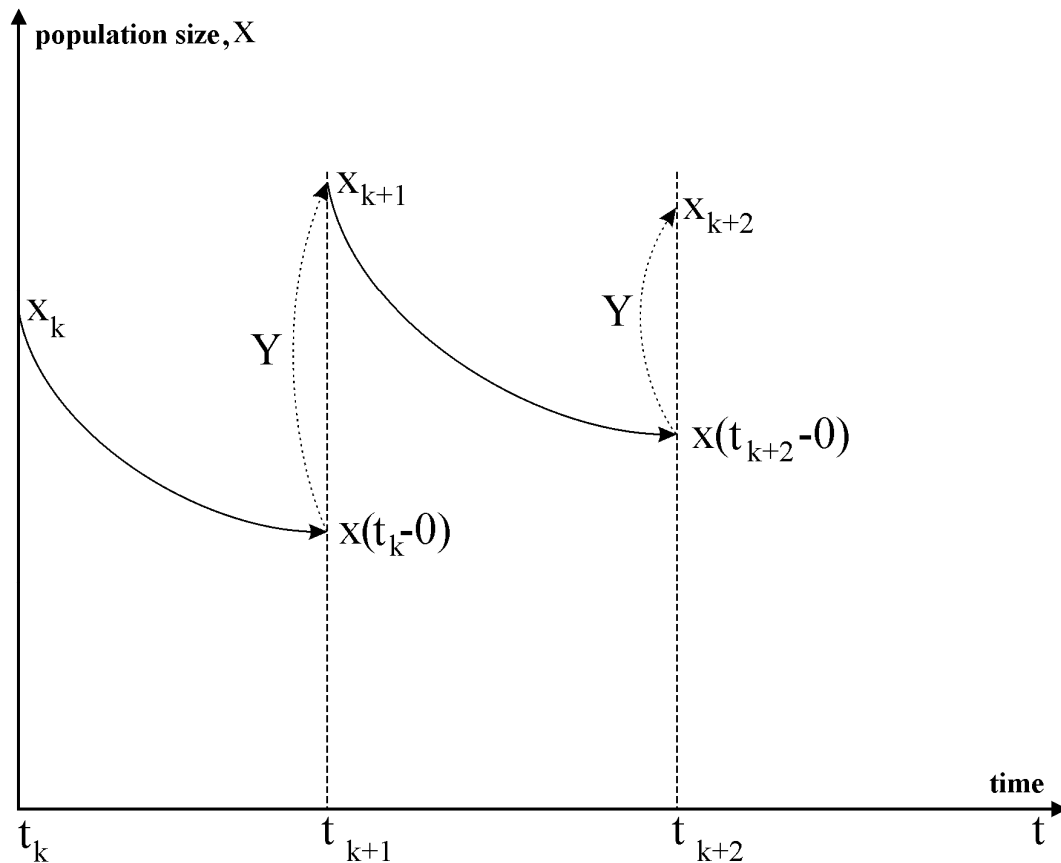
Fig. 1 Population size changing in time.

Thus, introduced time lag into model can be interpreted as indirect description of competition between individuals for food resource. This assumption and interpretation are valid if population fluctuations are not strong enough. And this assumption is truthful for various groups of insects in boreal zone (for example, for indifferent species and for various prodromal species; Isaev et al., 1984, 2001, 2009). But this assumption is not valid for prodromal species with sufficient big fluctuations of population size and for outbreak species – for such species we can observe dependence of population birth rates on conditions of population sizes in previous vegetation periods.

3 Properties of Model (1)-(3)

(1) For all non-negative initial values of population size solutions of model (1)-(3) are non-negative too: if $x(0) = x_0 \geq 0$ then for all $k > 0$ $x_k \geq 0$.

(2) All trajectories of model (1)-(3) are bounded, and it is possible to point out constant C, $C = const > 0$, with the following property: if $x(0) < C$ then $x_k < C$ for all $k > 0$.

(3) If the following inequality

$$Y < e^{R(0)h}$$

stationary state 0 is global stable equilibrium of considering model (condition of population extinction). If the inverse inequality is truthful origin is unstable stationary state: in such a condition population cannot extinct for all initial values of its size.
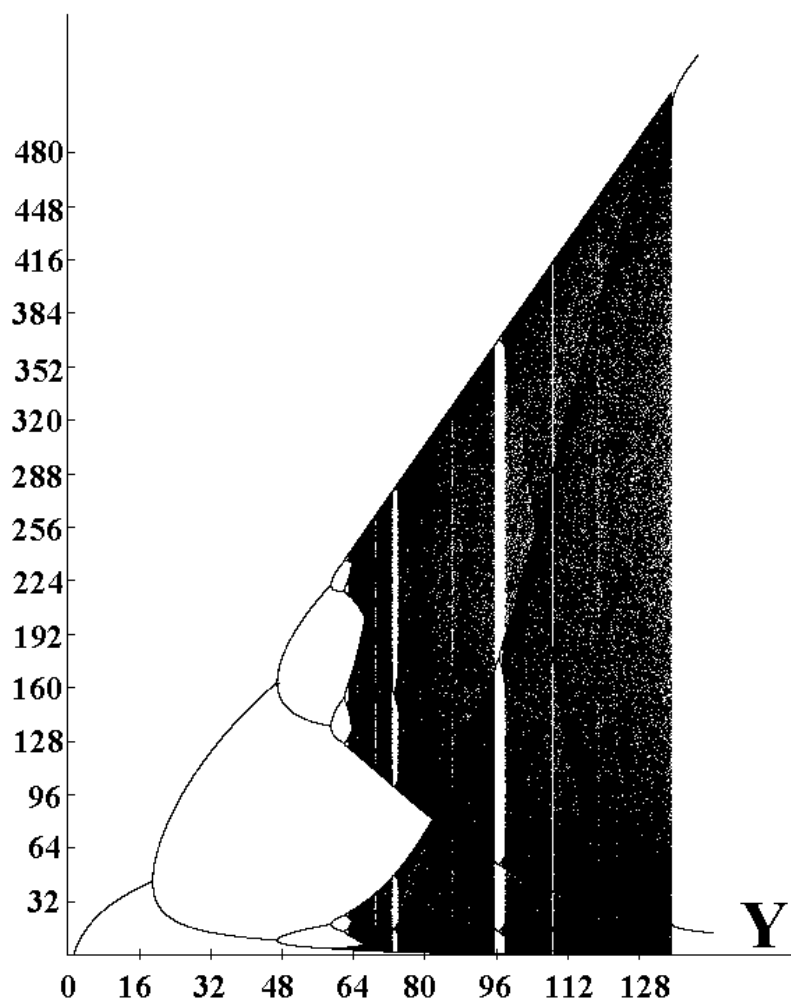
Fig. 2 Bifurcation diagram for model (4) obtained for the following values of model parameters: $\alpha = 0.2$, $\beta = 0.4$, $h = 1$. Ordinate line: coordinates of stable attractors; abscissa line: values of coefficient of productivity

(4) For particular case when $R = \alpha + \beta\theta$ model (1)-(3) can be presented in the following form

$$x_{k+1} = 4Yx_k\left(\alpha^2 + 2\beta x_k\right)\frac{e^{-h\sqrt{\alpha^2 + 2\beta x_k}}}{\left[\sqrt{\alpha^2 + 2\beta x_k} + \alpha + \left(\sqrt{\alpha^2 + 2\beta x_k} - \alpha\right)e^{-h\sqrt{\alpha^2 + 2\beta x_k}}\right]^2} . \tag{4}$$

In Fig. 2, there is the bifurcation diagram for model (4) which was obtained for $\alpha = 0.2$, $\beta = 0.4$, $h = 1$, $0 \le Y \le 160$. As we can see from this picture, if coefficient of productivity Y is rather small population eliminates for all initial values of population size. Increase of coefficient Y leads to appearance of non-trivial stationary state, and population size stabilizes at this level at positive initial values. Further increasing of coefficient Y leads to appearance of stable fluctuations: at initial stages we can observe stable cycles of the lengths 2, 4, 8 etc (Fig. 2). When coefficient Y is big enough we can observe a stable cycle of the length 2 again.

It is important to note that observed complicated dynamical regimes were appeared in a result of existence of time lag in a reaction of self-regulative mechanisms. As it was proved before (Nedorezov and Nedorezova,

1995), if $R = R(x)$ and satisfies to conditions (3) there are no cyclic regimes in a set of model of (1)-(3) type.
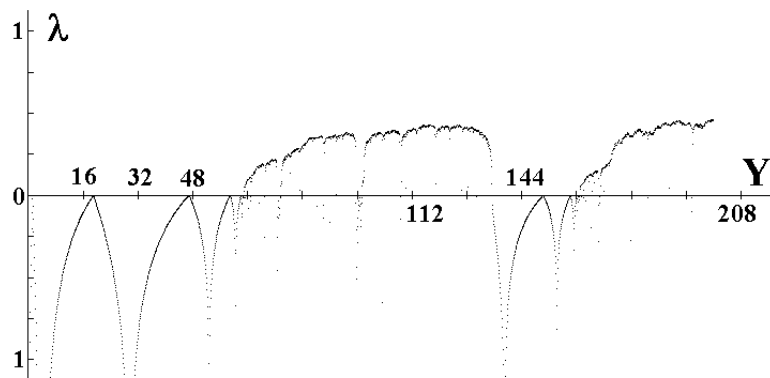

Fig. 3 Behavior of Lyapunov characteristics for $\alpha = 0.2$, $\beta = 0.4$, $h = 1$.

In Fig. 3 there is the graphic of changing of Lyapunov characteristics with respect to coefficient of productivity (for the same values of model parameters $\alpha = 0.2, \beta = 0.4, h = 1$)

$$\lambda(x_0) = \lim_{N \to \infty} \frac{1}{N} \sum_{i=0}^{N-1} \ln\left|f'(x_i)\right|,$$

where f is the function in right-hand side of equation (4), f' is a derivative of function f. As we can see from this picture for determined values of model parameters there is exponential divergence of model trajectories (positive values of Lyapunov characteristics are observed on the picture). Thus, for concrete values of parameters the chaotic behavior of trajectories can be observed.

Theorem (Diamond, 1976): Let I be a set in R^N and $f : I \to R^N$ is a continuous mapping. Suppose that there is a nonempty compact set $X \subset I$ satisfying the conditions

(1) $X \cup f(X) \subset f^{(2)}(X) \subset I$,

(2) $X \cap f(X) = \varnothing$.

Then

For every $k = 1, 2, 3...$ there is a k-periodic set in I;

There is an uncountable set $S \subset I$ containing no periodic points and satisfying the following relations

- $f(S) \subset S$;
- for arbitrary two different points $p \in S$ and $q \in S$ we have

$$\overline{\lim_{k \to \infty}}\left|f^{(k)}(p) - f^{(k)}(q)\right| > 0.$$

- for every point $p \in S$ and every periodic point $q \in I$ we have

$$\overline{\lim_{k \to \infty}} \left| f^{(k)}(p) - f^{(k)}(q) \right| > 0 \,.$$

In Diamond' theorem $f^{(k)}(\cdot)$ is k th iteration of map f. From this theorem we can conclude if conditions 1 and 2 are truthful (for map determined by the relations (1)-(3)) then in phase space of model chaotic trajectories are observed. Results of numerical calculations with model (4) are presented on figures 4 and 5.
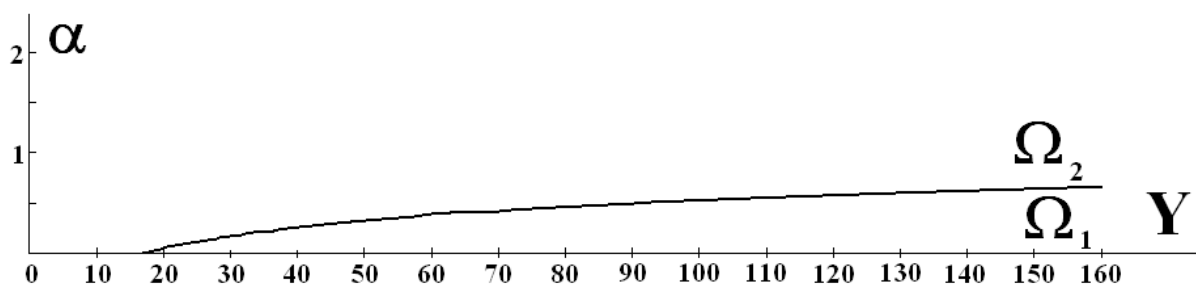

Fig. 4 Structure of the plane (Y, α) at $\beta = 0.4$ and $h = 1$. In domain Ω_1 conditions of Diamond' theorem are truthful; in Ω_2 conditions of theorem are not truthful.

For the situation presented on fig. 4 we can conclude that for fixed coefficient of productivity Y increase of intensity of death rate leads to stabilization of system behavior – increase of value of α leads to disappearance of chaotic trajectories. At the same time for every fixed value of parameter α increase of individuals productivity leads to destabilization of system behavior – increase of parameter Y leads to appearance of chaotic trajectories in phase space.

It is important to note that boundary between domains Ω_1 and Ω_2 (Fig. 4) is below the line $\alpha = \mathrm{Ln}(Y)$ which is the boundary for the domain of population elimination. Thus, for every fixed value of Y increase of death coefficient α leads to impossibility for the realization in phase space of chaotic trajectories, and after that (for big values of parameter α) the regime of non-conditional elimination of population is observed in phase space (elimination for all possible initial values of population size).
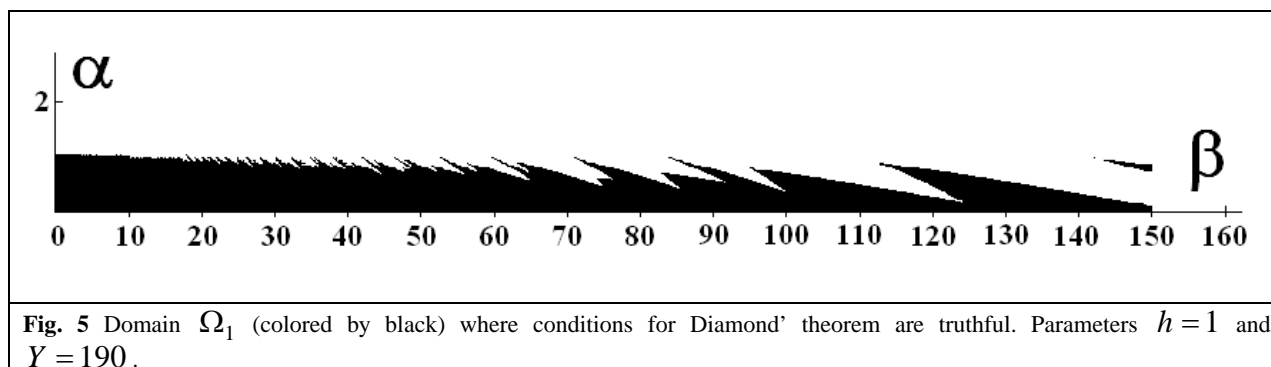

Fig. 5 Domain Ω_1 (colored by black) where conditions for Diamond' theorem are truthful. Parameters $h = 1$ and $Y = 190$.

In Fig. 5 there is the structure of the plane (β, α) for $h = 1$ and $Y = 190$. Boundary between sets Ω_1 and Ω_2 are very complicated, and it doesn't allow giving a description of role of the parameter β in a process of population regulation. Anyway, it allows us to conclude that increase of parameter β leads to the decrease of the interval of parameter α changing where chaotic regimes can be observed.

4 Conclusion

As it was proved before (Nedorezov and Nedorezova, 1995), if regulative mechanisms haven't time lag in their reaction onto population size changing, and productivity of individuals is constant there are no oscillation regimes for population, and population stabilizes asymptotically at unique level for all positive initial values. If regulative mechanisms have a time lag chaotic and oscillation regimes can be observed for population even with constant productivity.

Constructing of models with discrete time is based on the assumption that coefficient of population birth rate (it is determined as relation of population sizes or densities of two nearest generations) can be presented as rather simple function with respect to population size. In most cases investigators present this coefficient as simplest monotonic decreasing function (Nedorezov and Utyupin, 2011) with obvious biological interpretation of model parameters. All classic discrete models of population dynamics were constructed under these assumptions.

But very often investigators meet with serious problems of model parameters interpretation. In particular, if parameter was announced as a characteristics of influence of intra-population self-regulative mechanisms and its increasing corresponds to strengthening of these mechanisms (i.e. coefficient of birth rate is smaller for the same value of population size), then natural question arises: what concrete biological mechanism is on the base of this situation (increasing of value of parameter)? It can be observed, for example, in the results of decreasing of surviving of individuals during the winter time or in a result of strengthening of intra-population competition among individuals. Within the framework of discrete model it is impossible to give an answer in principle.

At the same time using of continuous-discrete models of the type (1)-(3) or (4) allows for investigators to separate all regulative mechanisms, and finally to give an answer on pointed out question. Moreover, within the framework of model (1)-(3) where every parameter has its own biological sense and respective interpretation, we can get very complicated models with discrete time (like model (4)) which doesn't practically allow giving biological interpretation of model parameters. In these discrete models parameters are complicated and depend on characteristics of various population mechanisms.

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