On two-stage continuous-discrete model of population dynamics

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Abstract. In paper two-age continuous-discrete model is analyzed. Within the framework of model it is assumed that appearance of individuals of new generations is realized at fixed time moments $t_k = hk$, $t_0 = 0$, $k = 1,2,...$, $h = const > 0$; at the same time death process of individuals has a continuous nature. Dynamic regimes of model are analyzed.

Introduction

Within the frameworks of simplest mathematical models of population dynamics it is assumed that all individuals haven't age, sex, phase of development etc. (Kostitzin, 1937; Hassell, 1975; Bellows, 1981; Kot, 2001; Nedorezov, 1986, 1997, 2012; Nedorezov, Utyupin, 2011 and others). But it is well-known that individuals of various types have their own sets of predators and parasites; individuals have their own specific reaction on influence of climatic factors, on changing of population size and so on (Odum, 1983; Isaev et al., 1984, 2001, 2009). Individuals of various ages have qualitatively different reactions on influence of climatic factors, self-regulative and regulative mechanisms, and play various roles in reproductive processes. The similar features can be pointed out for individuals of various sexes. Thus, analysis of population dynamics is of special interest when individuals are divided on some special groups with various features. Determination of role of these groups in population dynamics is of special interest too (Caswell, 1989; Logofet, 1993; Brauer, Castillo-Chavez, 2001; May, 1974 and others).

In particular, determination of real role of one or other population structure assumes finding of an answer onto the following question: can considering population structure be a basic reason of the appearance of periodic and/or chaotic fluctuations of population size? If yes, what kind of conditions must be observed for realization of these types of dynamics? In current publication we'll consider a model of population dynamics when individuals are divided onto two groups: it can correspond to existence of simple age or phase structure. Main goal of providing analysis is following: what kind of dynamic regimes can be observed within the framework of considering model?

It is impossible to present an overview of existing models of population dynamics with age (or phase) structures. First model of population dynamics with phase structure was presented in book by V.A. Kostitzin (1937). And this model was applied for the description of insect population dynamics. First model of population dynamics with age structure was created by Leslie (1945, 1948). Analysis of this model and its basic properties (together with various modifications of model) can be found in all textbooks and overviews on ecological modeling (Pielou, 1977; Cushing et al., 1996, 2001; Caswell, 1989; Kot, 2001; Logofet, 1993, 2008 and others).

Within the framework of Leslie model it is assumed that time has a discrete nature, $t = 0,1,2...$, at every time moment we have individuals of several age classes 1,...,*N*. Let $x_k(t)$ be a number of individuals of age class k at moment t. Population condition at moment t is determined by vector $\vec{x}(t) = (x_1(t), x_2(t),..., x_N(t))$. It is also assumed that $x_1(t)$ is number of youngest individuals, and after one time step all individuals of class j, $j < N$, becomes older with coefficient $p_j = const$, $0 \le p_j < 1$. Thus, we have the following system of equations:

$$x_{k+1}(t+1) = p_k x_k(t),\ k = 1,..., N-1. \tag{1}$$

Let $m_j = const \ge 0$ be a number of individuals of first class which are generated by individuals of class j after one time step. Thus, dynamics of individuals of the first class can be described by the following equation:

$$x_1(t+1) = \sum_{k=1}^{N} m_k x_k(t). \tag{2}$$

Leslie model (1)-(2) can be presented in matrix form. Let

$$P = \begin{pmatrix} m_1 & m_2 & \dots & m_{N-1} & m_N \\ p_1 & 0 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & p_{N-1} & 0 \end{pmatrix}.$$

Model (1)-(2) with matrix P has the form

$$\vec{x}(t+1) = P\vec{x}(t). \tag{3}$$

Modifications of Leslie model

It is possible to point out several basic directions in modification of Leslie model (1)-(3):

1. It is naturally to assume that model coefficients m_k and p_k depend on population size or on combination of sizes of age classes when researches try to take into account non-equivalence input of

classes into functioning of self-regulative mechanisms (see, for example, Kot, 2001; Schaffer, Kot, 1985, 1986; Ugarcovici, Weiss, 2004; Eizi, 1983). Really, increasing of population size

$$\theta(t) = x_1(t) + ... + x_N(t),$$

or "weighted" population size

$$\theta(t) = r_1 x_1(t) + ... + r_N x_N(t),$$

where $r_j = const \geq 0$, $j = 1,...,N$, are non-negative coefficients, can lead to increase of death rate (in a result of strengthening of intra-population competition for resources). Respectively, it can lead to decrease of amounts of coefficients p_k. At the same time it can lead to decrease of productivity of individuals (if Allee effect doesn't observe in population; Allee, 1931; Odum, 1983). Thus, following conditions for functions m_k and p_k look rather natural:

$$\forall \theta: \ m_k = m_k(\theta) \geq 0, \ p_k = p_k(\theta) \geq 0; \ \frac{dm_k}{d\theta} \leq 0, \ \frac{dp_k}{d\theta} \leq 0.$$

2. In various situations it is very difficult to determine a real age of individual. In this situation we have to talk about age classes, and for every individual it is possible to say it belongs to any age class or doesn't belong to this class. Modification of Leslie model for considering situation has the name "Leslie – Lefkovitch model" (Lefkovitch, 1965; Logofet, 1993, 2005, 2008; Logofet et al., 2006; Law, 1983; Csetenyi, Logofet, 1989). Basic equation is the same like in Leslie model (3). But matrix P has other structure.

In particular, in publication by D.O. Logofet and I.N. Klochkova (2002) dynamics of *Aporrectodea caliginosa* was analyzed. For individuals the following phases of development were selected: cocoon, juvenile phase, and four phases corresponding to adults. Matrix P for *Aporrectodea caliginosa* had the form:

$$P = \begin{pmatrix} 0 & 0 & m_3 & m_4 & m_5 & m_6 \\ s_1 & r_1 & 0 & 0 & 0 & 0 \\ 0 & s_2 & r_2 & 0 & 0 & 0 \\ 0 & 0 & s_3 & r_3 & 0 & 0 \\ 0 & 0 & 0 & s_4 & r_4 & 0 \\ 0 & 0 & 0 & 0 & s_5 & r_5 \end{pmatrix}. \quad (4)$$

In this matrix (4) m_j are coefficients of productivities of adults of four different age classes. In first row of matrix two elements are equal to zero: cocoons and individuals in juvenile phase cannot produce cocoons. s_j are coefficients of transmission of individuals from one group to another one. In particular, s_1 is coefficient of transition from the phase "cocoon" to phase "individual in juvenile state". r_j are coefficients of lag in respective phase. Thus, from model (3) with matrix (4) changing in one time step of individuals in juvenile phase will be determined by the equation

$$x_2(t+1) = s_1 x_1(t) + r_1 x_2(t).$$

In this equation $x_2(t)$ is number of individuals of juvenile group at time t, $x_1(t)$ is number of cocoons at the same time moment, r_1 is a quota of individuals which will stay in this phase one more time step.

Following the biological sense of model parameters next inequalities are truthful:

$$0 < s_j \le 1,\ 0 \le r_j < 1,\ r_j + s_{j+1} \le 1.$$

Remark. Within the framework of Leslie model (1)-(3) lifetime of every individual is finite and less than N. If in Leslie – Lefkovitch model one of coefficients r_j is positive lifetime of individuals in population becomes unlimited.

3. It is possible to point out a group of non-linear models with fixed phase structure. For example, it is LPA model (larvae –pupae – adult; Costantino et al., 1997; Henson et al., 2002; Cushing et al., 1996, 2001; Rinaldi, Candaten, Casagrandi, 2001). As we can see from the name of model it is oriented onto description of insect population dynamics:

$$L_{k+1} = bA_k e^{-c_1 A_k - c_2 L_k},$$

$$P_{k+1} = (1-\mu_1)L_k,$$

$$A_{k+1} = P_k e^{-c_3 A_k} + (1-\mu_2)A_k. \qquad (5)$$

In system of equations (5) L_k is a number of feeding larvae at moment k, P_k is a total number of non-feeding larvae, cocoons and immature adults, A_k is a number of adults which can produce individuals of new generation. As it was assumed by authors (Costantino et al., 1997; Henson et al., 2002; Cushing et al., 1996, 2001) time step in model (5) is equal to two weeks – it is close to sojourning of individuals in phases L and P (for provided laboratory experiments with *Tribolium*).

In model (5) coefficient b is equal to (average) number of larvae which are produced by one adult for one time step (without cannibalism). Quotas μ_1 and μ_2 are equal to probabilities of the death for adults and larvae on non-cannibalism reasons. Additionally, c_j are coefficients of cannibalism, and, respectively, exponents in expressions (5) are equal to quotas of survived individuals.

Model

Let $x(t)$ and $y(t)$ be numbers of “young” (first year old) and “old” (second year old) individuals respectively at time moment t. Let’s assume that changing of population conditions is realized at fixed time moments $t_k = hk$, $t_0 = 0$, $k = 1,2,\ldots$, $h = const > 0$ - these are moments of appearance of individuals of new generations. We will assume that total number of young individuals of new generation depends on current number of young and old individuals. Let $p,\quad 0<p<1,\quad p\equiv const$, be a quota of individuals in population developing in one-year generation. In general case p isn't a constant: its amount can depend on a lot of factors and, in particular, it can depend on food conditions for individuals. For example, it was proved for Siberian pine moth (*Dendrolimus sibiricus superans* Tschetv.; Isaev et al., 1984, 2001, 2009).

Let $x(t_k-0)$ and $y(t_k-0)$ be the numbers of survived individuals to moment t_k of appearance of new generation, and let Y_i, $i=1,2$, be their reproductive coefficients. Thus, at moments t_k following relations are truthful:

$$x_k = x(t_k) = Y_1 p x(t_k-0) + Y_2 y(t_k-0),$$
$$y_k = y(t_k) = (1-p)x(t_k-0). \qquad (6)$$

It is assumed that on time intervals $t\in[hk, h(k+1))$ monotonic decreasing of sizes of both age groups is observed:

$$\frac{dx}{dt} = -\alpha_1 x - \beta_1 x(x+\gamma y),$$
$$\frac{dy}{dt} = -\alpha_2 y - \beta_2 y(x+\gamma y). \qquad (7)$$

In equations (7) $\alpha_i = const > 0$, $i=1,2,$ are coefficients of natural death of individuals of first and second age classes respectively; $\beta_i = const > 0$, $i=1,2,$ are coefficients of death rates which are explained by the influence of self-regulative mechanisms; $\gamma = const > 0$ is coefficient which describes non-equal inputs of individuals of various age groups into functioning of self-regulative mechanisms.

Combining equations (7) together with conditions (6) we obtain mathematical model which describes changing of sizes of two age classes in time. Additionally we have to point out initial values of sizes $x(0)=x_0$ and $y(0)=y_0$ which are non-negative values.

Properties of model

Model (6)-(7) has the following properties:

1. For non-negative initial values of variables x_0, y_0, model's trajectories cannot intersect boundaries of first quota of plane (it means that for all time moments numbers of individuals of both classes will be non-negative).
2. There exists stable invariant compact Δ in R_+^2. Let

$$x^* = \frac{\alpha_1 e^{-\alpha_1 h}}{\beta_1 - \beta_1 e^{-\alpha_1 h}},\ y^* = \frac{\alpha_2 e^{-\alpha_2 h}}{\beta_2 \gamma - \beta_2 \gamma e^{-\alpha_2 h}}.$$

Compact Δ has the form:

$$\Delta = [0, Y_1 p x^* + Y_2 y^*] \times [0, (1-p) x^*].$$

If $(x_0, y_0) \in \Delta$ then for all $t > 0$ we have $(x(t), y(t)) \in \Delta$. All stationary states on Poincare' equator are unstable points. Thus, for all initial values population size is limited.

3. Point $(0,0)$ is stationary state of model (6)-(7). If $x(0) = 0$ then for all $t > 0$ $x(t) \equiv 0$; the same property is realized for other variable: if $y(0) = 0$ then for all $t > 0$ $y(t) \equiv 0$. Let

$$q_1 = Y_1 p e^{-\alpha_1 h},\ q_2 = Y_2 e^{-\alpha_2 h},\ q_3 = (1-p) e^{-\alpha_1 h}.$$

If inequality $q_1 > 2$ is truthful or two inequalities $q_1 < 2$ and $q_1 + q_2 q_3 > 1$ are truthful then stationary state $(0,0)$ is unstable point. In both cases with $x(0) + y(0) > 0$ population doesn't extinct. There are no other stationary states of model on coordinate lines.

4. If the following inequality is truthful $q_1 + q_2 q_3 < 1$ there are no non-trivial stationary states in Δ, and point $(0,0)$ is global stable equilibrium. Population size converges to zero for all initial values from Δ.

5. Numerical analysis of solutions of model (6)-(7) showed that we can get as regimes of asymptotic stabilization of sizes at any positive levels (figure 1a), as regimes of periodic fluctuations with various periods (fig. 1b).

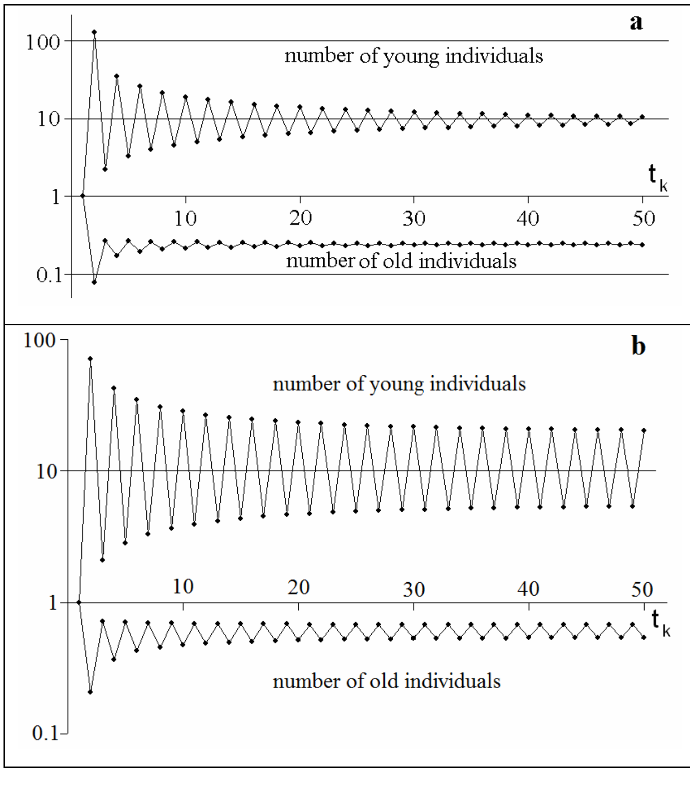

Fig. 1. Some dynamic regimes of model (6)-(7). a – fading fluctuations: $x_0 = 1$, $y_0 = 1$, $Y_1 = 3.5$, $Y_2 = 750$, $p = 0.2$, $\alpha_1 = 0.07$, $\beta_1 = 1.1$, $\alpha_2 = 0.05$, $\beta_2 = 1.4$, $\gamma = 2$;
b – cycle of the length 2 $x_0 = 1$, $y_0 = 1$, $Y_1 = 10$, $Y_2 = 400$, $p = 0.2$, $\alpha_1 = 0.01$, $\beta_1 = 1.1$, $\alpha_2 = 0.02$, $\beta_2 = 1.4$, $\gamma = 2$. Both graphics are in logarithmic scale.

Thus, within the framework of rather simple mathematical model (6)-(7) of population dynamics with two-age structure we can observe cyclic regimes for certain values of model parameters. At the same time within the framework of non-parametric model (model of Kolmogorov type) which is based on the similar assumptions (but with continuous birth process) oscillation regimes cannot be realized (Nedorezov, 1979, 1986). Taking into account that discrete nature of any population processes isn't a sufficient condition for appearance in model of oscillation regimes we can assume that realization of cyclic regimes can be partly explained by the existence of age structure.

Conclusion

Continuous-discrete model considered in paper cannot be applied directly to description of population dynamics of Siberian pine moth (*Dendrolimus superans sibiricus* Tschetv.) or any other species which have two-age structure. There are several reasons for it but, first of all, it is necessary to take into account influence of winter conditions on population dynamics (like it was realized for simpler models in several our publications; Nedorezov, Nekljudova, 2000; Nedorezov, Volkova, 2005; Nedorezov, Volkova, Sadykov, 2007).

The second, we have to take into account dependence of coefficient of transition of individuals from first class into first class p on population density. Yu.P. Kondakov showed (Isaev et al., 1984, 2001, 2009) that amount of this coefficient can increase at increasing of population size – finally, it leads to increase of number of individuals which are developed in one-year generation. It is obvious that such a modification of model will lead to increase of number of dynamic regimes which can be observed in model.

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