About one stochastic model of population dynamics

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Abstract

In current publication a new probabilistic model of population dynamics is analyzed. Conditions of asymptotic degeneration with probability one for the population which development is given by system with random coefficients, are determined. Dynamic regime of population dynamics which is on the verge of disappearance is investigated; this regime is characterized by the following property: if population size is less than minimal critical level after that restoration of population becomes impossible with probability one. Results of analysis are illustrated by examples with various biological populations.

Keywords: stochastic model of population dynamics, probability of population degeneration

Introduction

It is considered, that mathematical models of biological population development can be conditionally divided on deterministic (mechanistic) and stochastic. In most cases deterministic models are simpler than stochastic models but they don't allow getting an information about correspondence of theoretical curve to observed datasets which are under the influence of various random external factors. Well-known stochastic models of population dynamics are based on branching processes, birth and death processes, and the stochastic differential equations (Kostitzin, 1937; Harris, 1966; Bharucha-Reid, 1969; Sevastyanov, 1971; Poulsen, 1979; Aagard-Hansen, Yeo, 1984; Nagaev, Nedorezov, Wachtel, 1999; Pertsev, Loginov, 2011; Vatutin, 2012 and many others).

Considering in current publication a new stochastic model is generalization of models described in works (Nedorezov, 1997; Nedorezov, Utyupin 2003, 2011), and based on the theory of differential equations with random coefficients and differential equations with impulses. Within the framework of deterministic mathematical models of isolated population dynamics it is assumed that the death of individuals has continuous character, and appearance of individuals of new generations takes place in some fixed time moments τ_k . For considering in current paper we assume that population development on time intervals (τ_k, τ_{k+1}) , as well as the moments τ_k are depend on various changes of an environment, and therefore dynamics of population is described by system with random coefficients. For considering situation population dynamic regimes are investigated, and conditions of asymptotical elimination of population with probability one are determined. Presented results can be applied for solution of practical problems on changing of population size (preservation of rare types of animals from the Red book), or on its reduction (control of the number of harmful insects, epidemiology problems etc.).

According to A.N. Kolmogorov (1972) publication, the deterministic models describe dynamics of population for a case when its number is great, and at low values these models are inapplicable. A similar assumption we made for the stochastic model cosidered below. We assume that population disappears not only in a situation when its size tends to zero asymptotically. Population degenerates when its size becomes less than minimal critical value x_* . If population size becomes rather small surviving of population from the biological point of view is impossible, despite the fact that the solution of the model describing population changing, after achievement of minimal value can increase. If we talk about population of animals, we say that they are on the verge of disappearance; and the given type of animals can disappear if during of some years it will be exposed to successively adverse conditions (shortage of a forage, destruction by poachers).

Examples of discrete-continuous models of population growth

At first we will consider examples of deterministic models which were studied in publications (Nedorezov, 1997; Nedorezov, Utyupin, 2003, 2011). Models considered in these publications will form a basis for construction of stochastic model.

Example 1. The expediency of application of this model is connected by that in realization of process of birth, appearance of new individuals is observed a synchronism. At the same time death process has continuous nature, each individual can die at any moment under the influence of various factors. For the description of population dynamics differential equations with impulse are required. Trajectories of these equations suffer discontinuity in the certain moments of time (the moments of appearance of new generations) $\tau_k = kT$, where T > 0, $k = 1, 2, \ldots$ Within the limits of model it is possible to suppose, that appearance of new generation happens instantly in time moments τ_k , as the time range of its appearance is much less than time of life of separate individuals. It is supposed that population size changes

according to the following differential equation:

$$\dot{z} = -zr(z), \quad t \neq \tau_k, \quad \Delta z \Big|_{t=\tau_k} = lz,$$

where $\Delta z|_{t=\tau_k} = z(\tau_k + 0) - z(\tau_k - 0)$, l = const > 0 is the coefficient of reproduction, and it is equal to quantity of new individuals, falling to the one individual survived to moment of reproduction. Function r(z) is intensity of death rate of individuals; it is differentiated and satisfied to following conditions which are realized in many models of population dynamics:

$$r(0) > 0$$
, $r'(z) > 0$, $\lim_{z \to +\infty} r(z) = +\infty$.

In book by of L.V. Nedorezov (1997) it was shown that at performance of given conditions population size fixed at moments τ_k changes monotonously, and thus there always exists unique globally stable stationary state in phase space.

Example 2. There are various models of population dynamics (for example, models with phase structure, age structure, models describing dynamics of individuals of different types and various age classes) in which suppose that transition from one type or a class into another has jump character, and it is carried out in fixed time moments τ_k . These models with continuous-discrete behavior of trajectories are described by system of differential equations with impulses; the same behavior of trajectories will be considered for population with gender structure (examples of the description of these models can be found in Nedorezov, 1997; Nedorezov, Utyupin, 2003; Iannelli, Martcheva, Milner, 2005). Let's consider a model of population dynamics describing by the following control system

$$\dot{x} = f(t, x, u), \quad t \neq \tau_k,$$

$$\Delta x \big|_{t=\tau_k} = g(x, w), \quad (t, x, u, w) \in \mathbb{R} \times \mathbb{R}^n \times \mathbb{R}^m \times \mathbb{R}^p,$$
(1)

where $\tau_k = kT$, $k = 1, 2, ..., \mathbb{R}^n$ is a standard Euclidean *n*-dimension space with scalar product $\langle x, y \rangle$ and norm $|x| = \sqrt{\langle x, x \rangle}$. Let's designate through $\operatorname{comp}(\mathbb{R}^n)$ the space of nonempty compact subsets of Euclidean space \mathbb{R}^n . Admissible controls u(t) are limited measurable functions with values in set $U \in \operatorname{comp}(\mathbb{R}^m)$, w is control vector influencing behavior of system in time moments τ_k and accepting values in set $W \in \operatorname{comp}(\mathbb{R}^p)$. Let's also assume that functions f(t, x, u) and g(x, w) are continuous on set of variables.

Let's associate with system (1) differential inclusion

$$\dot{x} \in F(t,x), \quad F(t,x) = \operatorname{co} \widetilde{F}(t,x),$$

where for each fixed point $(t, x) \in \mathbb{R}^{n+1}$ set $\widetilde{F}(t, x)$ consists of all limiting values of function $(t, x) \to f(t, x, U)$ as $(t_i, x_i) \to (t, x)$, record co $\widetilde{F}(t, x)$ means short circuit of a convex co-

ver of set $\widetilde{F}(t, x)$. The solution of system (1) is such piecewise-continuous function $x = \varphi(t)$ (absolutely continuous on intervals (τ_k, τ_{k+1}) with discontinuity of first type at $t = \tau_k$), which at almost all t satisfies to inclusion $\dot{\varphi}(t) \in F(t, \varphi(t))$ and to a jump condition $t = \tau_k$, that is

$$\Delta \varphi \big|_{t=\tau_k} = \varphi(\tau_k + 0) - \varphi(\tau_k - 0) = g(\varphi(\tau_k - 0), w).$$

Let's assume, that function $\varphi(t)$ is continuous at the left, and as value of function $\varphi(t)$ in a point $t = \tau_k$ we will understand $\varphi(\tau_k - 0) = \lim_{t \to \tau_k - 0} \varphi(t)$.

Description of stochastic discrete-continuous model of population dynamics

Now we'll make a modification of model (1) and transform it into stochastic one. It is natural to suppose that population size changing on intervals (τ_k, τ_{k+1}) , as well as moments τ_k , are determined by various natural conditions. Therefore we have to assume that on each time interval (τ_k, τ_{k+1}) function f depends on random parameter ψ_k , accepting value in the set Ψ , and lengths of intervals $\theta_k = \tau_k - \tau_{k-1}$, $k = 2, 3, \ldots$ between the moments of appearance of new generation are random variables with distribution function G(t). We assume that this distribution is concentrated on a segment $[\alpha, \beta]$, where $0 < \alpha < \beta < \infty$, that is G(t) = 0 if $t < \alpha$ and G(t) = 1 if $t \ge \beta$. In that specific case when all variables φ_k , θ_k are constants, stochastic model coincides with deterministic one, therefore it is a generalization of the deterministic model.

Let's result the description of stochastic model. Let's assume that dynamics of population size is given by control system

$$\dot{x} = f(h^t \sigma, x, u), \quad t \neq \tau_k(\sigma),$$

$$\Delta x \big|_{t=\tau_k(\sigma)} = g(x, w), \quad (t, \sigma, x, u, w) \in \mathbb{R} \times \Sigma \times \mathbb{R}^n \times \mathbb{R}^m \times \mathbb{R}^p,$$
(2)

that generated by metric dynamical system $(\Sigma, \mathfrak{A}, \mu, h^t)$. We assume that function $(x, w) \to g(x, w)$ and function $(t, x, u) \to f(h^t \sigma, x, u)$ for every fixed $\sigma \in \Sigma$ is continuous on set of variables and controls u and w accept values in sets $U \in \text{comp}(\mathbb{R}^m)$ and $W \in \text{comp}(\mathbb{R}^p)$ accordingly.

Let's remind, that a metric dynamical system is four elements $(\Sigma, \mathfrak{A}, \mu, h^t)$, where Σ is a phase space of dynamic system; \mathfrak{A} is some sigma-algebra of subsets of Σ ; h^t is oneparametrical group of measurable transformations of phase space Σ in itself (measurability means that $h^t A \in \mathfrak{A}$ for every $A \in \mathfrak{A}$ and for any $t \in \mathbb{R}$). Further, μ is a probability measure, invariant concerning a flow h^t , that is $\mu(h^t A) = \mu(A)$ for all $A \in \mathfrak{A}$ and any $t \in \mathbb{R}$ (Kornfeld, Sinai, 1980). Let's describe metric dynamical system $(\Sigma, \mathfrak{A}, \mu, h^t)$, which parameterized control system (2), and thus control system turns to the system with random coefficients (the similar systems are described in Rodina, 2012, 2013). Let's define probability space $(\Sigma, \mathfrak{A}, \mu)$ as direct product of probability spaces $(\Sigma_1, \mathfrak{A}_1, \mu_1)$ and $(\Sigma_2, \mathfrak{A}_2, \mu_2)$. Here Σ_1 is the set of numerical sequences $\theta = (\theta_1, \ldots, \theta_k, \ldots)$, where $\theta_k \in (0, \infty)$, system of sets \mathfrak{A}_1 is the least sigma-algebra generated by cylindrical sets

$$E_k \doteq \{\theta \in \Sigma_1 : \theta_1 \in I_1, \dots, \theta_k \in I_k\},\$$

where $I_i \doteq (t_i, s_i]$, and the probabilistic measure μ_1 is defined as follows. For each interval I_i , $i \ge 2$, we define a probability measure $\tilde{\mu}_1(I_i) = G(s_i) - G(t_i)$ by means of distribution function G(t), and for I_1 by means of distribution function

$$G_1(t) = \frac{1}{m_{\theta}} \int_0^t (1 - G(s)) ds, \quad t \in (0, \infty),$$
(3)

where m_{θ} is the mathematical expectation of a random variable with distribution G(t). On algebra of cylindrical sets we construct a measure

$$\widetilde{\mu}_1(E_k) = \widetilde{\mu}_1(I_1)\widetilde{\mu}_1(I_2)\ldots\widetilde{\mu}_1(I_k),$$

then owing to theorem of A. N. Kolmogorov (Shiryaev, p.176, 1989) on measurable space $(\Sigma_1, \mathfrak{A}_1)$ there is a unique probabilistic measure μ_1 , which is continuation of $\tilde{\mu}_1$ on sigmaalgebra \mathfrak{A}_1 .

Further, let are fixed set Ψ and the sigma-algebra of its subsets \mathfrak{A}_0 , on which the probabilistic measure $\tilde{\mu}_2$ is defined. Let's designate through Σ_2 the set of sequences

$$\Sigma_2 \doteq \{ \varphi : \varphi = (\psi_0, \psi_1, \dots, \psi_k, \dots), \, \psi_k \in \Psi \},\$$

through \mathfrak{A}_2 we designate the least sigma-algebra generated by cylindrical sets

$$D_k \doteq \{\varphi \in \Sigma_2 : \psi_1 \in \Psi_1, \dots, \psi_k \in \Psi_k\}, \text{ where } \Psi_i \in \mathfrak{A}_0.$$

We define a measure $\tilde{\mu}_2(D_k) = \tilde{\mu}_2(\Psi_1)\tilde{\mu}_2(\Psi_2)\dots\tilde{\mu}_2(\Psi_k)$ and a measure μ_2 as measure continuation of $\tilde{\mu}_2$ on sigma-algebra \mathfrak{A}_2 .

Let's enter sequence $\{\tau_k\}_{k=0}^{\infty}$ as follows: $\tau_0 = 0$, $\tau_k(\theta) = \sum_{i=1}^k \theta_i$, where $\theta \in \Sigma_1$. We will designate through $z = z(t, \theta)$ the number of points of sequence $\{\tau_k\}_{k=0}^{\infty}$, located left then t, thus $z = z(t, \theta) = \max\{k : \tau_k \leq t\}$, where $t \geq 0$. The variable $z(t, \theta)$ is called a *renewal process*. As function of distribution of a random variable θ_1 is given by equality (3), $z(t, \theta)$ is a *stationary renewal process* (Korolyuk et al., p. 145 - 147, 1985).

On probabilistic space $(\Sigma_1, \mathfrak{A}_1, \mu_1)$ we define the shift transformation

$$h_1^t \theta = (\tau_{z+1} - t, \theta_{z+2}, \theta_{z+3}, \dots), \quad t > 0.$$

As $z(t, \theta)$ is a stationary renewal process, the transformation h_1^t keeps the measure μ_1 , that is for any set $A \in \mathfrak{A}_1$ and all $t \ge 0$ are satisfied equalities $\mu_1(h_1^t A) = \mu_1(A)$. On space $(\Sigma_2, \mathfrak{A}_2, \mu_2)$ at everyone fixed $\theta \in \Sigma_1$ we define shift transformation

$$h_2^t(\theta)\varphi = (\psi_z, \psi_{z+1}, \dots).$$

From definition of measure μ_2 follows, that h_2^t keeps given measure. On probabilistic space $(\Sigma, \mathfrak{A}, \mu)$ we also define transformation $h^t \sigma = h^t(\theta, \varphi) = (h_1^t \theta, h_2^t(\theta)\varphi)$. The constructed dynamical system $(\Sigma, \mathfrak{A}, \mu, h^t)$ is called the slanting product of dynamical systems $(\Sigma_1, \mathfrak{A}_1, \mu_1, h_1^t)$ and $(\Sigma_2, \mathfrak{A}_2, \mu_2, h_2^t(\theta))$, and transformation $h^t \sigma$ keeps a measure $\mu = \mu_1 \times \mu_2$ (Kornfeld, Sinai, p. 190, 1980) which is direct product of probability measures μ_1 and μ_2 . It means, that $\mu_1 \times \mu_2(A \times B) = \mu_1(A)\mu_2(B)$ for all sets $A \in \mathfrak{A}_1$, $B \in \mathfrak{A}_2$.

Conditions of extinction of population. Auxiliary statements.

Results of this section both represent independent interest, and serve for research of conditions for degeneracy of population which dynamics is given by control system with random coefficients. Here is investigated the population that defined by the differential equation with influence of impulse

$$\dot{z} = q(h^t \sigma, z), \quad t \neq \tau_k(\sigma),$$

$$\Delta z \big|_{t=\tau_k(\sigma)} = l(z), \quad (t, \sigma, z) \in \mathbb{R} \times \Sigma \times \mathbb{R}.$$
(4)

This equation is parameterized by metric dynamical system $(\Sigma, \mathfrak{A}, \mu, h^t)$, which is constructed in previous section. We assume that the solutions of equation (4) are continuous at the left. To the equation (4) we associate the auxiliary determined equation with impulse influence

$$\dot{z} = q(t, \psi, z), \quad t \neq \tau_k,$$

$$\Delta z \big|_{t=\tau_k} = l(z), \quad (t, \psi, z) \in \mathbb{R} \times \Psi \times \mathbb{R},$$
(5)

where $\tau_k = kT$, $T \in [\alpha, \beta]$, $0 < \alpha < \beta < \infty$, $k = 1, 2, \ldots$ Let's notice, that the equation (5) can be considered as a special case of the equation with random coefficients (4) at fixed $\sigma = ((T, \psi), (T, \psi), \ldots) \in \Sigma$. We assume that for everyone $\psi \in \Psi$ function $(t, z) \to q(t, \psi, z)$ is defined and continuous together with a derivative $q'_z(t, \psi, z)$ on set $(0, \infty) \times (0, \infty)$ and $q(t, \psi, 0) = 0$. We consider the function $L(z) \doteq l(z) + z$ and assume that L(z) is differentiated, increasing, L(0) = 0 and $L(z) \ge 0$ if z > 0.

Let $\varphi(t, \psi, z)$ is a solution of equation $\dot{z} = q(t, \psi, z)$ at fixed value $\psi \in \Psi$ (without impulse influence), satisfying the initial condition $\varphi(0, \psi, z) = z$. We enter into consideration the function

$$H(t,\psi,z) \doteq L(\varphi(t,\psi,z)) = l(\varphi(t,\psi,z)) + \varphi(t,\psi,z),$$

which, as it will be shown further, defined for all $(t, \psi, z) \in [0, \infty) \times \Psi \times [0, \infty)$. At fixed t = Tand $\psi \in \Psi$ function $z \to H(T, \psi, z)$ defines character of behavior of the population given by determined equation (5). We designate through $z_k = z(kT, \psi)$ the size of population (5) at the time moment kT in assumption that in the initial moment the size of this population is equal $z(0, \psi) = z_0 \ge 0$, then

$$z_{k+1} = z((k+1)T, \psi) = H(T, \psi, z_k), \quad k = 0, 1, \dots$$

Let's notice, that the equation $H(T, \psi, z) = z$ always has the solution z = 0. It is known, that if this equation has the unique positive solution z_+ and $H'_z(T, \psi, z_+) < 1$, then number of population z_k (considered in the moments kT) monotonously tends to z_+ as $k \to \infty$. If the equation $H(T, \psi, z) = z$ has no positive solutions and $H'_z(T, \psi, 0) < 1$, then the sequence $\{z_k\}_{k=0}^{\infty}$ asymptotically tends to zero for any initial size z_0 (see, for example, Nedorezov, 1997, p. 27, 37-38).

In this work it is shown that for probabilistic model (4) there exist more dynamical regimes of change of population size. For the description of these regimes it is necessary to investigate properties of function $(t, z) \to H(t, \psi, z)$ for fixed $\psi \in \Psi$. We assume that for every $(t, \psi) \in (0, \infty) \times \Psi$ equation $H(t, \psi, z) = z$ has finite number of solutions and designate greatest of these solutions through $\tilde{z}(t, \psi)$.

Lemma 1. Let $\psi \in \Psi$ is fixed. Function $H(t, \psi, z)$ satisfy following properties:

1) if $\varphi(t, \psi, z)$ is continued on a segment $[\alpha, \beta]$ for all z > 0, then $H(t, \psi, z)$ is defined and continuous together with its derivative $H'_z(t, \psi, z)$ for all $t \ge 0$, z > 0;

- 2) $H(t, \psi, z) \ge 0$ for all $t \ge 0$, z > 0 and $H(t, \psi, 0) = 0$ for any $t \ge 0$;
- 3) function $z \to H(t, \psi, z)$ is increasing for any $t \in (0, \infty)$.

Proof. As $\varphi(t, \psi, 0) \equiv 0$ and L(0) = 0, then $H(t, \psi, 0) = 0$ for any $t \in [0, \infty)$. Let's show that $\varphi(t, \psi, z) > 0$ for all z > 0. We assume the opposite: let there is a point t^* such that $\varphi(t^*, \psi, z) = 0$, z > 0. Then through a point $(t^*, 0)$ pass two solutions of the equation $\dot{z} = q(t, \psi, z)$: the initial solution $\varphi(t, \psi, z)$ and the solution identically equal to zero; we received the contradiction with a condition of uniqueness of the solution. Let's notice that $L(z) \ge 0$ if z > 0, therefore $H(t, \psi, z) \ge 0$ for all $t \ge 0$, z > 0. The continuity of functions $H(t, \psi, z)$ and $H'_z(t, \psi, z)$ for all t > 0, z > 0 follows from differentiability of function L(z) and theorems of differentiability on initial values. From uniqueness of the solution $\varphi(t, \psi, z)$ also follows that function $z \to \varphi(t, \psi, z)$ is increasing. Really, if exist such $z_1 < z_2$, that $\varphi(t, \psi, z_1) \ge \varphi(t, \psi, z_2)$, then will be a point $t_* \in (0, t]$ such that $\varphi(t_*, \psi, z_1) = \varphi(t_*, \psi, z_2)$; we come to contradiction. Thus, function L(z) is increasing, then function $z \to H(t, \psi, z) = L(\varphi(t, \psi, z))$ also increases.

Let's notice, that if we can't write out function $H(t, \psi, z)$ in an explicit form, may be possible to estimate function $q(\sigma, z)$ by some function $q_0(\sigma, z)$, then to construct function $H_0(t, \psi, z)$ and use the theorem of differential inequalities.

Conditions of extinction of populations satisfied for all $\sigma \in \Sigma$ and satisfied with probability one

Let's designate through $z(t, \sigma, z_0)$ the size of population which dynamics is given by the equation (4), through z_0 we designate the initial size of population. We also define the number sequence $\{s_k\}_{k=1}^{\infty}$, where

$$s_0 = z_0, \quad s_k = h(s_{k-1}), \quad h(z) = \sup_{t \in [\alpha, \beta], \psi \in \Psi} H(t, \psi, z), \quad k = 1, 2, \dots$$

Lemma 2. If the equation h(z) = z has no positive solutions and h'(0) < 1, then the equality $\lim_{t \to \infty} z(t, \sigma, z_0) = 0$ is true for every $\sigma \in \Sigma$ and any $z_0 \ge 0$.

Proof. Let $\sigma = ((\theta_1, \psi_1), (\theta_2, \psi_2), ...)$ be any point of set Σ , $\theta_1 \in [0, \beta]$, $\theta_k \in [\alpha, \beta]$, k = 2, 3, ... Let's consider solution $z(t, \sigma, z_0)$ of equation (4) with initial condition $z_0 \ge 0$. If $z_0 = 0$ the lemma statement is obvious, we assume therefore that $z_0 > 0$. To the solution $z(t, \sigma, z_0)$ we associate the sequence $\{z_k(\sigma)\}_{k=1}^{\infty}$, where

$$z_0(\sigma) = z_0, \quad z_k(\sigma) = z(\tau_k(\sigma), \sigma) = H(\theta_k, \psi_k, z_{k-1}(\sigma)), \quad k = 1, 2, \dots$$
 (6)

For sequence $\{s_k\}_{k=1}^{\infty}$ under conditions of the lemma we have the equality $\lim_{k\to\infty} s_k = 0$ (Nedorezov, 1997, p. 27). It is obvious, that for all $\sigma \in \Sigma$ the inequality $z_k(\sigma) \leq s_k$ is true for any natural k; besides, owing to a lemma 1 takes place $z_k(\sigma) = H(\theta_k, \psi_k, z_{k-1}(\sigma)) > 0$. Thus, we have

$$\lim_{k \to \infty} z_k(\sigma) = \lim_{k \to \infty} s_k = 0.$$

From continuity of function $(t, z) \to H(t, \psi, z)$ and condition $H(t, \psi, 0) = 0$ follows that $\lim_{t \to \infty} z(t, \sigma, z_0) = 0 \text{ for every } \sigma \in \Sigma \text{ and any } z_0 \ge 0.$

In the theorem 1 we receive the conditions of extinction of population with probability

one in a case, when the equation $H(\beta, \psi, z) = z$ has no positive solutions for any $\psi \in \Psi$. About solutions of equation $H(\alpha, \psi, z) = z$ we assume only that for every fixed $\psi \in \Psi$ number of such solutions is finite. Thus the quantity of positive solutions can be optional and various for different values $\psi \in \Psi$.

Theorem 1. Let's assume that there exists a measurable set $I \subseteq [\alpha, \beta]$ such that $\mu(I) > 1/2$, for everyone $t \in I$, $\psi \in \Psi$ the equation $H(t, \psi, z) = z$ has no positive solutions and is true the inequality

$$\sup_{t\in I,\psi\in\Psi,z>0}\frac{H(t,\psi,z)}{z}\cdot\sup_{t\in[\alpha,\beta],\psi\in\Psi,z>0}\frac{H(t,\psi,z)}{z}<1.$$
(7)

Then the population, which dynamics is given by model (4), degenerates with probability one, that is there is a set $\Sigma_0 \subseteq \Sigma$ such that $\mu(\Sigma_0) = 1$ and $\lim_{t\to\infty} z(t,\sigma,z_0) = 0$ for all $\sigma \in \Sigma_0$ and any $z_0 \ge 0$.

Proof. For any $\sigma \in \Sigma$ we consider the sequence of independent random variables $\{\zeta_k(\sigma)\}_{k=1}^{\infty}$, where $\zeta_k(\sigma) = 1$, if $\theta_k \in [\alpha, \beta] \setminus I$ and $\zeta_k(\sigma) = -1$, if $\theta_k \in I$. From the conditions of the theorem follows that

$$\mu(\zeta_k(\sigma) = -1) = \mu(I) > \frac{1}{2}, \quad \mu(\zeta_k(\sigma) = 1) = \mu([\alpha, \beta] \setminus I) < \frac{1}{2}$$

Let's also consider the sequence $\{S_k(\sigma)\}_{k=0}^{\infty}$, where $S_0(\sigma) = 0$, $S_k(\sigma) = \zeta_1(\sigma) + \ldots + \zeta_k(\sigma)$, which is random wandering on integer points of axis; then from an inequality

$$\mu(\zeta_k(\sigma) = -1) > \frac{1}{2}$$

follows that with probability one random wandering leaves in $-\infty$ (Korolyuk et al., p. 154, 1985). It means, that there is a set $\Sigma_0 \subset \Sigma$ such that $\mu(\Sigma_0) = 1$ and $\lim_{k \to \infty} S_k(\sigma) = -\infty$ for all $\sigma \in \Sigma_0$.

If the equation h(z) = z has no positive solutions, then owing to the lemma 2 equality $\lim_{t\to\infty} z(t,\sigma,z_0) = 0$ is true for all $\sigma \in \Sigma$, $z_0 \ge 0$. Further we consider a case when for every $t \in [\alpha,\beta] \setminus I$ there exist a set $\Psi_+(t) \subseteq \Psi$ such that for every $\psi \in \Psi_+(t)$ the equation $H(t,\psi,z) = z$ has positive solutions. We remind, that through $\tilde{z}(t,\psi)$ we designate the greatest solution of the equation $H(t,\psi,z) = z$, then $\tilde{z}(t,\psi) > 0$ for all $t \in [\alpha,\beta] \setminus I$, $\psi \in \Psi_+(t)$.

$$\text{Let } c = \sup_{t \in [\alpha,\beta], \psi \in \Psi, z > 0} \frac{H(t,\psi,z)}{z}, \ d = \sup_{t \in I, \psi \in \Psi, z > 0} \frac{H(t,\psi,z)}{z} \cdot \sup_{t \in [\alpha,\beta], \psi \in \Psi, z > 0} \frac{H(t,\psi,z)}{z} < 1.$$
 From the conditions of theorem follows that if $\psi \in \Psi_+(t)$, then

$$\widetilde{z}(t,\psi) = H(t,\psi,\widetilde{z}(t,\psi)) = \frac{H(t,\psi,\widetilde{z}(t,\psi))}{\widetilde{z}(t,\psi)} \cdot \widetilde{z}(t,\psi) \leqslant c\widetilde{z}(t,\psi),$$

therefore $c \ge 1$, $\frac{c}{d} > 1$. For each point $z_0 > 0$ and $\sigma \in \Sigma$ we define the sequence of random variables $\{y_k(\sigma)\}_{k=1}^{\infty}$, where $y_0(\sigma) = z_0$, $y_k(\sigma) = \left(\frac{c}{d}\right)^{\zeta_k(\sigma)} \cdot y_{k-1}$, $k = 1, 2, \dots$ Then $y_k(\sigma) = \left(\frac{c}{d}\right)^{\zeta_1(\sigma) + \dots + \zeta_k(\sigma)} \cdot z_0 = \left(\frac{c}{d}\right)^{S_k(\sigma)} \cdot z_0,$

hence, if $\lim_{k\to\infty} S_k(\sigma) = -\infty$, then $\lim_{k\to\infty} y_k(\sigma) = 0$. Let's consider sequence $\{z_k(\sigma)\}_{k=1}^{\infty}$, given by equality (6). We will show, that under conditions of theorem inequalities $z_k(\sigma) < y_k(\sigma), \ k = 1, 2, \dots$ are true. If $\theta_1 \in [\alpha, \beta] \setminus I$, then $\zeta_1(\sigma) = 1$; therefore for any $\psi_1 \in \Psi$ we have

$$z_1(\sigma) = H(\theta_1, \psi_1, z_0) = \frac{H(\theta_1, \psi_1, z_0)}{z_0} \cdot z_0 \leqslant c^{\zeta_1(\sigma)} z_0 < \left(\frac{c}{d}\right)^{\zeta_1(\sigma)} \cdot z_0 = y_1(\sigma).$$

If $\theta_1 \in I$, then $\zeta_1(\sigma) = -1$, thus from (7) we received

$$z_{1}(\sigma) = H(\theta_{1}, \psi_{1}, z_{0}) = \frac{H(\theta_{1}, \psi_{1}, z_{0})}{z_{0}} z_{0} \leqslant \sup_{t \in I, \psi \in \Psi, z > 0} \frac{H(t, \psi, z)}{z} \cdot z_{0} = \frac{dz_{0}}{c} = \left(\frac{c}{d}\right)^{\zeta_{1}(\sigma)} \cdot z_{0} = y_{1}(\sigma).$$

Further, if $\theta_2 \in [\alpha, \theta^*)$, then $\zeta_2(\sigma) = 1$, hence,

$$z_2(\sigma) = H(\theta_2, \psi_2, z_1(\sigma)) \leqslant c^{\zeta_2(\sigma)} z_1(\sigma) < \left(\frac{c}{d}\right)^{\zeta_2(\sigma)} z_1(\sigma) < \left(\frac{c}{d}\right)^{\zeta_2(\sigma)} y_1(\sigma) = y_2(\sigma).$$

We can similarly show that $z_2(\sigma) < y_2(\sigma)$, if $\theta_2 \in I$ and also that the inequality

$$0 < z_k(\sigma) < y_k(\sigma)$$

is true for all $k = 1, 2, \ldots$. Thus, if $\sigma \in \Sigma_0$, then for the sequence $\{z_k(\sigma)\}_{k=1}^{\infty}$ is true the equality $\lim_{k\to\infty} z_k(\sigma) = 0$, from which follows that $\lim_{t\to\infty} z(t,\sigma,z_0) = 0$ for all $\sigma \in \Sigma_0$ and any $z_0 > 0.$

Example 3. Let "free" (without exploitation) population dynamics is described by the equation $\dot{z} = z(1-z)$. We assume that at the random moments of time τ_k some quantity of biomass is taken off the population. Thus, we consider the exploited population which dynamics is given by the equation

$$\dot{z} = z(1-z), \quad t \neq \tau_k(\sigma),$$

$$\Delta z \big|_{t=\tau_k(\sigma)} = -cz, \quad (t,z) \in \mathbb{R}^2,$$
(8)

that parameterized by metric dynamical system $(\Sigma, \mathfrak{A}, \mu, h^t)$, which is constructed above; $c \in (0,1)$. We suppose that on each time interval (τ_k, τ_{k+1}) function f(z) = z(1-z) does

not depend on random parameter, but lengths of intervals $\theta_k = \tau_k - \tau_{k-1}$, k = 2, 3, ... between the moments of appearance of new generations are random variables with distribution function G(t), concentrated on a segment $[\alpha, \beta]$.

Let's calculate function $H(t,z) = \frac{ze^t(1-c)}{z(e^t-1)+1}$ and solutions of equation

$$H(t,z) = z$$
: $z_1 = 0$, $z_2 = \frac{e^t(1-c)}{e^t - 1}$

From lemma 2 follows that if $\beta < -\ln(1-c)$, then the equality $\lim_{t\to\infty} z(t,\sigma,z_0) = 0$ is true for every $\sigma \in \Sigma$ and any $z_0 \ge 0$.

Let's consider a case, when $\beta \ge -\ln(1-c)$. We will find a segment $I = [\alpha, \beta_0] \subseteq [\alpha, \beta]$ that satisfies the conditions of theorem 1. We notice that

$$\sup_{t \in [\alpha,\beta], z > 0} \frac{H(t,\psi,z)}{z} = e^{\beta}(1-c), \quad \sup_{t \in I, z > 0} \frac{H(t,\psi,z)}{z} = e^{\beta_0}(1-c).$$

Therefore, if $\beta_0 \leq -\ln(1-c)$, $\beta_0 + \beta < -2\ln(1-c)$ and $\mu(I) > 1/2$, then from theorem 1 follows that the population (8) degenerates with probability one, that is there exist a set $\Sigma_0 \subseteq \Sigma$ such that $\mu(\Sigma_0) = 1$ and $\lim_{t \to \infty} z(t, \sigma, z_0) = 0$ for all $\sigma \in \Sigma_0$ and any $z_0 \geq 0$.

In the following theorem we will also receive the conditions of extinction of population, satisfied with probability one, but unlike previous, here it is impossible to assert that for almost all $\sigma \in \Sigma$ the equality $\lim_{t\to\infty} z(t,\sigma,z_0) = 0$ is true. We will notice, that population also degenerates under weaker conditions, because for this purpose enough that in some moment of time t_* the size of population has appeared less than critical value $z_* > 0$, at which further restoration of its number is impossible. Let's remind that we designate the greatest of solutions of equation $H(t, \psi, z) = z$ through $\tilde{z}(t, \psi)$.

Theorem 2. Let following conditions are satisfied:

1) $H'_z(t,\psi,\widetilde{z}(t,\psi)) < 1$ for every $t \in [\alpha,\beta]$, $\psi \in \Psi$ and $\sup_{t \in [\alpha,\beta], \psi \in \Psi} \widetilde{z}(t,\psi) < \infty$; 2) there are sets $I^* \subseteq [\alpha,\beta]$ and $\Psi^* \subseteq \Psi$ such that $\mu(I^*) > 0$, $\mu(\Psi^*) > 0$, equation

2) there are sets $I^* \subseteq [\alpha, \beta]$ and $\Psi^* \subseteq \Psi$ such that $\mu(I^*) > 0$, $\mu(\Psi^*) > 0$, equation $g(z) \doteq \sup_{t \in I^*, \psi \in \Psi^*} H(\theta^*, \psi, z) = z$ has no positive solutions and g'(0) < 1.

Then there is a set $\Sigma_0 \subseteq \Sigma$ such that $\mu(\Sigma_0) = 1$ and for any $z_* > 0$, $z_0 > 0$ and $\sigma \in \Sigma_0$ there is such $t_* = t_*(z_*, \sigma, z_0)$, that $z(t_*, \sigma, z_0) < z_*$.

Proof. Let designate $\bar{z}(t) = \sup_{\psi \in \Psi} \tilde{z}(t, \psi)$. Let's notice, that $\bar{z}(t) = 0$ only in that case, when the equation $H(t, \psi, z) = z$ has no positive solutions for every $\psi \in \Psi$; therefore if $\bar{z}(t) = 0$ for all $t \in [\alpha, \beta]$, then owing to a lemma 2 the equality $\lim_{t \to \infty} z(t, \sigma, z_0) = 0$ is true for all $\sigma \in \Sigma$, that is the theorem statement is obviously satisfied. Further we consider a case when $\bar{z}(t) > 0$ for some $t \in [\alpha, \beta]$. We show, that with probability one since some moment of time $\tau_r = \tau_r(\sigma, z_0)$ for all solutions of the equation (4) the inequality $0 < z(t, \sigma, z_0) \leq \sup_{t \in [\alpha, \alpha]} \bar{z}(t) \doteq \bar{z}$ is satisfied.

Let's consider events A_k , consisting that $(\theta_k, \psi_k) \in I^* \times \Psi^*$, $k = 1, 2, \ldots$ Random variables $\theta_1, \theta_2, \ldots$ and ψ_1, ψ_2, \ldots are independent, therefore events A_k are independent and for $k \ge 2$ they have equal probabilities $\mu(A_k) = \mu(I^*)\mu(\Psi^*) > 0$. Owing to lemma 2 as equation g(z) = z has no positive solutions, therefore if there occur only events A_k , then the solution $z(t, \sigma, z_0)$ asymptotical tends to zero at any initial condition z_0 . If, on the contrary, events A_k never occur, then the solution $z(t, \sigma, z_0)$ or tends to value $\tilde{z}(t, \psi) \le \bar{z}$ as $t \to \infty$ (for example, in a case when $\theta_k = \alpha$, $\psi_k = \psi$ for all $k = 1, 2, \ldots$), or reaches values, smaller then $\bar{z}(\alpha)$.

It is known, that if events A_k are independent and the series $\sum_{k=1}^{\infty} \mu(A_k)$ diverges, then with probability one will be carried out infinitely many events A_k (Feller, 1985, p. 216). It means, that at any initial condition $z_0 > 0$ the inequality $0 < z(t, \sigma, z_0) \leq \bar{z}$ will be executed after realization of certain number of events A_k , that is during some moment of time τ_r , $r \geq k$. We notice, that if the inequality $0 < z(t, \sigma, z_0) \leq \bar{z}$ is true for some $t = \tau_r$, then it is true for all $t = \tau_{r+1}, \tau_{r+2} \dots$ Really, if $0 < z(\tau_r, \sigma, z_0) \leq \bar{z}$, then

$$0 < z(\tau_{r+1}, \sigma, z_0) = H(\theta_r, \psi_r, z(\tau_r, \sigma, \sigma)) \leqslant H(\theta_r, \psi_r, \bar{z}) \leqslant \bar{z}.$$

Let's consider the solution $z(\tau_k, \sigma, z_0)$ of (4) for $k \ge r$, then $0 < z(\tau_k, \sigma, z_0) \le \bar{z}$. Let it is fixed $z_* > 0$. We designate through s such number, that after consecutive realization of s events A_k for the solution $z(t, \sigma, z_0)$, satisfying the condition $z(\tau_k, \sigma, z_0) \le \bar{z}$, it will be true an inequality $z(\tau_k, \sigma, z_0) < z_*$, that is the size of population will appear below minimal permissible level. Such number s exists, as if there appeared only events A_k , then the solution $z(\tau_k, \sigma, z_0)$ asymptotical tends to zero. We enter into consideration the next events:

$$B_1 = A_{r+1} \cap \ldots \cap A_{r+s}, \quad B_2 = A_{r+s+1} \cap \ldots \cap A_{r+2s}, \quad \ldots, \quad r \ge 1.$$

Let $p = \mu(A_k) > 0$, $k = 2, 3, \ldots$ From independence of events A_k follows that events B_k are also independent and $\mu(B_k) = p^s > 0$, therefore the series $\sum_{k=1}^{\infty} \mu(B_k)$ diverges and with probability one will be carried out at least one of events B_k , that is the size of population will be less minimal value $z_* > 0$ in some moment of time $t_* = t_*(z_*, \sigma)$.

Theorem 3. Let following conditions are satisfied: 1) $H'_{z}(t,\psi,\widetilde{z}(t,\psi)) < 1$ for every $t \in [\alpha,\beta], \ \psi \in \Psi$ and $\sup_{t \in [\alpha,\beta],\psi \in \Psi} \widetilde{z}(t,\psi) < \infty;$ 2) there are sets $I^* \subseteq [\alpha, \beta]$ and $\Psi_* \subseteq \Psi$ such that $\mu(I^*) > 0$, $\mu(\Psi_*) > 0$ and for every $t \in I^*$, $\psi \in \Psi_*$ inequality $\widetilde{z}(t, \psi) < z_*$ is true.

Then there is a set $\Sigma_0 \subseteq \Sigma$ such that $\mu(\Sigma_0) = 1$ and for any $\sigma \in \Sigma_0$ and $z_0 \ge 0$ there is such $t_* = t_*(z_*, \sigma, z_0)$, that $z(t_*, \sigma, z_0) < z_*$.

The proof is similar to the proof of theorem 2.

Let's designate through $\hat{z}(t, \psi)$ the minimal positive solution of equation $H(t, \psi, z) = z$ (if such solution does not exist, we will put $\hat{z}(t, \psi) = 0$). In the following statement we will receive the conditions at which population does not degenerate, that is all time its size surpasses critical value $z_* > 0$. The proof is analogous to the proof of lemma 2.

Lemma 3. Let it is fixed $z_* > 0$. If $\inf_{t \in [\alpha,\beta], \psi \in \Psi} \widehat{z}(t,\psi) > z_*, z_0 > z_*$ and $H'_z(t,\psi,\widehat{z}(t,\psi)) < 1$

for all $t \in [\alpha, \beta]$, $\psi \in \Psi$, then the inequality $z(t, \sigma, z_0) > z_*$ is true for all $t \ge 0$, $\sigma \in \Sigma$.

Let's notice, that in the model given by the equation (4), there are also other dynamical regimes of development. For example, we consider a case, when the equation $H(t, \psi, z) = z$ for each pair $(t, \psi) \in [\alpha, \beta] \times \Psi$ has exactly one positive solution $\hat{z}(t, \psi)$ such that $H'_z(t, \psi, \hat{z}(t, \psi)) > 1$. Then $\lim_{t\to\infty} z(t, \sigma, z_0) = +\infty$, if $z_0 \ge \sup_{t\in[\alpha,\beta],\psi\in\Psi} \hat{z}(t,\psi)$, and $\lim_{t\to\infty} z(t, \sigma, z_0) = 0$, if $z_0 \le \inf_{t\in[\alpha,\beta],\psi\in\Psi} \hat{z}(t,\psi)$. If $z_0 \in \left(\inf_{t\in[\alpha,\beta],\psi\in\Psi} \hat{z}(t,\psi), \sup_{t\in[\alpha,\beta],\psi\in\Psi} \hat{z}(t,\psi)\right)$, then the solution $z(t, \sigma, z_0)$ with probability one or leaves to infinity, or tends to zero. The probability of that $z(t, \sigma, z_0) \to +\infty$ and that $z(t, \sigma, z_0) \to 0$ as $t \to \infty$ depends from the initial size of population z_0 .

Example 4. Let's consider the population which dynamics is given by the equation

$$\dot{z} = -z(az+b), \quad t \neq \tau_k(\sigma),$$

$$\Delta z\Big|_{t=\tau_k(\sigma)} = (c-1)z, \quad (t,z) \in \mathbb{R}^2,$$
(9)

that parameterized by metric dynamical system $(\Sigma, \mathfrak{A}, \mu, h^t)$, which is constructed above. Here constants a > 0, b > 0, c > 0. It is obvious, that if $c \in (0, 1]$, then the size of population $z(t, \sigma, z_0)$ tends to zero as $t \to \infty$. Therefore we assume further that c > 1. We suppose that on each time interval (τ_k, τ_{k+1}) function f(z) = -z(az + b) does not depend on random parameter, but lengths of intervals $\theta_k = \tau_k - \tau_{k-1}$, $k = 2, 3, \ldots$ between the moments of appearance of new generations are random variables with distribution function G(t), which is concentrated on a segment $[\alpha, \beta]$. Let's find function $H(t, z) = \frac{bcz}{az(e^{bt} - 1) + be^{bt}}$ and solutions of equation H(t, z) = z: $z_1 = 0, \ z_2(t) = \frac{b(c - e^{bt})}{a(e^{bt} - 1)}$. We notice, that $z_2(t) > 0$ for $t < \frac{\ln c}{b}$. From lemma 2 follows that if $a \ge \frac{\ln c}{b}$, then the equality $\lim_{t \to \infty} z(t, \sigma, z_0) = 0$ is true for every $\sigma \in \Sigma$ and any $z_0 \ge 0$. Let's consider a case, when $\alpha < \frac{\ln c}{b}$. If there exist $\theta^* \in (\alpha, \beta)$ such that $\theta^* \ge 2\frac{\ln c}{b} - \alpha$ and $\mu([\theta^*, \beta]) > \frac{1}{2}$, then from theorem 1 follows that the population (9) degenerates with probability one. If there is $\theta^* \in (\alpha, \beta)$ such that $\theta^* > \frac{\ln c}{b}$ and $\mu([\theta^*, \beta]) > 0$, then for population (9) there is a set $\Sigma_0 \subseteq \Sigma$ such that $\mu(\Sigma_0) = 1$ and for any $z_* > 0, \ z_0 > 0, \ \sigma \in \Sigma_0$ there is such $t_* = t_*(z_*, \sigma, z_0)$, that $z(t_*, \sigma, z_0) < z_*$.

It is simple to show that the inequality $z_2(\theta^*) < z_*$ is true for $\theta^* \in \left(\frac{1}{b}\ln\frac{az_* + bc}{az_* + b}, \frac{\ln c}{b}\right)$. Therefore, owing to the theorem 3, if $\mu([\theta^*, \beta]) > 0$, then there is a set $\Sigma_0 \subseteq \Sigma$ such that $\mu(\Sigma_0) = 1$ and for any $\sigma \in \Sigma_0$ and $z_0 > 0$ there is such $t_* = t_*(z_*, \sigma, z_0)$, that $z(t_*, \sigma, z_0) < z_*$. The solution of inequality $\inf_{t \in [\alpha, \beta], \psi \in \Psi} \widehat{z}(t, \psi) = z_2(\beta) > z_*$ is $\beta > \frac{1}{b} \ln \frac{az_* + bc}{az_* + b}$, hence for these β and any $\alpha > 0$ the inequality $z(t, \sigma, z_0) > z_*$ is true for all $t \ge 0$, $\sigma \in \Sigma$.

Conclusion

In this work the stochastic model which is taking into account influence of random changes of environmental conditions on dynamics of population size, is developed. As it was shown, considered model contains more dynamic regimes in comparison with known deterministic models. We investigate different conditions of population extinction and, in particular, received conditions when population size can stay less than minimal permissible level, that also leads to its disappearance. Results of analysis can find application to solution of various problems of population dynamics, epidemiology, etc.

References

- Aagard-Hansen H., Yeo G.F. 1984. A Stochastic Discrete Generation Birth, Continuous Death Population Growth Model and its Approximate Solution // J. Math. Biol. 20. 69-90.
- Bharucha-Reid A.T. 1969. Elements of the Theory of Markov Processes and their Applications. Moscow: Nauka.
- Iannelli M., Martcheva M., Milner F.A. 2005. Gender-Structured Population Modeling. Mathematical Methods, Numerics, and Simulations. Society for Industrial and Applied Mathematics. Philadelphia.
- Feller W. 1984. An Introduction to Probability Theory and its Applications (Vol. 1). Moscow:

Mir.

- Harris T.E. 1966. Theory of Stochastic Branching Processes. Moscow: Mir.
- Kolmogorov A.N. 1972. Qualitative Study of Mathematical Models of Population Dynamics // Problemy Kibernetiki, 25. Moscow: Nauka: 101-106.
- Kornfeld I. P., Sinai Ya. G., Fomin S.V. 1980. The Ergodic Theory. Moscow: Nauka.
- Korolyuk V. S., Portenko N. I., Skorokhod A. V., Turbin A. F. 1985. Reference Book on Probability Theory and Mathematical Statistics. Moscow: Nauka.
- Kostitzin V. A. 1937. La Biologie Mathematique. Paris: A. Colin.
- Nagaev S. V., Nedorezov L. V., Vakhtel' V. I. 1999. A Probabilistic Continuous-Discrete Model of the Size of an Isolated Population // Sib. Zh. Ind. Mat. 2(2): 147-152.
- Nedorezov L. V. 1997. Course of Lectures on Ecological Modeling. Novosibirsk: Siberian Chronograph.
- Nedorezov L. V., Utyupin Yu. V. 2003. A Discrete-Continuous Model for a Bisexual Population Dynamics // Sibirsk. Mat. Zh. 44 (3): 650-659.
- Nedorezov L. V., Utyupin Yu. V. 2011. Continuous-Discrete Models of Population Dynamics: An Analytical Overview. Ser. Ecology. Vip. 95. Novosibirsk: State Public Scientific-Technical Library, Siberian Branch, Russian Academy of Sciences.
- Pertsev N. V., Loginov K.K. 2011. Stochastic Model of Dynamics of Biological Community in the Conditions of Consumption by Individuals of Harmful Food Resources // Mathematical Biology and Bioinformatics. 6 (1): 1-13.
- Poulsen E.T. 1979. A Model for Population Regulation with Density- and Frequency-Dependent Selection // J. Math. Biol. 8: 325-348.
- Rodina L.I. 2012. Invariant and Statistically Weakly Invariant Sets of Control Systems // Izv. Inst. Mat. Inform. Udmurtsk. Gos. Univ. 2 (40): 3-164.
- Rodina L.I. 2013. On Some Probability Models of Dynamics of Population Growth // Vestn. Udmurtsk. Univ. Mat. Mekh. Komp. Nauki. 4: 109-124.
- Sevastyanov B.A. 1971. Branching Processes. Moscow: Nauka.
- Shiryaev A.N. 1989. Probability. Moscow: Nauka.
- Svirezhev Yu. M. 1987. Nonlinear waves, dissipative structures and catastrophes in ecology. Moscow: Nauka.
- Vatutin V.A. 2012. Total Population Size in Critical Branching Processes in a Random Environment // Mat. Zametki. 91(1): 12-23.