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Stochastic modelling of age-structured population with time and size dependence of immigration rate

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Abstract — A stochastic age-structured population model with immigration of individuals is considered. We assume that the lifespan of each individual is a random variable with a distribution function which may differ from the exponential one. The immigration rate of individuals depends on the time and total population size. Upper estimates for the mean and variance of the population size are established based on the theory of branching processes with constant immigration rate. A Monte Carlo simulation algorithm of population dynamics is developed. The results of numerical experiments with the model are presented.

Keywords: stochastic age-structured and size-dependent population model, branching stochastic processes with immigration, nonlinear immigration rate, non-exponential distribution of the lifespan of individuals, Monte Carlo simulation

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In the construction of mathematical models of population dynamics, it is essential to consider the following factors: (1) the dependence of the immigration or reproduction rate of individuals on the population size; (2) the finiteness of life time of individuals or the time of their stay in some stages with the ability to produce new individuals including individuals from other populations; (3) the interaction between individuals leading to death of individuals or their transition to other populations; (4) the environmental impact.

As a rule, stochastic models taking into account the total population size are based on random birth and death processes [3, 4]. Stochastic models using the age or stages of development of individuals are based on the theory of branching random processes [11, 24]. An important aspect in the creation of stochastic models of population dynamics is the consideration of immigration and reproduction processes of individuals. Mathematical foundations for construction of models of this family were given in [10, 12, 18, 25]. The development of the results of [10, 12, 18, 25] with respect to problems of dynamics of different populations was presented in [2, 9, 15].

The consideration of indicated and other factors entails the need for special methods and algorithms for analytical and numerical study of stochastic model. Examples of development of such methods and algorithms for stochastic models of

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specific types were presented in [7, 19, 20, 27, 28]. It should be noted that in the case of exponential distribution of lifespan of individuals the models allow analytical studies.

As a rule, deterministic models of population dynamics taking into account the above factors are based on partial differential equations, differential equations with delay, integro-differential or integral equations. Examples of such models were given in [5,6,8,22,23,29]. An important aspect of the creation of deterministic models in such subject areas as immunology, hematology, epidemiology, ecology, etc., is the consideration of compartment and age structures of studied populations. Incoming flows of individuals into different compartments can be regulated according to the feedback principle. The stay lengths of individuals in different compartments and the lifespan of individuals can be described by rather arbitrary distribution functions. The presence of a large number of compartments or intermediate stages of development of individuals leads to increase the dimension of the vector of used variables and at the same time to reduction of typical sizes of individual components of this vector. Therefore, using differential or integral equations in models, we encounter the problem of interpretation of their solutions taking into account the integer nature of variables. In addition, the description of the duration of stay of an individual in a particular compartment by non-exponential distribution functions actually means the use of the individual-based (agent-based) approach. Hence, in some problems the adequate simulation of some or other process requires transition from a deterministic model to a stochastic one, each based on the same basic assumptions. The stochastic model should take into account the integer nature of variables and the age composition of the population.

The general idea of the paper is to construct and study a stochastic analogue of the deterministic models of population dynamics [21, 22] under the following assumptions: the rate of appearance of new individuals depends on the time and population size; the distribution of lifespan of individuals differs from the exponential one. These assumptions lead to appearance of a new and previously unstudied family of stochastic models of population dynamics.

The aims of the paper are: (1) the mathematical formalization of the stochastic model; (2) the development of an approach to analytic study of some characteristics of the population size; (3) the elaboration of a modelling algorithm based on the Monte Carlo method; (4) numerical experiments with the stochastic model and comparison of the simulation results with solutions to a deterministic analogue in the form of integral equation.

1. Description of the model

Let the function r(t,x), $t \in \mathbb{R}$, $x \in \mathbb{Z}_+$, and the distribution function F(t) be given. We consider a population of individuals, where

- new individuals appear with the rate r(t, x(t)), where x(t) is the population size at the time moment *t*;

- each individual lives random time with the distribution function F(t) and dies

without leaving offspring;

- individuals do not interact with each other.

We assume that the function r(t,x) is nonnegative and piecewise-continuous from the right with respect to t, and the function F(t) is such that F(+0) = 0.

Let us give a formal definition of the random process describing such population. To do that, we introduce the following notations:

-W is a fixed set of individuals isomorphic to the set \mathbb{Z} of integer numbers;

 $-b_i$ is the moment of appearance of the individual $i \in W$ in the population;

 $-\ell_i$ is the lifespan of the individual $i \in W$. We assume that the random variables ℓ_i have the distribution function

$$F(t) = \mathsf{P}(\ell_i < t)$$

and are independent in common;

 $-d_i = b_i + \ell_i$ is the moment of death of the individual $i \in W$;

 $-X(t) = \{i \in W : t \in [b_i; d_i)\}$ is the set of individuals existing at the moment *t* in the population;

-x(t) = |X(t)| is the population size at the moment *t*;

 $-X(t,s) = \{i \in X(t) : s \in [b_i; d_i)\}, t \leq s$, is the set of individuals of the population existing at the moment *t* and living to the moment *s*;

 $-x(t,s) = |X(t,s)|, t \le s$, is the number of individuals in the population existing at the moment *t* and living to the moment *s*;

 $-v(t) = \max\{i \in W : b_i \leq t\}$ is the last individual among all individuals appeared before the time *t* inclusive;

 $-\mathscr{F}_t = \sigma\{X(s), \ell_i, s \leq t, i \in X(s)\}$ is the σ -algebra of events generated by the moments of appearance and lifespans of all individuals existing in the population to the moment *t* inclusive. We call the family of σ -algebras $\{\mathscr{F}_t\}_{t\in\mathbb{R}}$ the history of population.

We assume that for any t and h > 0 and for h tending to zero the following equalities hold:

$$\mathsf{P}(X(t+h) = X(t) \cup \{v(t)+1\} \mid \mathscr{F}_t) = r(t, x(t))h + o(h)$$
(1.1)

$$\mathsf{P}(X(t+h) = X(t) \mid \mathscr{F}_t) = 1 - r(t, x(t))h + o(h).$$
(1.2)

Formula (1.1) specifies the probability that exactly one individual *i* appears in the population in the time (t;t+h] and this individual is chosen from the set *W* according to the equality i = v(t) + 1. For this individual we have $b_i \in (t;t+h]$. Formula (1.2) specifies the probability that in the time (t;t+h] the content of the population does not change. The probability of other possible changes in the population content in the time (t;t+h] is o(h).

Point out two peculiarities in definition (1.1)–(1.2). First, the individuals do not die for small *h*. This follows from the fact that the random variables d_i , $i \in X(t)$, are measurable relative to \mathscr{F}_t and hence *h* can be taken so that $t + h < \min_{i \in X(t)} d_i$.

Second, probabilities (1.1)–(1.2) are measurable relative to the σ -algebra $\sigma\{x(t)\}$. Therefore, for small *h* the appearance of a new individual during the time interval [t;t+h) depends only on the population size at the moment *t* and does not depend on other events $A \in \mathscr{F}_t \setminus \sigma\{x(t)\}$.

2. Time distribution of intervals between appearance of individuals in the population

Consider the set X(t) of individuals of the population existing at the moment t. If no new individual appears in the population in the time interval (t;s) and individuals only die during this period, then we have the inclusion $X(s) \subset X(t)$. By

$$\xi(t) = \sup\{s \in \mathbb{R} : X(s) \subset X(t)\}$$

we denote the closest to t from the right moment of appearance of a new individual in the population. Some properties of $\xi(t)$ are presented in the following lemmas.

Lemma 2.1. For any $t \in \mathbb{R}$ and $s \ge t$ the following relation holds:

$$\mathsf{P}(\boldsymbol{\xi}(t) < s \mid \mathscr{F}_t) = 1 - \exp\left(-\int_t^s r(u, x(t, u)) \,\mathrm{d}u\right). \tag{2.1}$$

Proof. Fix a moment $t \in \mathbb{R}$ and consider the function

$$G(s) = \mathsf{P}(\xi(t) < s \mid \mathscr{F}_t), \quad s \ge t$$

for this moment. In this case for $s \ge t$ and h > 0 we have

$$\begin{aligned} G(s+h) &= \mathsf{P}(\xi(t) < s+h \mid \mathscr{F}_t) = \mathsf{P}(\xi(t) < s \mid \mathscr{F}_t) \,\mathsf{P}(\xi(t) < s+h \mid \xi(t) < s, \mathscr{F}_t) \\ &+ \mathsf{P}(\xi(t) \ge s \mid \mathscr{F}_t) \,\mathsf{P}(\xi(t) < s+h \mid \xi(t) \ge s, \mathscr{F}_t) \\ &= G(s) + (1 - G(s)) \mathsf{P}(\xi(t) < s+h \mid \xi(t) \ge s, \mathscr{F}_t). \end{aligned}$$

The probability $P(\xi(t) < s + h | \xi(t) \ge s, \mathscr{F}_t)$ is equal to the probability that a new individual appears in the population in the time interval [s; s + h) under the condition that the history of the population is known until the moment *t* inclusive and no new individuals appear during the time period [t; s).

According to formula (1.1), the probability that a new individual appears in the population in the time period [s;s+h) depends on the size of the population at the moment *s* only. By construction, the σ -algebra \mathscr{F}_t contains information on the moments of birth and death of all individuals appeared in the population until the moment *t* inclusive. Therefore, the random variable x(t,s) is measurable relative to \mathscr{F}_t and equals the size of the population at the moment *s* under the condition $\{\xi(t) \ge s\}$. Therefore,

$$\mathsf{P}(\xi(t) < s+h \mid \xi(t) \ge s, \mathscr{F}_t) = r(s, x(t,s))h + o(h).$$

Substituting the obtained expression into the formula for G(s+h), we get

$$G(s+h) = G(s) + (1 - G(s)) (r(s, x(t,s))h + o(h)).$$

Dividing this equality by *h* and passing to the limit for $h \rightarrow +0$ we obtain the Cauchy problem

$$G'(s) = (1 - G(s)) r(s, x(t, s)), \quad G(t) = 0$$

Function (2.1) is the solution to this problem.

Lemma 2.2. The equality $b_{i+1} = \xi(b_i)$ is valid for each $i \in W$.

Proof. Consider the moments $t = b_i$ and $s = \xi(t)$. Since no new individuals appear in the population in the time period [t;s), then the individual *i* is the last in the population for all time moments $u \in [t;s)$, i.e., i = v(u) for all $u \in [t;s)$. Therefore, X(s) equals $X(t,s) \cup \{i+1\}$. This means that at the time moment *s* the individual i + 1 appears in the population. Thus, $s = b_{i+1}$.

3. The case of constant rate of appearance of new individuals

Lemma 3.1. If $r(t,x) \equiv r^* = \text{const}$, then for any t > 0 and under the condition \mathscr{F}_0 the random variable x(t) - x(0,t) has the Poisson distribution with the parameter

$$\lambda(t) = r^* \int_0^t (1 - F(s)) \,\mathrm{d}s. \tag{3.1}$$

In particular,

$$E(x(t) | \mathscr{F}_0) = x(0,t) + \lambda(t) E(x^2(t) | \mathscr{F}_0) = x^2(0,t) + (2x(0,t)+1)\lambda(t) + \lambda^2(t).$$

Proof. Lemmas 2.1 and 2.2 imply that for $r(t,x) \equiv r^* = \text{const}$ the difference $b_{i+1} - b_i$ between subsequent moments of appearance of individuals has the exponential distribution with the parameter r^* . In this case we can use the results of [10] where it was established that the generating function

$$H(s,t) = \mathsf{E}(s^{z(t)} \mid \mathscr{F}_0)$$

of the variable z(t) = x(t) - x(0,t) has the form

$$H(s,t) = \exp\left(-r^* \int_0^t (1-h_0(\Phi(s,u))) \,\mathrm{d}u\right)$$

where in the case of considered model the functions h_0 and $\Phi(s,t)$ are

$$h_0(x) = x, \quad \Phi(s,t) = \mathsf{E}s^{\mathbb{I}(t \le \ell)} = s + (1-s)F(t).$$

Here $\mathbb{I}(\cdot)$ is an indicator function and ℓ is a random variable with the distribution function F(t). Substituting h_0 and $\Phi(s,t)$ into the expression for H(s,t), we get

 $H(s,t) = \exp\left(\lambda(t)\left(s-1\right)\right).$

Therefore, under the condition \mathscr{F}_0 the random variable x(t) - x(0,t) has the Poisson distribution with the parameter $\lambda(t)$.

The variable x(0,t) is measurable relative to \mathscr{F}_0 . Therefore,

$$\mathsf{E}(x(t) \mid \mathscr{F}_0) = x(0,t) + \mathsf{E}(x(t) - x(0,t) \mid \mathscr{F}_0) = x(0,t) + \lambda(t).$$

The formula for $E(x^2(t) | \mathscr{F}_0)$ can be proved similarly.

The assertion of Lemma 3.1 is formulated relative to the zero time moment, but it remains valid for any other basic time moment t_0 . In this case the assertion of the lemma can be formulated as follows: for any $t > t_0$ and under the condition \mathscr{F}_{t_0} the random variable $x(t) - x(t_0, t)$ has the Poisson distribution with the parameter $\lambda(t - t_0)$.

4. Upper estimate of the population size

Theorem 4.1. Let there exist a constant $r^* \ge 0$ such that

$$r(t,x) \leqslant r^*, \quad t \in \mathbb{R}, \quad x \in \mathbb{Z}_+.$$

In this case the inequality $x(t) \leq x(0,t) + z(t)$ holds under the condition \mathscr{F}_0 , where the random variable z(t) has the Poisson distribution with the parameter $\lambda(t)$ determined by formula (3.1).

In particular,

$$\mathsf{E}(x(t) \mid \mathscr{F}_0) \leq x(0,t) + \lambda(t) \\ \mathsf{E}(x^2(t) \mid \mathscr{F}_0) \leq x^2(0,t) + (2x(0,t)+1)\lambda(t) + \lambda^2(t).$$

Proof. Let *V* be one more fixed set of individuals isomorphic to \mathbb{Z} and not intersecting *W*. We define the random process $Y(t) \subset V$ similar to the process X(t) and introduce the following notations:

 $-b_j$ is the moment of appearance of the individual $j \in V$ in the population Y; $-\ell_j$ is the lifespan of the individual $j \in V$, $\{\ell_j\}_{j \in V}$ are independent in common random variables with the distribution function F(t);

 $-d_j = b_j + \ell_j$ is the moment of death of the individual $j \in V$; $-Y(t) = \{j \in V : t \in [b_j; d_j)\}$ is the set of individuals of the population *Y* existing at the moment *t*;

 $-\eta(t) = \max\{j \in V : b_j \leq t\}$ is the last individual among all individuals of the population *Y* appeared before the moment *t* inclusive;

 $-\mathscr{G}_t = \sigma\{\mathscr{F}_t, Y(s), \ell_j, s \leq t, j \in Y(s)\}$ is the σ -algebra of events generated by the moments of appearance and lifespans of all individuals existing in the populations *X* and *Y* until the moment *t* inclusive.

We assume that $Y(t) = \emptyset$ for $t \le 0$ and define the appearance of new individuals in the population *Y* in the following way:

$$P(Y(t+h) = Y(t) \cup \{j\} | \mathscr{G}_t) = (r^* - r(t, x(t)))h + o(h)$$

$$P(Y(t+h) = Y(t) | \mathscr{G}_t) = 1 - (r^* - r(t, x(t)))h + o(h)$$

where $t \ge 0$, h > 0, $j = \eta(t) + 1 \in V$.

Consider the random process

$$Z(t) = \emptyset, \ t \leq 0, \qquad Z(t) = (X(t) \setminus X(0)) \cup Y(t), \ 0 \leq t.$$

Under the condition \mathscr{F}_0 for any $t \ge 0$ and h > 0 we have

$$(X(t) \setminus X(0)) \subset Z(t)$$

$$x(t) - x(0,t) = |X(t) \setminus X(0)| \leq z(t) := |Z(t)|$$
(4.1)

$$P(Z(t+h) = Z(t) \cup \{i\} \mid \mathcal{G}_t) = r(t, x(t))h + o(h)$$
(4.2)

$$\mathsf{P}(Z(t+h) = Z(t) \cup \{j\} \mid \mathscr{G}_t) = (r^* - r(t, x(t)))h + o(h)$$
(4.3)

$$\mathsf{P}(Z(t+h) = Z(t) \mid \mathscr{G}_t) = 1 - r^* h + o(h)$$

where i = v(t) + 1, $j = \eta(t) + 1$.

Since the sum of probabilities (4.2) and (4.3) equals $r^*h + o(h)$, the rate of appearance of new individuals in the population *Z* is constant and equal to r^* . Therefore, according to Lemma 3.1, under the condition \mathscr{F}_0 the random variable z(t) has the Poisson distribution with the parameter $\lambda(t)$, which together with estimate (4.1) completes the proof.

Similar to Lemma 3.1, the assertion of Theorem 4.1 is valid not only relative to zero time moment, but relative to any other moment t_0 .

5. Simulation algorithm

Construct an algorithm for generation of implementations of the random process x(t) on the time segment [0; T]. Each implementation of the random process x(t) is a piecewise-constant function continuous from the right. Therefore, in order to construct implementations of x(t), we have to generate the moments

$$0 < t_1 < t_2 < \dots < t_n \leqslant T$$

at which the process x(t) changes its value and the values $x_k = x(t_k)$, k = 1, ..., n, at those time moments.

The size of the population x(t) can change in two following cases: at the moment of death of an individual (or a group of individuals) and at the moment of appearance

of a new individual. If at the moment t we know the moments d_i of death of all individuals $i \in X(t)$, then the function x(t,s) is determined and hence distribution (2.1) of the closest to t from the right moment $\xi(t)$ of appearance of a new individual in the population is also determined.

The direct simulation of the random variable $\xi(t)$ requires the solution of the nonlinear equation

$$1 - \exp\left(-\int_{t}^{s} r(u, x(t, u)) \,\mathrm{d}u\right) = \alpha \tag{5.1}$$

relative to the variable $s \in (t; \infty)$ for each t, where α is a random number uniformly distributed in (0; 1). To avoid this procedure, assume that $r(t, x) \leq \hat{r}(x) < +\infty$ for all $t \geq 0$ and $x \in \mathbb{Z}_+$, where $\hat{r}(x)$ is some bounding function. This assumption allows us to use the algorithm of maximal section (see [26, p. 227] and [1]) for generation of the random variable $\xi(t)$ and not to solve equation (5.1) at each step.

As a result we come to Algorithm 1 where we use the following notations: |D| is the number of elements in the list D, minD is the first (minimal) element in the list D (if the list D is empty, then we assume that min $D = +\infty$), uniform(0, 1) is a generator of pseudo-random numbers uniformly distributed on (0; 1). For generation of the values α and ℓ indicated in Algorithm 1 we can use the formulas and pseudo-random generators described in [13, 14, 16].

6. Computational experiments

The aim of numerical experiments with the model was the study of typical modes of population dynamics.

6.1. Influence of the function r(t,x) on the population dynamics

In the first experiment we compare the cases of constant and controlled inflows of individuals, i.e., $r(t,x) = r_1(t,x) = r^*$ or $r(t,x) = r_2(t,x) = (a_1 + a_2 x)/(1 + a_3 x^2)$, where r^* , a_1 , a_2 , and a_3 are positive constants. The function $r_2(t,x)$ relates to the family of unimodal functions. Such functions are often used in control models for biological processes and reflect positive and negative feedback between the size of the population and the rates of inflow or reproduction of individuals. The function $r_2(t,x)$ is nonnegative, continuous, and bounded from above for $x \ge 0$.

For F(t) we used the uniform distribution in $(0; \omega)$. In this case the function $\lambda(t)$ defined by formula (3.1) has the form

$$\lambda(t) = r^* \left(t - \frac{t^2}{2\omega} \right), \ t \in (0; \omega), \quad \lambda(t) = \frac{1}{2} r^* \omega, \ t \in [\omega; +\infty).$$

The values of scalar parameters were the following: x(0) = 0, $\omega = 10$, $r^* = 17320$, $a_1 = 10^7$, $a_2 = 1.5 \cdot 10^7$, and $a_3 = 10^{-2}$.

Let $E_1(t)$, $\sigma_1(t)$, $E_2(t)$, $\sigma_2(t)$ be the mathematical expectations and mean square deviations of x(t) for the cases $r(t,x) = r_1(t,x)$ and $r(t,x) = r_2(t,x)$, respectively.

Algorithm 1: Generation of an implementation of the random process x(t) on the segment [0; T].

Input:

T > 0 is a finite time moment;

D is an ordered list of real numbers with repetitions containing the death moments d_i of individuals $i \in X(0)$ existing at the moment t = 0;

Output:

n is the number of time moments of population size changes in the time segment [0; T];

 $0 < t_1 < \cdots < t_n \leq T$ are the time moments of population size changes; x_1, \ldots, x_n are the population sizes at the moments t_1, \ldots, t_n ;

1: t := 0 is the current time moment;

- 2: x := |D| is the current population size;
- 3: n := 0 is the number of generated moments for changes in the population size;

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4: While t < T do:
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5: $d := \min D$ is the closest moment of death of an individual;

6: $\alpha := uniform(0, 1);$

- 7: $\xi := -\ln(\alpha)/\hat{r}(x)$ is the supposed moment of appearance of a new individual;
- 8: If $d \leq \xi$, then:

9: t := d;

10: If T < t, then exit;

11: Remove all moments equal to *d* from the list *D*;

- 12: $n := n + 1; \quad t_n := t; \quad x_n := x := |D|;$
- 13: **Else**:

14:	$t := \xi;$
15:	If $T < t$, then exit;
16:	$\alpha := \text{uniform}(0, 1);$
17:	If $\alpha \hat{r}(x) < r(t,x)$, then:
18:	Generate the random variable ℓ with the distribution func-
	tion $F(t)$;
19:	Add the moment $d := t + \ell$ into the list D;
20:	$n := n + 1; t_n := t; x_n := x := D .$

The interval estimates of $E_j(t)$, $\sigma_j(t)$, j = 1, 2, with the confidence level 95% are presented in Tables 1 and 2 for different time moments. For each of two variants of specification of the function r(t,x) we generated 1000 implementations of the random process x(t).

Table 1 shows that the dynamics and numeric values of $E_1(t)$, $\sigma_1(t)$ completely correspond to the assertion of Lemma 3.1 and to the values of the function $\lambda(t)$. The data of Table 1 can be considered as a result of test calculations confirming the

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Table 1. Interval of $E_1(t)$, $\sigma_1(t)$.	estimates	t	$\lambda(t)$	$\sqrt{\lambda(t)}$	$E_1(t)$	$\sigma_1(t)$
		0	0	0	0	0
		0.5	8443.5	91.89	8443.01 ± 5.85	94.21 ± 4.32
		2.5	37887.5	194.65	37894.64 ± 12.37	199.35 ± 9.14
		4.5	60403.5	245.77	60408.82 ± 15.61	251.59 ± 11.54
		8.5	84651.5	290.95	84674.48 ± 18.27	294.41 ± 13.51
		12.5	86600	294.28	86602.97 ± 17.92	288.74 ± 13.24
		20	86600	294.28	86602.04 ± 17.89	288.31 ± 13.22
		30	86600	294.28	86592.64 ± 18.76	302.31 ± 13.86
		50	86600	294.28	86605.33 ± 18.25	294.07 ± 13.49

Table 2. Interval estimates of $E_2(t)$, $\sigma_2(t)$.

t	$E_2(t)$	$\sigma_2(t)$
0	0	0
0.5	37755.61 ± 7.08	114.19 ± 5.24
2.5	75709.56 ± 10.54	169.83 ± 7.79
4.5	89790.12 ± 12.56	202.41 ± 9.28
8.5	91039.43 ± 12.84	206.93 ± 9.49
12.5	85187.99 ± 12.85	207.12 ± 9.51
20	86682.08 ± 13.16	212.11 ± 9.73
30	86614.34 ± 13.03	209.99 ± 9.63
50	86610.28 ± 13.03	210.01 ± 9.63

proper work of the simulation algorithm described above.

Table 2 shows that the dynamics of $E_2(t)$, $\sigma_2(t)$ has an expressed transition character going out to a steady level.

The parameters of the model were chosen so that the confidence intervals for $E_1(t)$, $E_2(t)$ were distinct in the interval [0;20) and intersect on the segment [20;50]. At the same time, the estimates of $\sigma_1(t)$, $\sigma_2(t)$ are essentially different on the whole segment [0;50]. In particular, for $t \in [12;50]$ we can write $\sigma_1(t) \approx 1.42 \sigma_2(t)$ and this relation is caused by distinct behavior of the functions r_1 and r_2 in a neighbourhood of the point $x^* = \lambda(\omega) = 86600$. Therefore, taking into account this type of feedback in the inflow rate of new individuals $(r(t,x) = r_2(t,x))$, we get a lesser amplitude range for the size of the population with respect to its mean value in comparison to the case of constant inflow rate $(r(t,x) = r^*)$.

According to Lemma 3.1, for $r(t,x) = r_1(t,x)$ and for any fixed *t* the random variable x(t) has the Poisson distribution with the parameter $\lambda(t)$. If the parameter of this Poisson distribution is large, then it can be approximated by a normal distribution. Given the generated implementations, we applied the Pearson χ^2 criterion to test the hypothesis that the variable x(t) has a normal distribution at the time moments t = 1, 2, ..., 50. This hypothesis was accepted at the 5% level of significance for each indicated time moment and for each of the cases $r(t,x) = r_1(t,x)$ and $r(t,x) = r_2(t,x)$ (the minimal observed p-value was equal to 0.074). The fact that the distribution law of the function x(t) is normal allows us to use justifiably a set of well-known statistical methods for processing real data within the framework of the studied model.

6.2. Comparison with deterministic model

In the second experiment we compared the constructed stochastic model with the deterministic model in the form of an integral equation [21, 22]:

$$y(t) = \int_{t}^{\infty} P(a) e^{-\mu a} \varphi(t-a) da + \int_{0}^{t} P(a) e^{-\mu a} f(y(t-a)) da, \quad t \ge 0.$$
(6.1)

The following notations are used in equation (6.1): y(t) is the size of the population at the moment *t*, $\varphi(t)$ is the rate of appearance of individuals before the moment t = 0, f(y) is the inflow rate of new individuals depending on the population size, $\mu > 0$ is a constant, P(a) does not increase and is non-negative on $[0;\infty)$, P(0) = 1, and there exists a constant $\sigma > 0$ such that $P(\sigma) = 0$.

Model (6.1) is based on the same assumptions as those presented at the beginning of Section 1: the function f(y) has the same sense as the function r(t,x) in the stochastic model, and the role of the distribution function for the lifespan of individuals is implemented by the function

$$L(t) = 1 - P(t) e^{-\mu t}, \quad t \in [0; \infty).$$

The general properties of solutions to equation (6.1) and to its more general form were established in [21], namely, those are the existence, uniqueness, and non-negativity on the semiaxis $[0;\infty)$. The following assertions were proved in [22]: (1) if the solution y(t) to equation (6.1) has a limit y^* for $t \to +\infty$, then y^* is a root of the equation

$$y^* = J_{P,\mu} f(y^*), \quad J_{P,\mu} = \int_0^\infty P(a) e^{-\mu a} da$$
 (6.2)

(2) all nonnegative solutions to equation (6.2) are steady state solutions to equation (6.1), (3) if the functions P(a), $\varphi(t)$, f(y) are sufficiently smooth, y^* is a root of equation (6.2), the function f(y) satisfies the Lipschitz condition on \mathbb{R} and $J_{P,\mu} f'(y^*) < 1$, then the stationary solution y^* is asymptotically stable relative to small perturbations of the function $\varphi(t)$ in the sense of mean.

Assume that $\mu = 0.0475$, $P(t) = \max\{0, 1 - t/12\}, t \ge 0$,

$$f(x) = \begin{cases} 0.1x + 50, & x \in [0;800] \\ x - 670, & x \in [800;1000] \\ \max\{-1.8x + 2130, 0\}, & x \in [1000; +\infty). \end{cases}$$

The function f(x) is unimodal, nonnegative, continuous, and bounded from above. The parameters were taken so that $J_{P,\mu} = 5$, equation (6.2) has three roots

$$y_1^* = 500, \quad y_2^* = 837.5, \quad y_3^* = 1065$$

and the following inequalities hold:

$$J_{P,\mu} f'(y_1^*) < 1, \quad J_{P,\mu} f'(y_2^*) > 1, \quad J_{P,\mu} f'(y_3^*) < 1.$$



Figure 1. Heat map of implementations of the random process x(t).

Figure 1 presents the heat map of implementations of the random process x(t)in the case when the inflow of individuals is described by the function r(t, x) = f(x)and the lifespan is described by the function $F(t) = 1 - P(t)e^{-\mu t}$. The darker areas correspond to points (t,x) such that implementations of the random process x(t)occur more frequently in the neighbourhoods of those points. The lines of constant frequency are drawn for the levels 0.24, 0.12, 0.06, 0.03, 0.015, 0.0075, 0.0037, 0.0019. To construct this heat map, we generated 500000 implementations of the random process x(t). In all the implementations the initial population size was taken randomly and uniformly from the set $\{300, 301, \dots, 1200\}$, the ages of initial individuals were distributed uniformly in (0; 12).

It is seen that for large t the distribution of the variable x(t) is concentrated in neighbourhoods of the points y_1^* and y_3^* , and the value of x(t) almost never falls into a neighbourhood on the point y_2^* even if the initial size of the population is close to y_2^* . This observation is in accordance with the stability of the stationary solutions y_1^* and y_3^* of deterministic model (6.1).

7. Conclusion

In this paper we present the model of population dynamics in the form of a random process where the inflow rate of new individuals depends on time and the total size of the population and the distribution of lifespan of individuals may differ from exponential one. The model develops and generalizes stochastic models of population dynamics with constant inflow of individuals or models with exponential distribution functions of lifespan of individuals.

The paper contains the results of analytical and numerical studies of the constructed model including its comparison with the deterministic analogue in the form of an integral equation. The analytical results of the study of the stochastic model are used twice. First, they are used to test the numerical simulation algorithm and

compare the results of numerical experiments with theoretical values of the mathematical expectation and variance of the population size at constant rate of inflow of individuals. Second, the presence of upper estimates of the mathematical expectation and variance of the population size in the case of a non-constant rate of inflow of individuals provides the finiteness of these numerical characteristics in a fixed time interval. As a consequence, the application of standard methods of mathematical statistics becomes feasible for determination of point and interval estimates of the mathematical expectation of population size.

The results of computational experiments indicate some similarities and differences in the behavior of solutions of the stochastic and deterministic models constructed under the same assumptions. The analysis of solutions of the deterministic model allows us to evaluate the behavior of implementations of the stochastic model. The presence of stable or unstable stationary solutions of the integral model determines possible areas of attraction of implementations of the stochastic model. In particular, the estimate of the mathematical expectation of the population size relative to implementations falling within a neighbourhood of the asymptotically stable stationary solution y^* to the integral equation practically coincides with y^* . Such *a priori* information is quite important from the viewpoint of planning computational experiments with the stochastic model.

The approach proposed in the present paper can be used to construct stochastic models of population dynamics in immunology and epidemiology. Thus, in particular, the studies of the dynamics of small populations in the human immune system taking into account the structure of lymphoid system [17] or in processes of epidemic spread described within the framework of the SEIRS formalization [29] are rather important. Initial stages of infection in the human body or first few days (weeks) of the spread of an epidemic process in the population of a certain region require consideration of the discreteness of studied variables. The results of stochastic simulations can be used as initial data for the corresponding deterministic models.

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