Continuous Monocyclic and Polycyclic Age Structured Models of Population Dynamics

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Abstract

This paper focuses on the study of continuous age-structured models, or more general, physiologically structured models, which used for detailed and accurate study of population dynamics in many ecological, biological applications and medicine. In contrast to simpler unstructured models, these models allow us to relate the individual life-histories described as fertility and mortality rates of an individual at a given age with population dynamics. Depending from the particularity of reproduction mechanism continuous age-structured models are divided into monocyclic (reproduction occurs only at the one fixed age of individuals) and polycyclic (reproduction occurs with age-dependent probability at some age reproductive window) models. The linear monocyclic age-structured models are used often in cell cycles modelling, in population dynamics of plants, etc. In this case continuous age-structured models allow for obtaining the exact analytical solution. Since the linear and non-linear polycyclic age-structured models are more general then monocyclic models, they cover wider range of applications in life science. But in this case solution of model can be obtained only in the form of recurrent formulae and can be used only in numerical algorithms. Both solutions obtained in this work allow us to study numerically the important dynamical regimes – population outbreaks of three types: oscillations with large magnitude, pulse sequence and single pulse. Thus, analysis of continuous age-structured models of population dynamics provides insight into features and particularities of complex dynamical regimes of populations in many applications in biology, ecology and medicine.

Keywords: Age-structured model, exact solution, population outbreaks
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1. INTRODUCTION

Advanced continuous monocyclic and polycyclic age-structured models occupy important place in the study of complex processes of population dynamics in various applications of life science. Since these models provide the theoretical analysis and practical insights into the demographical processes of populations (i.e. reproduction and mortality of individuals) they can be used for deep analysis of dynamical regimes of populations in biology, ecology, medicine and others fields. The Kermack and McKendrick models [14], [15], [16] put the beginning of a large number of scientific works dealing with the theoretical analysis of the systems of linear and semi-linear hyperbolic equations with non-local integral boundary conditions for the continuous age-structured models of population dynamics [10] , [11], [12], [13], [17], [18], [20], [21]. Now the demographical processes in populations play an important role in the most theoretical and applied biological studies, such as the bacterial population dynamics, modeling of label-structured cell populations, modelling of dynamics and treatment of cancer, and many others.

In this paper we study the continuous age-structured monocyclic [1] and polycyclic [3] models of population dynamics. The feature of the first one is that individuals of population can give offspring with some likelihood only at some fixed age. If individuals do not give offspring, they lose their ability to reproduce. We derive the exact solution of linear model and obtain its asymptotic which was not considered in work [1]. In the second model individuals can give offspring at any age of the fixed reproductive window (age interval). In this work we consider the age reproductive window with maximum reproductive age less than individual's maximum lifespan that is more realistic than those one used in work [3]. We derive the explicit recurrent formulae for the solution. Both solutions obtained in this work are used in the developed accurate numerical algorithms for study of the special types of dynamical regimes – population outbreaks. The results of modelling for three types of polycyclic population outbreaks – oscillations with large magnitude, pulse sequence and single pulse are shown in the last section.

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2. Exact Solution of The Linear Monocyclic Model

The age-structured monocyclic population is divided at the age a_p into the two sub classes: individuals of the first one are born, mature, and either give offspring at the fixed age a_p (θ new individuals of zero age) and die, or move at the second (matured) subclass. The matured individuals do not reproduce, and can die or live up to a maximal age (lifespan) a_d ($a_p < a_d$). The age-specific densities of first and second subpopulations $u_1(a,t)$ and $u_2(a,t)$ are defined in domains $\overline{\Omega}^{(1)} = \{(a,\ t) : 0 \le a \le a_p, 0 \le t \le T\}$, and $\overline{\Omega}^{(2)} = \{(a,\ t) : a_p \le a \le a_d,\ 0 \le t \le T\}$, respectively. The quantity of individuals in each subclass are defined as $U_1(t) = \int\limits_0^{a_p} u_1(a,t)da$, $U_2(t) = \int\limits_{a_p}^{a_d} u_2(a,t)da$. The dynamics of $u_1(a,t)$, $u_2(a,t)$ are described by the system of initial-boundary value problems for the linear hyperbolic equations of the first order:

$$\frac{\partial u_1}{\partial t} + \frac{\partial u_1}{\partial a} = -s_1(a,t)\,u_1(a,t), \quad (a,t) \in \Omega^{(1)}, \tag{1}$$

$$\begin{aligned} u_1(0,t) &= \theta\,\sigma(t)\,u_1(a_p,t), \quad t \in (0,T), \\ u_1(a,0) &= \phi_1(a), \quad a \in [0,a_p]\,, \end{aligned} \tag{2}$$

$$\frac{\partial u_2}{\partial t} + \frac{\partial u_2}{\partial a} = -s_2(x,t)\,u_2(a,t), \quad (x,t) \in \Omega^{(2)}, \tag{3}$$

$$\begin{aligned} u_2(a_d,t) &= (1-\sigma(t))\,u_1(a_d,t), \quad t \in (0,T), \\ u_2(a,0) &= \phi_2(a), \quad a \in [a_p,a_d], \end{aligned} \tag{4}$$

where $\sigma(t)$ is a fertility rate at the age a_p; $\theta = const > 0$ is a mean number of offspring; $s_m(a,t)$ are death rates of each subclasses ($m = 1,2$); $\phi_m(a)$ are initial values of subclasses density. The period $[0,\ T]$ is divided into the set of time cuts $[t_{k-1},t_k]$, $t_k = ka_p$, $k = 1,..K$, $t_0 = 0$, $t_K = T$, which create the consequence of sets (Fig.1):

$$\begin{aligned} \overline{\Omega}_k^{(11)} &= \{(a,t)\,|\,t \in [(k-1)a_p, a+(k-1)a_p]\,,\ a \in [0,a_p]\,\}\,, \\ \overline{\Omega}_k^{(12)} &= \{(a,t)\,|\,t \in [a+(k-1)a_p, ka_p]\,,\ a \in [0,a_p]\,\}\,, \end{aligned} \tag{5}$$

$$\begin{aligned} \overline{\Omega}^{(21)} &= \{(a,t)\,|\,t \in [0,a-a_p],\ a \in [a_p,a_d]\,\}\,, \\ \overline{\Omega}^{(22)} &= \{(a,t)\,|\,t \in [a-a_p,T],\ a \in [a_p,a_d]\,\} \end{aligned} \tag{6}$$

where $\overline{\Omega}^{(1)} = \bigcup\limits_{k=1}^{K} \overline{\Omega}_k^{(1)} = \bigcup\limits_{k=1}^{K} \left(\overline{\Omega}_k^{(11)} \bigcup \overline{\Omega}_k^{(12)}\right)$, $\overline{\Omega}^{(2)} = \overline{\Omega}^{(21)} \bigcup \overline{\Omega}^{(22)}$. In the new characteristics variables $v_m = a - t$ ($m = 1,2$), $v_m \in \overline{\Omega}^{(m)}$, and time t system (1) - (4) is reduced to the Cauchy problem for the linear ODE system described propagation of "travelling wave" fronts along the characteristics $v_m = const$ [18], [19]:

$$\frac{\partial u_m}{\partial t} = -s_m(v_m+t,t)\,u_m, \quad u_m(v_m,0) = \phi_m(v_m), \quad (m = 1,2), \tag{7}$$

with additional conditions (2), (4). Solution of Equation (7) in $\overline{\Omega}_1^{(11)}$, $\overline{\Omega}_1^{(12)}$, ($k = 1$, $m = 1$) is given [19]:

$$u_1(a,t) = \begin{cases} u_1^{(0)}(v_1,t) = \phi_1(v_1)\,\exp\left(-\int\limits_0^t s_1(v_1+\xi,\xi)d\xi\right), & if\ (a,t) \in \overline{\Omega}_1^{(11)}, \\ u_1^{(1)}(v_1,t) = F_1^{(1)}(v_1)\,\exp\left(-\int\limits_{-v_1}^t s_1(v_1+\xi,\xi)d\xi\right), & if\ (x,t) \in \overline{\Omega}_1^{(12)}, \end{cases} \tag{8}$$

where the auxiliary functions $F^{(1)}(v_1)$ are defined from the Equation (2) (see Fig.1):

$$u_1^{(1)}(-t,t) = F_1^{(1)}(-t) = \theta\sigma(t)u_1^{(0)}(a_p - t, t). \tag{9}$$

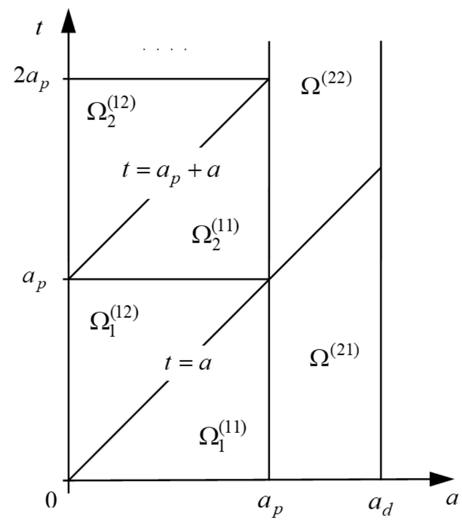

Figure 1: Splitting of domain $\overline{\Omega} = \overline{\Omega}^{(1)} \bigcup \overline{\Omega}^{(2)} = \bigcup_{k=1}^{K} \left(\bar{\Omega}_k^{(11)} \bigcup \bar{\Omega}_k^{(12)} \right) \bigcup \bar{\Omega}^{(21)} \bigcup \bar{\Omega}^{(22)}$

.

Since $F_1^{(1)}(v_1)$ depends only from the new variable $v_1 = a - t$ (Eq.(8)), we have:

$$F_1^{(1)}(v_1) = \theta\sigma(-v_1)u_1^{(0)}(v_1 + a_p, -v_1). \tag{10}$$

Substituting (13) in (11) yields the solution $u_1^{(1)}(a,t)$:

$$u_1^{(1)}(v_1,t) = \theta\sigma(-v_1)\phi_1(v_1 + a_p)\exp\left(-\int_0^t s_1(v_1+\xi,\xi)d\xi\right) \tag{11}$$

Eqs. (8), (10), (11) provide the exact solution of the first equation of system (7) $u_1(a,t)$ $(m = 1)$ in domains $\overline{\Omega}_1^{(11)}$, $\overline{\Omega}_1^{(12)}$ $(k = 1)$. The particular solutions $u_1^{(k)}(a,t)$ are defined consequently at the next time steps $k = 2, ..., K$ in domains $\overline{\Omega}_k^{(11)}$, $\overline{\Omega}_k^{(12)}$. Thus, the final solution $u_1(a,t)$ $(m = 1)$ can be given by two different but equivalent expression. The first form is described by the following recurrent formula $(k = 1, ..., K)$:

$$u_1(a,t) = \begin{cases} u_1^{(k-1)}(v_1,t) = u_1^{(k-1)}(a-t,t), \quad if\ (a,t) \in \overline{\Omega}_k^{(11)}, \\ u_1^{(k)}(v_1,t) = \theta\sigma(-v_1)u_1^{(k-1)}(v_1+a_p,-v_1)\exp\left(-\int_{-v_1}^{t} s_1(v_1+\xi,\xi)d\xi\right), \quad if\ (a,t) \in \overline{\Omega}_k^{(12)}, \end{cases} \tag{12}$$

$$u_1^{(0)}(v_1,t) = \phi_1(v_1)\exp\left(-\int_0^t s_1(v_1+\xi,\xi)d\xi\right). \tag{13}$$

The other form of solution is described explicitly for each particular solution $u_1^{(k)}(a,t)$, $k=1,...,K$:

$$\begin{aligned} u_1^{(k)}(v_1,t) &= \phi_1(v_1+ka_p)\theta\sigma(-v_1)\exp\left(-\int\limits_0^{-v_1-(k-1)a_p} s_1(v_1+ka_p+\xi,\xi)d\xi\right) \\ &\times \exp\left(-\int\limits_{-v_1}^{t} s_1(v_1+\xi,\xi)d\xi\right)\prod_{l=1}^{k-1}\theta\sigma(-(v_1+la_p))\exp\left(-\int\limits_{-v_1-la_p}^{-v_1-(l-1)a_p} s_1(v_1+la_p+\xi,\xi)d\xi\right), \end{aligned} \tag{14}$$

where $u_1^{(0)}(v_1,t)$ is given by Eq.(13). To complete the derivation of solution $u_1(a,t)$ we have to consider the compatibility condition for the two branches of solution (12) using the particular solutions (13), (14). The continuity condition of solution $u_1(a,t)\in C\left(\Omega^{(1)}\right)$ at the points $a=t-t_{k-1}$ in directions $a=const$, $t=const$ is given:

$$\begin{aligned} \lim_{a\to(t-t_{k-1})^-} u_1(a,t) &= \lim_{a\to(t-t_{k-1})^+} u_1(a,t), \\ \lim_{t\to(t_{k-1}+a)^-} u_1(a,t) &= \lim_{t\to(t_{k-1}+a)^+} u_1(a,t). \end{aligned} \tag{15}$$

Solution (12) provides the continuity condition (15) in the explicit form:

$$u_1^{(k-1)}(-t_{k-1},t) = u_1^{(k)}(-t_{k-1},t). \tag{16}$$

Substituting Eq.(14) in (16) yields the continuity condition for the initial value $\phi_1(x)$:

$$\phi_1(0) = \theta\,\sigma(0)\,\phi_1(a_p). \tag{17}$$

The smoothness condition of solution $u_1(a,t)\in C^{(1)}\left(\Omega^{(1)}\right)$ at the points of characteristics $a=t-t_{k-1}$ in directions $a=const$, $t=const$ is given:

$$\begin{aligned} \lim_{a\to(t-t_{k-1})^-} \frac{\partial u_1}{\partial a} &= \lim_{a\to(t-t_{k-1})^+} \frac{\partial u_1}{\partial a}, \\ \lim_{t\to(t_{k-1}+a)^-} \frac{\partial u_1}{\partial t} &= \lim_{t\to(t_{k-1}+a)^+} \frac{\partial u_1}{\partial t}, \end{aligned} \tag{18}$$

$$\left(\theta\left(\frac{d\sigma}{dt}\bigg|_{t\,=\,0}\phi_1(a_p) + \frac{d\phi_1}{da}\bigg|_{a\,=\,a_p}\sigma(0)\right) - \frac{d\phi_1}{dt}\bigg|_{a\,=\,0}\right) - \phi_1(0)s_1(0,0) = 0. \tag{19}$$

The general solution of the second problem (3), (4) (including (9), $m=2$) in domains $\overline{\Omega}^{(21)}$, $\overline{\Omega}^{(22)}$ is given:

$$u_2(a,t) = \begin{cases} u_2^{(1)}(v_2,t) = \phi_2(v_2)\exp\left(-\int\limits_0^t s_2(v_2+\xi,\xi)d\xi\right), & if\ (a,t)\in\overline{\Omega}^{(21)}; \\ u_2^{(2)}(v_2,t) = F_2(v_2-a_p)\exp\left(-\int\limits_{-v_2+a_p}^{t} s_2(v_2+\xi,\xi)d\xi\right), & if\ (a,t)\in\overline{\Omega}^{(22)}; \end{cases} \tag{20}$$

where function $F_2(v_2)$ is defined by analogy with $F_1(v_1)$ from the boundary condition (4):

$$F_2(v_2-a_p) = (1-\sigma(-(v_2-a_p)))u_1(v_2,a_p-v_2), \tag{21}$$

where $u_1(a,t)$ is given by Eq.(12). By analogy with compatibility (continuity and smoothness) conditions (15), (18), we obtain the corresponding compatibility conditions for solution $u_2(a,t)$:

$$\phi_2(x_d) = (1-\sigma(0))\,\phi_1(x_d), \tag{22}$$

$$\frac{d\sigma}{dt}\bigg|_{t=0}\phi_1(a_p)+\frac{d\phi_1}{da}\bigg|_{a=a_p}(1-\sigma(0))-\frac{d\phi_2}{da}\bigg|_{a=a_p}+(1-\sigma(0))\,\phi_1\,(a_p)\,s_1\,(a_p,0)-\phi_2\,(a_p)\,s_2\,(a_p,0)=0. \tag{23}$$

Thus, the unique smooth solution $u_m\,(a,t)\in C^{(1)}\left(\Omega^{(m)}\right)\cap C\left(\overline{\Omega}^{(m)}\right)$, $(m=1,2)$ of problem (1) - (4) given by Eqs. (12), (13), (14), (17), (19), (20) - (23) exists if the coefficients of system (1)-(4) and initial values (2), (4) satisfy the conditions:

$$\begin{aligned} &\phi_1(a)\in C^{(1)}\left([0,a_p]\right), \quad \phi_2(a)\in C^{(1)}\left([a_p,a_d]\right),\\ &s_m(a,t)\in C\left(\Omega^{(m)}\right), \quad \sigma(t)\in C^{(1)}\left([0,T]\right), \end{aligned} \tag{24}$$

$$\theta = const>0, \quad 0\le \phi_m(a), \quad 0<s_m(a,t), \quad 0<\sigma(t)<1. \tag{25}$$

By analogy with [1], from all result obtained above we arrive to the following theorem.

Theorem 2.1. *Let θ, $\phi_m(a)$, $\sigma(t)$, $s_m(a,t)$, $(m=1,2)$ satisfy conditions (24), (25), then the unique smooth solution of problem (1) - (4) $u_m\,(a,t)\in C^{(1)}\left(\Omega^{(m)}\right)\cap C\left(\overline{\Omega}^{(m)}\right)$ exists and is given in the two different but equivalent forms: (12), (13), (20), (21) or (12), (13), (14), (20), (21).*

Corollary 2.1.1. *Solution (13), (14), of the system (1)-(5) with constant coefficients provides us the asymptotic behavior of monocyclic population model with $t\to\infty$ ($K\to\infty$). In particular, solution (14) with σ, s_1, $\phi_1=const>0$ at instants $t_k=ka_p$ (Fig.1) is:*

$$u_1^{(k)}(a,t_k)=\phi_1(\theta\sigma)^k\exp\left(-ka_ps_1\right), \quad (a,t_k)\in\bar{\Omega}_k^{(1)}. \tag{26}$$

Hence, if the basic reproductive number $R_0=\theta\sigma\exp(-a_ps_1)<1$ the monocyclic population declines to extinction $u_1^{(k)}(a,t_k)\to 0$, if $R_0=1$ it remains at the initial value $u_1^{(k)}(a,t_k)\to\phi_1$, and if $R_0>1$ it grows infinitely $u_1^{(k)}(a,t_k)\to\infty$.

3. Solution of Nonlinear Policyclic Model

Nonlinear continuous age-structured model of polycyclic population dynamics with a density-dependent death rate is studied in this section. In contrast with the model of monocyclic population in this model individuals can proliferate at any age $a\in[a_p,a_f]$, where a_p is an age of maturation (the onset of reproduction), a_f is a maximum individual's reproductive age, $[a_p,a_f]$ is an age reproductive window. We assume that individuals have the finite maximal lifespan a_d and they all die when reach the maximal age a_d. Age-specific population density $u(a,t)$ is defined in domain $\overline{\Omega}=\{(a,\ t)\,|a\in[0,a_d],\ t\in[0,T]\}$. We will use also domain $\Omega=\{(a,\ t)\,|a\in(0,a_d)\,,\ t\in(0,T)\}$. The quantity of individuals at instant t is $U(t)=\int\limits_0^{a_d}u(a,t)da$. The dynamics of $u(a,t)$ is described by the initial-boundary value problem for the nonlinear hyperbolic equation with integral boundary condition:

$$\frac{\partial u}{\partial t}+\frac{\partial u}{\partial a}=-(s(a,t)+\delta\tilde{\sigma}(a,t)+r(t)U(t))u, \quad (a,t)\in\Omega, \tag{27}$$

$$\begin{aligned} &u(0,t)=\theta\int\limits_{a_p}^{a_f}\sigma(a,t)u(a,t)da, \quad 0<t\le T,\\ &u(a,0)=\phi(a), \quad 0\le a\le a_d \end{aligned} \tag{28}$$

where $s(a,t)$ is a death rate, $r(t)$ is a coefficient of proportionality of nonlinear death rate, $\theta > 0$ is a coefficient of reproduction, δ denotes the biological type of population and takes only values 0 or 1: $\delta = 1$ when individuals die or are eliminated after reproduction (like biological cells after dividing, some species of fishes and insects, etc.), $\delta = 0$ when individuals can survive the birth of offspring (for example, the cell of yeast, most species of animals, people, etc.), $\sigma(a,t)$ is a fertility rate, function $\tilde{\sigma}(a,t)$ is defined as

$$\tilde{\sigma}(a,t) = \begin{cases} \sigma(a,t), & if\ a \in [a_p, a_d] \\ 0, & if\ a \notin [a_p, a_d] \end{cases}, \tilde{\sigma}(a,t) \in C(\Omega). \tag{29}$$

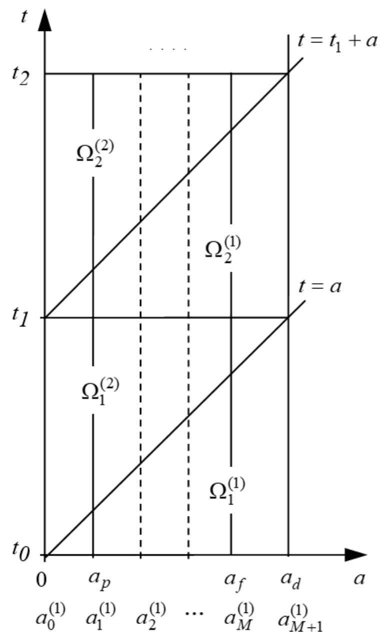

Figure 2: Splitting of domain $\overline{\Omega} = \bigcup\limits_{k=1}^{K} \left(\Omega_k^{(1)} \bigcup \Omega_k^{(2)}\right)$ and the age intervals $\left[a_m^{(1)}, a_{m+1}^{(1)}\right]$, $m = 0, ..., M$.

The period $[0,T]$ is divided on time cuts $[t_{k-1}, t_k]$, $t_k = ka_d$, $k = 1, ..., K$, $t_0 = 0$, which define the domains:

$$\begin{aligned} \Omega_k^{(1)} &= \{(a,t)\,|\,t \in [(k-1)a_d, a + (k-1)a_d]\,,\ a \in [0, a_d]\}\,, \\ \Omega_k^{(2)} &= \{(a,t)\,|t \in [a + (k-1)a_d, ka_d]\,,\ a \in [0, a_d]\}\,, \end{aligned} \tag{30}$$

where $\overline{\Omega} = \bigcup\limits_{k=1}^{K} \left(\Omega_k^{(1)} \bigcup \Omega_k^{(2)}\right)$ (see Fig.2). We define the sets of age-specific intervals:

$$Q^{(k)} = \left\{ \left[-a_m^{(k)}, -a_{m+1}^{(k)}\right] \,\middle|\, a_m^{(k)} = ma_p + (k-1)a_d, m = 0, 1, ..., M-1,\ a_M^{(k)} = a_f + (k-1)a_d,\ a_{M+1}^{(k)} = ka_d \right\}, \tag{31}$$

$$M = \begin{cases} [a_f/a_p] + 1, & if\ \ a_f/a_p - [a_f/a_p] > 0, \\ [a_f/a_p]\,, & if\ \ a_f/a_p - [a_f/a_p] = 0, \end{cases} \tag{32}$$

where $[a]$ - is an integer part of real number a. Using the new variables $v = a - t$, $t' = t$ we reduce the problem (27) – (28) to the Cauchy problem for the nonlinear ODE

$$\frac{\partial u}{\partial t'} = -\left(\tilde{s}(v + t', t') + r(t')U(t')\right) u(v, t')\,, \quad u(v, 0) = \phi(v), \tag{33}$$

where $\tilde{s}(a,t) = s(a,t) + \delta\tilde{\sigma}(a,t)$ is a linear part of death rate which does not depend from the population density. The boundary condition (28) will be used also in Cauchy problem (33). Solution of problem (33) in domains $\Omega_1^{(1)}$ and $\Omega_1^{(2)}$ is defined in variables a, t by analogy with [3], [5]:

$$u(a,t) = \begin{cases} u_1^{(1)}(v,t) = F_1^{(1)}(a-t)\,W(a-t,t_0,t)U_1(t), & if\ (a,t) \in \Omega_1^{(1)}; \\ u_1^{(2)}(v,t) = F_1^{(2)}(a-t)\,W(a-t,t-a,t)U_1(t), & if\ (a,t) \in \Omega_1^{(2)}; \end{cases} \tag{34}$$

$$W(v,t_k,t) = \exp\left(-\int\limits_{t_k}^{t} \tilde{s}(v+\xi,\xi)d\xi\right), \tag{35}$$

$$U_1(t) = \exp\left(-\int\limits_{t_0}^{t} r(\xi)U(\xi)d\xi\right). \tag{36}$$

Differentiating Eq.(36) by t and substituting $U(t) = \int\limits_0^t u_1^{(2)}(a-t,t)da + \int\limits_t^{a_d} u_1^{(1)}(a-t,t)da$, the first and second part of Eq. (34) in the obtained expression yields the Cauchy problem for unknown function $U_1(t)$:

$$U_1{}'(t) = -r(t)\left(\int\limits_0^t F_1^{(2)}(a-t)W(a-t,t-a,t)da + \int\limits_t^{a_d} F_1^{(1)}(a-t)W(a-t,t_0,t)da\right)U_1^2(t), \tag{37}$$

$$U_1(t_0) = 1 \tag{38}$$

Solution of problem (37), (38) is given:

$$U_1(t) = \left(1 + \int\limits_0^t r(\eta)\left(\int\limits_0^\eta F_1^{(2)}(a-\eta)W(a-\eta,\eta-a,\eta)da \ + \int\limits_\eta^{a_d} F_1^{(1)}(a-\eta)W(a-\eta,t_0,\eta)da\right)d\eta\right)^{-1}, \quad t \in [t_0,t_1]. \tag{39}$$

Substituting the initial value (28) in the upper part of Eq. (34) yields:

$$u_1^{(1)}(v,t_0) = F_1^{(1)}(v) = \phi(v). \tag{40}$$

Function $F_1^{(2)}(v)$ is obtained from the integral Eq. (28):

$$u_1^{(2)}(-t,t) = F_1^{(2)}(-t)U_1(t) = \theta\int\limits_{a_p}^{a_f} \sigma(a,t)u(a,t)da, \quad t \in [0,a_d). \tag{41}$$

From (34) it follows that $F_1^{(2)}(u)$ is defined by auxiliary functions $\Phi_{1m}(z)$ step by step at the intervals $z \in \left[-x_m^{(1)}, -x_{m-1}^{(1)}\right]$, $m = 1,...,M$:

$$\Phi_{11}(z) = \theta\int\limits_{a_p+z}^{a_f+z} \sigma(y-z,-z)\,F_1^{(1)}(y)W(y,t_0,-z)dy, \quad z \in \left[-a_1^{(1)}, -a_0^{(1)}\right], \tag{42}$$

$$\Phi_{1m}(z) = \theta \int\limits_{a_p+z}^{-a_{m-2}^{(1)}} \sigma(y-z,-z)\Phi_{1m-1}(y)\, W(y,-y,-z)dy + \theta \sum_{j=0}^{m-3} \int\limits_{-a_{j+1}^{(1)}}^{-a_j^{(1)}} \sigma(y-z,-z)\Phi_{1j+1}(y)W(y,-y,-z)dy$$
$$+ \theta \int\limits_{-a_0^{(1)}}^{a_f+z} \sigma(y-z,-z)F_1^{(1)}(y)W(y,t_0,-z)dy, \quad z \in \left[-a_m^{(1)}, -a_{m-1}^{(1)}\right], \quad m = 2, ..., M, \tag{43}$$

where the sum in Eq.(43) is not used when $m = 2$. Solution of equation (41) $F^{(1)}(v)$ is:

$$F_1^{(2)}(v) = \Phi_{1m}(v), \quad v \in \left[-a_m^{(1)}, -a_{m-1}^{(1)}\right], \quad m = 1, ..., M. \tag{44}$$

$$F_1^{(2)}(v) = \theta \int\limits_{a_p+v}^{a_f+v} \sigma(y-v,-v)\, F_1^{(2)}(y)W(y,-y,-v)dy, \quad v \in \left[-a_{M+1}^{(1)}, -a_M^{(1)}\right]. \tag{45}$$

Substituting (39), (40), (44), (45) in (34) yields the solution of problem (27) - (28) in domains $\Omega_1^{(1)}$, $\Omega_1^{(2)}$, $(k = 1)$. We consider solution of problem (27) - (28) in domains $\Omega_k^{(1)}$, $\Omega_k^{(2)}$ for the next $k > 1$. On the border of two domains $\Omega_{k-1}^{(1)} \cup \Omega_{k-1}^{(2)}$ and $\Omega_k^{(1)} \cup \Omega_k^{(2)}$, at the points $t = t_{k-1}$ solution $u(a, t)$ has to satisfy continuity condition:

$$u_k^{(1)}(a - t_{k-1}, t_{k-1}) = u_{k-1}^{(2)}(a - t_{k-1}, t_{k-1}), \quad k > 1. \tag{46}$$

Hence, common solution of problem (27) – (28) in domain $\overline{\Omega}$ for $k \in N$ is:

$$u(a,t) = \begin{cases} u_k^{(1)}(v,t) = F_k^{(1)}(a-t)W(a-t,t_{k-1},t)U_k(t), & if\ (x,t) \in \Omega_k^{(1)}; \\ u_k^{(2)}(v,t) = F_k^{(2)}(a-t)W(a-t,t-a,t)U_k(t), & if\ (x,t) \in \Omega_k^{(2)}; \end{cases} \tag{47}$$

$$F_1^{(1)}(v) = \phi(v), \tag{48}$$

$$F_k^{(1)}(v) = F_{k-1}^{(2)}(v)W(v,-v,t_{k-1})U_{k-1}(t_{k-1}), \quad v = a - t_{k-1}, \quad k > 1, \tag{49}$$

$$\Phi_{k1}(z) = \theta \int\limits_{a_p+z}^{a_f+z} \sigma(v-z,-z)\, F_k^{(1)}(v)W(v,t_{k-1},-z)dv, \quad z \in \left[-a_1^{(k)}, -a_0^{(k)}\right], \tag{50}$$

$$\Phi_{km}(z) = \theta \int\limits_{a_p+z}^{-a_{m-2}^{(k)}} \sigma(v-z,-z)\Phi_{km-1}(v)\, W(v,-v,-z)dv + \theta \sum_{j=0}^{m-3} \int\limits_{-a_{j+1}^{(k)}}^{-a_j^{(k)}} \sigma(v-z,-z)\Phi_{kj+1}(v)$$
$$\times W(v,-v,-z)dv + \theta \int\limits_{-a_0^{(k)}}^{a_f+z} \sigma(v-z,-z)F_k^{(1)}(v)\, W(v,t_{k-1},-z)dv,$$
$$z \in \left[-a_m^{(k)}, -a_{m-1}^{(k)}\right], \quad m = 2, ..., M, \tag{51}$$

$$F_k^{(2)}(v) = \Phi_{km}(v), \quad v \in \left[-a_m^{(k)}, -a_{m-1}^{(k)}\right], \quad m = 1, ..., M, \tag{52}$$

$$F_k^{(2)}(v) = \theta \int\limits_{a_p+v}^{a_f+v} \sigma(y-v,-v)\, F_k^{(2)}(y)W(y,-y,-v)dy, \quad v \in \left[-a_{M+1}^{(k)}, -a_M^{(k)}\right], \tag{53}$$

$$U_k(t) = \left(1 + \int\limits_{t_{k-1}}^{t} r(\eta)\left(\int\limits_{0}^{\eta - t_{k-1}} F_k^{(2)}(a-\eta)W(a-\eta, \eta - a, \eta)da \;+ \int\limits_{\eta - t_{k-1}}^{a_d} F_k^{(1)}(a-\eta)W(a-\eta, t_{k-1}, \eta)dx\right)d\eta\right)^{-1}, \tag{54}$$

where the sum in Eq.(50) is not used when $m = 2$. The continuity condition of solution $u(a,t) \in C\left(\bar{\Omega}\right)$ at the points $a = t - t_{k-1}$ across lines $a = const$, $t = const$ leads to the equation:

$$F_k^{(1)}(-t_{k-1}) = F_k^{(2)}(-t_{k-1}). \tag{55}$$

From this we arrive to the condition for the initial value:

$$\phi\,(0) = \theta \int\limits_{a_p}^{a_f} \sigma\,(v,0)\phi(v)dv. \tag{56}$$

The smoothness condition of solution $u(a,t) \in C^{(1)}(\Omega) \cap C(\overline{\Omega})$ at the points $a = t - t_{k-1}$ across lines $a = const$, $t = const$ leads to the equation:

$$F_k^{(1)'}(-t_{k-1}) = F_k^{(2)'}(-t_{k-1}). \tag{57}$$

From Eq.(57) it follows the restriction on the coefficients and initial value of system (27)-(28):

$$\frac{\partial \phi}{\partial a}(0) = \theta\left(\sigma(a_f,0)\phi(a_f) - \sigma(a_p,0)\phi(a_p) + \int\limits_{a_p}^{a_f}\left(\frac{\partial \sigma}{\partial a}(v,0) - \frac{\partial \sigma}{\partial t}(v,0) + \sigma(v,0)\tilde{s}(v,0)\right)\phi(v)dv\right). \tag{58}$$

Thus, the unique smooth solution $u(a,t) \in C^{(1)}(\Omega) \cap C(\overline{\Omega})$ of problem (27)-(28) given by Eqs. (47)-(54) exists if coefficients of system (27)-(28) and initial values (28) satisfy the conditions:

$$\phi(a) \in C^{(1)}\left([0,a_f]\right), \quad s(a,t) \in C\left(\Omega\right), \quad \tilde{\sigma}(a,t) \in C^{(1)}\left(\Omega\right), \quad r(t) \in C\left(R_{>0}\right), \tag{59}$$

$$\theta = const > 0, \quad \phi(a) \geq 0, \quad r(t) \geq 0, \quad s(a,t) > 0, \quad \sigma(a,t) \geq 0 \tag{60}$$

By analogy with [3], from all result obtained above we arrive to the following theorem.

Theorem 3.1. *Let initial value $\phi(a)$ and coefficients $s(a,t)$, $r(t)$, $\sigma(a,t)$, of problem (27)-(28) satisfy the conditions (59), (60), continuity and smoothness conditions (56), (58). Then there exists a unique solution $u(a,t) \in C^{(1)}(\Omega) \cap C(\overline{\Omega})$ of problem (27)-(28) which is defined by the explicit recurrent formulae (47)-(54).*

4. Population Outbreaks In Numerical Experiments

Explicit form of solutions obtained in Theorems 1 and 2 for age-structured models of monocyclic and polycyclic populations allows for developing of accurate numerical algorithms for simulation of different dynamical regimes of populations [1], [2], [3], [5], [6]. The one of the important classes of population dynamical regimes is a population outbreaks observed in various biological systems. Among different types of population outbreaks [8] we distinguish three main types of population density dynamics: oscillations with large magnitude, sequence of pulses and single pulse. For instance, oscillation with large magnitude of population density were observed in desert locusts populations [7], herbivorous insects, forest Lepidoptera, Cardiaspina albitextura Taylor [8], etc. The time series of NIH 3T3 cell population in the form of sequence of pulses were observed by using the FUCCI method in [9]. Outbreak in the form of single pulse of infected population density is observed in a result of quick epidemic invasion of infective disease [4]. According to the population outbreak classification oscillations with a large magnitude and sequence of pulses is inherent to the populations with periodical eruption dynamics [8].

In simulations of age-structured model of polycyclic population dynamics we observe these three types of population density outbreaks: oscillations with large magnitude (Fig.3a, 3b), pulse sequence (Fig.3c, 3d) and single pulse (Fig.3e, 3f). All dynamical regimes with outbreak are obtained for periodic by time functions of death and birth rates like in work [3]. It was expected that solution of system with periodic coefficients is oscillating function because according to Theorem 3.1 solution depends continuously from the coefficients of model. On the other hand, pulse sequence and single pulse exhibit quite new form of solution of age-structured model of polycyclic population dynamics which can be valuable in practice and applicable for the various applications in life science.

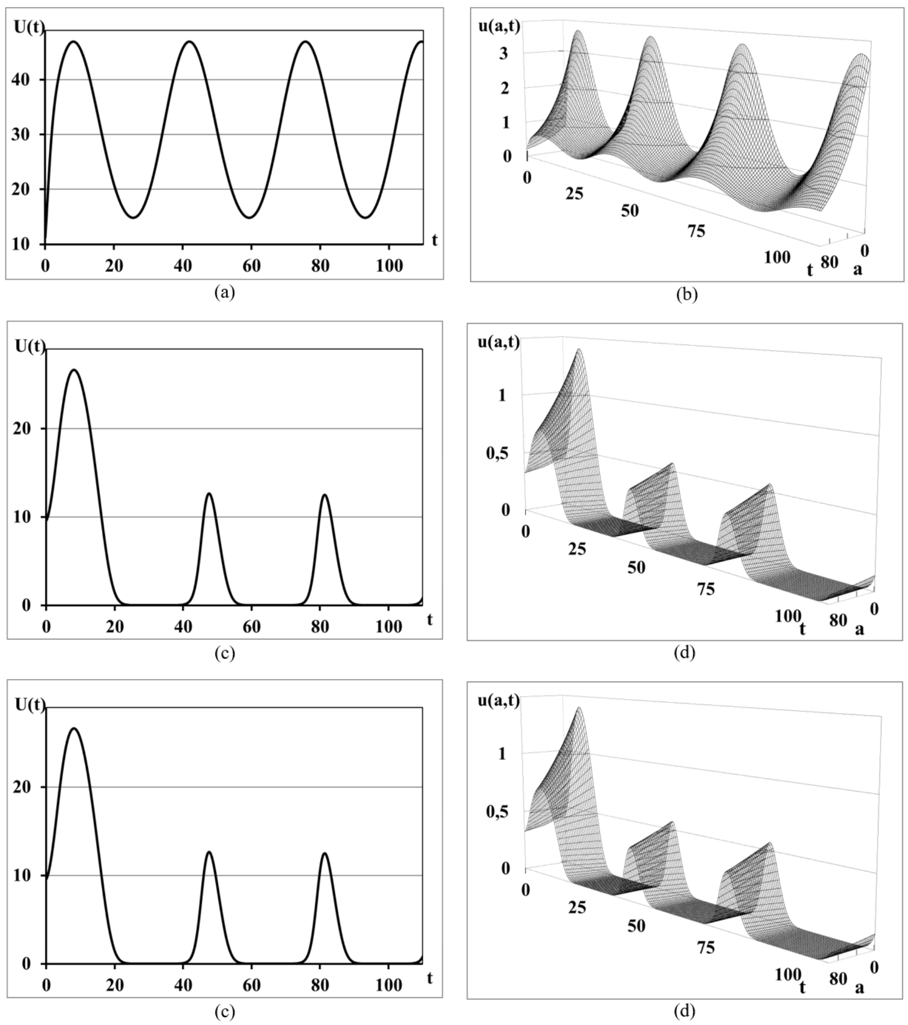

Figure 3: Graphs of the quantity of individuals $U(t)$ and population density $u(a,t)$ of polycyclic population outbreaks: (a), (b) – periodic regime with large magnitude, (c), (d) – pulse consequence, (e), (f) – single pulse.

5. Conclusion

In this work the exact solution of linear age-structured model of monocyclic population dynamics and the explicit recurrent formula for the solution of semi-linear age-structured model (with density-dependent death rate) of polycyclic population dynamics were obtained. The explicit form of obtained solutions allows for developing the accurate numerical algorithms for simulation of complex dynamical regimes of population such as population outbreaks. The theoretical and numerical study of nonlinear age-structured models of monocyclic and polycyclic population dynamics helps us understand better the different dynamical regimes of populations observed in various real-world applications in practice.

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