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A One-Sex Population Dynamics Model with Discrete Set of Offsprings and Child Care

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Abstract. We present a one-sex age-structured population dynamics deterministic model with a discrete set of offsprings, child care, environmental pressure, and spatial migration. All individuals have pre-reproductive, reproductive, and post-reproductive age intervals. Individuals of reproductive age are divided into fertile single and taking child care groups. All individuals of pre-reproductive age are divided into young (under maternal care) and juvenile (offspring who can live without maternal care) classes. It is assumed that all young offsprings move together with their mother and that after the death of mother all her young offsprings are killed. The model consists of integro-partial differential equations subject to the conditions of the integral type. Number of these equations depends on a biologically possible maximal newborns number of the same generation produced by an individual. The existence and uniqueness theorem is proved, separable solutions are studied, and the long time behavior is examined for the solution with general type of initial distributions in the case of non-dispersing population. Separable and more general (nonseparable) solutions, their large time behavior, and steady-state solutions are studied for the population with spatial dispersal, too.

Keywords: population dynamics, age–structured population, child care.

1 Introduction

Many species of animals care of their offsprings. This phenomenon is native for many species of mammals and birds and *forms the main difference between the behavior of the population taking care of offsprings and that without maternal (or parental) duties.* But child care for every species is different. Offsprings of mammals and birds spend some time with their mother or both parents, while young offsprings of fishes, reptilia, and amphibia are left to one's fate. Mammals and birds feed, warm, and defend their young offsprings from enemies. If one of these native duties is not realized, young offsprings die and the population vanishes. For many species of mammals [1], e.g. bear (*Thalarctos maritimus* and *Ursus arctos horribilis*), whale (*Balaenoptera musculus*), and panther (*Pannthera onca*), only a female takes care of her young offsprings. For some species of mammals and birds, e.g. red fox (*Vulpes vulpes*), gnawer (*Dolichotis patagonium*), penquin (*Pygoscelis adeliae*), heron (*Ardea purpurea*), falcon (*Falco ciolumbarius*), and tawny owl (*Strix aluco*), both parents take care of their young offsprings.

The Sharpe-Lotka-McKendrick-von Foerster (see, e.g., [2]) and Fredrickson-Hoppensteadt-Staroverov [3–5] models are well known in mathematical biology. In the case when information about sex ratio is not important the Sharpe-Lotka-McKendrick-von Foerster one sex model (or its Gurtin-MacCamy generalization [6]) is usually used to describe dynamics of age-structured population. The other one (or its Hadeler [7] modification involving a maturation period) describes the evolution of populations forming permanent pairs. All these models do not include a female gestation period.

Models involving a gestation period were first proposed and analyzed in papers [8–11]. However, all these models do not treat the child care phenomenon. Therefore, all models mentioned above have to be applied for the population which does non care its young offsprings, e.g. some species of fishes, reptilia, and amphibia. In papers [12–16] we proposed and examined four population dynamics models with child care: two for one-sex and the other two for two-sex population. The main requirement in these papers is that all offsprings under maternal (or parental) care are killed if their mother (or any of their parents) dies. These models are based on the notion of the density of young (under maternal or parental care) offsprings which has to be a C^1-function at least on the characteristic lines of the equation for this density. However, *the differentiability assumption of this density is questionable for many species of mammals and birds.* There exists the other essential requirement in the case of the population with the spatial diffusion. In this case, *all young offsprings have to move together with their mother (or pair of parents).* To describe the diffusion of young offsprings and their mothers the Ficke law for fluxes of young offsprings and their mothers with the same diffusion coefficient is used in models [14] and [15]. In the case of the homogeneous Neumann problem, each of these fluxes have to be zeroth on the boundary of the living area. But such the model does not ensure that young offsprings and their mothers move together. If we assume that diffusion flux of young offsprings is proportional to that of their mothers, then in the case of homogeneous Neumann problem at the same time these both fluxes will be zeroth on the boundary of their living region. But the gradient of the young offsprings density on this boundary may not be equal to zero and we have a loss or gain of youngs through the boundary. This shows that this model is biologically incorrect, too. Therefore, there arises *the problem of the construction of a biologically correct model in the case of a population with the spatial diffusion.*

This problem can be solved by using *a notion of the complex (family) which consists of mother (or both parents) and a discrete set of her (their) young offsprings.* In [17], we proposed a model for two-sex population taking into account temporal pairs, a discrete set of offsprings, and child care and examined its separable solutions. In [9], a model of two-sex population is studied taking into account permanent pairs, child care, and a discrete set of offsprings.

In the present paper we present and examine a one-sex age-structured population dynamics deterministic model with child care and a discrete set of offsprings of the same generation produced by an individual. A preprint version of this paper has been used in [18] (see literature cited there) for numerical solving of the model discussed in the present paper. This model could be used to describe the evolution of the population for which only one mother takes care (see above) of her young offsprings. We consider the population dynamics both with and without spatial diffusion ant take into account an environmental influence (pressure) which depends on population overcrowding. All individuals have pre-reproductive, reproductive, and post-reproductive age intervals. All individuals of reproductive age are divided into fertile single (without offsprings under maternal care at the given time) and individuals taking child care groups. Individuals of pre-reproductive age are divided into young and juvenile (offsprings who can live without maternal care) classes. We assume that the ecological pressure does not influence the dynamics of the young offsprings directly, that youngs move together with their mother, and that after the death of mother all her young offsprings are killed. The model consists of a system of integro-partial differential equations subject to conditions of the integral type. The number of these equations depends on a biologically possible maximal number of newborns of the same generation produced by an individual.

The paper is organized as follows. In Section 3, we present and examine the model for a non-dispersing population. In Section 3.1, separable solutions are studied for the general type of stationary vital rates. In Section 3.2, the existence and uniqueness theorem is proved for the unlimited population. Section 3.3 is devoted to the analysis of the long time behavior of the solution to the model without spatial diffusion and with general type of the initial distributions. In Section 4, we consider the model with spatial dispersal. Separable and more general solutions and their long time behavior are studied in Sections 4.1 and 4.2, respectively. The structure of steady-state solutions is examined in Section 4.3. Remarks in Section 5 conclude the paper.

2 Notation

The following notation is used for the analysis of the population dynamics.

$\mathbb{R}^m$: the Euclidean space of dimension m with $x = (x_1, \ldots, x_m)$,

κ: the diffusion modulus,

$(0, T)$ and (T_1, T_3) $(T < T_1 < T_3)$: the child care and reproductive age intervals, respectively,

$u(t, \tau_1, x)$: the age-space-density of individuals aged τ_1 at time t at the position x who are of juvenile ($\tau_1 \in (T, T_1)$), fertile single ($\tau_1 \in (T_1, T_3)$), or post-reproductive ($\tau_1 > T_3$) age,

$u_k(t, \tau_1, \tau_2, x)$: the age-space-density of individuals aged τ_1 at time t at the position x who take care of their k offsprings aged τ_2 at the same time,

$\nu(t, \tau_1, x)$: the natural death rate of individuals aged τ_1 at time t at the position x who are of juvenile or adult age,

$\nu_k(t, \tau_1, \tau_2, x)$: the natural death rate of individuals aged τ_1 at time t at the position x who take care of their k offsprings aged τ_2,

$\nu_{ks}(t, \tau_1, \tau_2, x)$: the natural death rate of $k - s$ young offsprings aged τ_2 at time t at the position x whose mother is aged τ_1 at the same time,

$\alpha_k(t, \tau_1, x)\,\mathrm{d}t$: the probability to produce k offsprings in the time interval $[t, t + \mathrm{d}t]$ at the location x for an individual aged τ_1,

N: sum of spatial densities of juvenile and adult individuals,

$\rho(N)$: the death rate conditioned by ecological causes (overcrowding of the population), $\rho(0) = 0$,

$u_0(\tau_1, x), u_{k0}(\tau_1, \tau_2, x)$: the initial age distributions,

$[u|_{\tau_1=\tau}]$: the jump discontinuity of u at the point $\tau_1 = \tau$,

$\alpha = \sum\limits_{k=1}^{n} \alpha_k,\ \gamma_1(\tau_1) = \max(0, \tau_1 - T_3), \gamma_2(\tau_1) = \min(\tau_1 - T_1, T),$

$\tilde{\nu}_k = \nu_k + \sum\limits_{s=0}^{k-1} \nu_{ks},$

$T_2 = T_1 + T$: the minimal age of an individual finishing care of offsprings of the first generation,

$T_4 = T_3 + T$: the maximal age of an individual finishing care of offsprings of the last generation,

$$\begin{aligned}
&\sigma_1 = (T_1, T_3), \qquad \sigma_2 = (T_1, T_4), \qquad \sigma_3 = (T_2, T_4),\\
&\sigma_1^* = (T, \infty) \setminus \sigma_1, \quad \sigma_2^* = (T, \infty) \setminus \sigma_2, \quad \sigma_3^* = (T, \infty) \setminus \sigma_3,\\
&Q = \{(\tau_1, \tau_2)\colon\ \tau_1 \in (T_1 + \tau_2, T_3 + \tau_2),\ \ \tau_2 \in (0, T)\}.
\end{aligned}$$

In what follows κ, T, T_1, and T_3 are assumed to be positive constants. In the case of non-dispersing populations all functions $u, u_k, \nu, \nu_k, \nu_{ks}, \alpha_k, u_0$, and u_{k0} do not depend on the spatial position x.

3 The non-dispersing population dynamics model

In this section, we present a deterministic model for a non-dispersing age-structured population with discrete set of offsprings of the same generation produced by an individual and prove the existence and uniqueness theorem. In the case of stationary vital rates, we examine separable solutions and find the long time behavior of the solution to this model with initial distributions of the general type. We take into account the environmental pressure by letting the death rates of juvenile and adult individuals depend on the sum of their spatial densities, N, and assume that young offsprings are subject to natural mortality and are protected from density related increases of mortality dependent on N directly. Note that in more general case the environmental pressure depends on N, x, t, and age of the individuals. At age $\tau_1 = T$ all young offsprings go to the juvenile group and at age $\tau_1 = T_1$ all juveniles become adult individuals. Let n be the biologically possible maximal number of newborns of the same generation produced by an individual. Using the balance law, we derive the density-dependent population dynamics model which consists of the equations

$$\partial_t u + \partial_{\tau_1} u + \big(\nu + \rho(N)\big) u = -\begin{cases} 0, & \tau_1 \in \sigma_1^*, \\ \alpha u, & \tau_1 \in \sigma_1 \end{cases}$$
$$+ \begin{cases} 0, & \tau_1 \in \sigma_2^*, \\ \int\limits_{\gamma_1(\tau_1)}^{\gamma_2(\tau_1)} \sum\limits_{k=1}^{n} \nu_{k0} u_k \,\mathrm{d}\tau_2, & \tau_1 \in \sigma_2 \end{cases} + \begin{cases} 0, & \tau_1 \in \sigma_3^*, \\ \sum\limits_{k=1}^{n} u_k|_{\tau_2 = T}, & \tau_1 \in \sigma_3, \end{cases} \quad t > 0, \tag{1}$$

$$\partial_t u_k + \partial_{\tau_1} u_k + \partial_{\tau_2} u_k + \left(\nu_k + \sum_{s=0}^{k-1} \nu_{ks} + \rho(N)\right) u_k$$
$$= \begin{cases} 0, & k = n, \\ \sum\limits_{s=k+1}^{n} \nu_{sk} u_s, & 1 \le k \le n-1, \end{cases} \quad (\tau_1, \tau_2) \in Q, \;\; t > 0, \tag{2}$$

$$N = \int\limits_{T}^{\infty} u \,\mathrm{d}\tau_1 + \int\limits_{0}^{T} \mathrm{d}\tau_2 \int\limits_{T_1+\tau_2}^{T_3+\tau_2} \sum_{k=1}^{n} u_k \,\mathrm{d}\tau_1 \tag{3}$$

subject to the conditions

$$\begin{cases} u|_{\tau_1 = T} = \int\limits_{\sigma_3} \sum\limits_{k=1}^{n} k u_k|_{\tau_2 = T} \,\mathrm{d}\tau_1, \\ u_k|_{\tau_2 = 0} = \alpha_k u, \\ u|_{t=0} = u_0, \;\; u_k|_{t=0} = u_{k0}, \\ [u|_{\tau_1 = \tau}] = 0, \;\; \tau = T_1, T_2, T_3, T_4. \end{cases} \tag{4}$$

Here ∂_t and ∂_{τ_k} signify partial derivatives. The first term on the right-hand side in equation (1) means the part of individuals who produces offsprings, the second and third terms describe the part of individuals whose all young offsprings die and who finish child care, respectively. The transition term $\sum\limits_{s=0}^{k-1} \nu_{ks} u_k$ on the lefth-hand side in equation (2) describes the part of individuals aged τ_1 at time t who take child care of k young offsprings and whose at least one young offspring dies. Similarly, the term on the right-hand side in this equation describes a part of individuals aged τ_1 at time t who take care of more than $k, 1 \le k \le n-1$, young offsprings aged τ_2 whose number after the death of the other offsprings is equal to k. The condition $[u|_{\tau_1=\tau}] = 0,\ \tau = T_1, T_2, T_3, T_4$ means that function u must be continuous at the point, $\tau_1 = \tau$, discontinuity of the right-hand side of equation (1).

As follows from the foregoing, the given functions $\nu, \nu_k, \nu_{ks}, \alpha_k, u_0,$ and u_{k0} and the unknown ones u and u_k are to be positively valued, otherwise they have no biological significance. The positive constants T and T_s are to be given, too. The assumption $T < T_1$ given in Section 2 is natural.

In order that conditions (4) would be consistent we formulate the following compatibility conditions:

$$\begin{cases} u_0|_{\tau_1=T} = \int\limits_{\sigma_3} \sum\limits_{k=1}^{n} k u_{k0}|_{\tau_2=T} \,\mathrm{d}\tau_1, \\ u_{k0}|_{\tau_2=0} = \alpha_k|_{t=0} u_0, \\ [u_0|_{\tau_1=\tau}] = 0, \;\; \tau = T_1, T_2, T_3, T_4. \end{cases} \tag{5}$$

Inserting

$$u(t,\tau_1) = f(t)U(t,\tau_1), \quad u_k(t,\tau_1,\tau_2) = f(t)U_k(t,\tau_1,\tau_2), \quad f(0) = 1 \tag{6}$$

into (1)–(4), we split this system into the problem for U and U_k,

$$\begin{aligned} \partial_t U + \partial_{\tau_1} U + \nu U = &- \begin{cases} 0, & \tau_1 \in \sigma_1^*, \\ \alpha U, & \tau_1 \in \sigma_1 \end{cases} \\ &+ \begin{cases} 0, & \tau_1 \in \sigma_2^*, \\ \int\limits_{\gamma_1(\tau_1)}^{\gamma_2(\tau_1)} \sum\limits_{k=1}^{n} \nu_{k0} U_k \,\mathrm{d}\tau_2, & \tau_1 \in \sigma_2 \end{cases} + \begin{cases} 0, & \tau_1 \in \sigma_3^*, \\ \sum\limits_{k=1}^{n} U_k|_{\tau_2=T}, & \tau_1 \in \sigma_3, \end{cases} \quad t > 0, \end{aligned} \tag{7}$$

$$\begin{aligned} &\partial_t U_k + \partial_{\tau_1} U_k + \partial_{\tau_2} U_k + \tilde{\nu}_k U_k \\ &\quad = \begin{cases} 0, & k = n, \\ \sum\limits_{s=k+1}^{n} \nu_{sk} U_s, & 1 \le k \le n-1, \end{cases} \quad (\tau_1,\tau_2) \in Q, \;\; t > 0 \end{aligned} \tag{8}$$

subject to the conditions

$$\begin{cases} U|_{\tau_1=T} = \int\limits_{\sigma_3} \sum\limits_{k=1}^{n} k U_k|_{\tau_2=T} \,\mathrm{d}\tau_1, \\ U_k|_{\tau_2=0} = \alpha_k U, \\ U|_{t=0} = u_0, \;\; U_k|_{t=0} = u_{k0}, \\ [U|_{\tau_1=\tau}] = 0, \;\; \tau = T_1, T_2, T_3, T_4, \end{cases} \tag{9}$$

and the equations for f and N,

$$f' = -\rho(f\beta) f, \quad f(0) = 1, \tag{10}$$

$$\beta = \int_T^{\infty} U \,\mathrm{d}\tau_1 + \int_0^T \mathrm{d}\tau_2 \int_{T_1+\tau_2}^{T_3+\tau_2} \sum_{k=1}^{n} U_k \,\mathrm{d}\tau_1, \tag{11}$$

$$N = f\beta. \tag{12}$$

Function f means the ratio of the total limited (under ecological pressure) population N and the total unlimited population β.

3.1 Separable solutions to problem (7)–(9)

In this section we restrict ourselves by the case where ν, ν_k, ν_{ks}, and α_k do not depend on t and are positive supported functions. Moreover, we assume that ν is continuous, while α_k, ν_k, and ν_{ks} are C^1-functions. We seek solutions of the form

$$\begin{aligned}
&U \ = \tilde{U} v^\lambda(\tau_1) \exp\{\lambda t\}, \quad u_0 = \tilde{U} v^\lambda(\tau_1), \quad v^\lambda(T) = 1,\\
&U_k = \tilde{U} v^\lambda(\tau_1 - \tau_2) v_k^\lambda(\tau_1, \tau_2) \exp\{\lambda t\}, \quad u_{k0} = \tilde{U} v^\lambda(\tau_1 - \tau_2) v_k^\lambda(\tau_1, \tau_2),\\
&v_k^\lambda|_{\tau_2 = 0} = \alpha_k,
\end{aligned} \tag{13}$$

where $\tilde{U} > 0$ is an arbitrary constant while the constant λ and positive functions v^λ and v_k^λ are to be determined. Note that separable solutions to the Gurtin-MacCamy model and their application to genetics were first studied in [19] and [20], respectively, (see also [21] and [2]). Inserting (13) into equations (7)–(9) gives the equations for v^λ and v_k^λ,

$$\begin{aligned}
v^{\lambda\prime} + (\nu + \lambda) v^\lambda = &- \begin{cases} 0, & \tau_1 \in \sigma_1^*, \\ \alpha v^\lambda, & \tau_1 \in \sigma_1 \end{cases}\\
&+ \begin{cases} 0, & \tau_1 \in \sigma_2^*, \\ \int\limits_{\gamma_1(\tau_1)}^{\gamma_2(\tau_1)} \sum\limits_{k=1}^{n} \nu_{k0} v_k^\lambda(\tau_1, \tau_2) v^\lambda(\tau_1 - \tau_2) \, \mathrm{d}\tau_2, & \tau_1 \in \sigma_2 \end{cases}\\
&+ \begin{cases} 0, & \tau_1 \in \sigma_3^*, \\ \sum\limits_{k=1}^{n} v_k^\lambda(\tau_1, T) v^\lambda(\tau_1 - T), & \tau_1 \in \sigma_3 \end{cases}
\end{aligned} \tag{14}$$

with the conditions

$$v^\lambda(T) = 1, \quad [v^\lambda(\tau)] = 0, \quad \tau = T_1, T_2, T_3, T_4,$$

$$\partial_{\tau_1} v_k^\lambda + \partial_{\tau_2} v_k^\lambda + (\tilde{\nu}_k + \lambda) v_k^\lambda = \begin{cases} 0, & k = n, \\ \sum\limits_{s=k+1}^{n} \nu_{sk} v_s^\lambda, & 1 \le k \le n-1 \ \text{ in } \ Q \end{cases} \tag{15}$$

with the condition

$$v_k^\lambda|_{\tau_2 = 0} = \alpha_k,$$

and the characteristic equation for λ,

$$1 = \int\limits_{\sigma_3} \sum_{k=1}^{n} k v_k^\lambda(\tau_1, T) v^\lambda(\tau_1 - T) \, \mathrm{d}\tau_1. \tag{16}$$

Here and in what follows the prime indicates differentiation. Equations (15) can be solved in the recurrent way starting with $k = n$ and have a unique positive C^1-solution.

Equations (14) can be solved explicitly for $\tau_1 \in [T, T_1] \cup [T_3, \infty)$, while, for $\tau_1 \in (T_1, T_3)$, they can be reduced into Volterra type integral equations with the delay T and, therefore, have a unique positive solution. Obviously, this solution is a C^1-function except the points $\tau_1 = T_1, T_2, T_3$, and T_4. From (14) and (15) it is easy to see that

$$v^\lambda = v^0(\tau_1)\exp\{-\lambda(\tau_1 - T)\}, v_k^\lambda = v_k^0(\tau_1, \tau_2)\exp\{-\lambda\tau_2\} \tag{17}$$

where v^0 and v_k^0 satisfies equations (14) and (15) for $\lambda = 0$. From equations (16) and (17) we get the characteristic equation for λ,

$$1 = I(\lambda), \quad I(\lambda) = \int\limits_{\sigma_1} \exp\{-x\lambda\} v^0(x) \sum_{k=1}^{n} k v_k^0(x+T, T)\,\mathrm{d}x. \tag{18}$$

The distribution of roots of this equation is well known. It has a unique real root λ_0 and a discrete set of complex conjugate roots. The real part of complex roots is less than λ_0. As a result we formulate

Theorem 1. *Let ν, ν_k, ν_{ks}, and α_k be positive functions and $\nu \in C^0([T,\infty))$, $\alpha_k \in C^0(\bar\sigma_1) \cap C^1(\sigma_1)$, ν_k and $\nu_{ks} \in C^0(\bar Q) \cap C^1(Q)$. Then problem* (7)–(9) *has a one-parameter class of separable solutions of type* (13) *with the properties*

$$U \in C^0\big([T,\infty)\big) \cap C^1\big((T,\infty) \setminus \{\tau_1 = T_1, T_2, T_3, T_4\}\big),$$

$$U_k \in \begin{cases} C^0(\bar Q) \cap C^1(Q \setminus \{\tau_1 = \tau_2 + T_2\}) & \textit{if} \;\; T_3 - T_1 > T, \\ U_k \in C^0(\bar Q) \cap C^1(Q) & \textit{if} \;\; T_3 - T_1 \le T. \end{cases}$$

From the biological point of view death rates increase with age increasing and need not stay bounded.

3.2 The existence and uniqueness theorem to system (7)–(9)

In this section, we consider the case $T_3 - T_1 > 2T$ (the opposite case can be examined similarly) and prove the existence and uniqueness theorem to system (7)–(9) with vital rates independent of t. We assume that conditions of Theorem 1 are satisfied and u_0 and u_{k0} are positive C^1-functions. Integrating of equation (8), for $t < \tau_2$, yields

$$U_n(t,\tau_1,\tau_2) = u_{n0}(\tau_1 - t, \tau_2 - t)\exp\left\{-\int\limits_{\tau_1 - t}^{\tau_1} \tilde\nu_n(\xi, \xi + \tau_2 - \tau_1)\,\mathrm{d}\xi\right\},$$

$$\begin{aligned} U_k(t,\tau_1,\tau_2) &= u_{k0}(\tau_1 - t, \tau_2 - t)\exp\left\{-\int\limits_{\tau_1 - t}^{\tau_1} \tilde\nu_k(\xi, \xi + \tau_2 - \tau_1)\,\mathrm{d}\xi\right\} \\ &+ \int\limits_{\tau_1 - t}^{\tau_1} \exp\left\{-\int\limits_{\eta}^{\tau_1} \tilde\nu_k(\xi, \xi + \tau_2 - \tau_1)\,\mathrm{d}\xi\right\} \sum_{s=k+1}^{n} (\nu_{sk} U_s)|_{(\eta + t - \tau_1, \eta, \eta + \tau_2 - \tau_1)}\,\mathrm{d}\eta \end{aligned} \tag{19}$$

with $1 \leq k \leq n-1$. Equation (19) can be solved in the recurrent way starting with $k = n-1$.

If $t > \tau_2$, we have

$$U_k(t,\tau_1,\tau_2) = U(t-\tau_2,\tau_1-\tau_2)v_k^0(\tau_1,\tau_2) \tag{20}$$

with v_k^0 defined in Section 1. It remains to determine $U(t,\tau_1)$.

Let $t < \tau_1 - T$. Set

$$\Pi(a,b;\nu+\alpha) = \exp\left\{-\int_a^b \big(\nu(x)+\alpha(x)\big)\,\mathrm{d}x\right\},$$

$$A(\tau_1,\tau_2) = \sum_{k=1}^n \big(\nu_{k0}v_k^0\big)\big|_{(\tau_1,\tau_2)},$$

$$B(t,\tau_1,\tau_2) = \sum_{k=1}^n \nu_{k0}(\tau_1,\tau_2)U_k(t,\tau_1,\tau_2),$$

$$C(t,\tau_1) = \sum_{k=1}^n U_k(t,\tau_1,T),$$

$$D(\tau_1) = \sum_{k=1}^n v_k^0(\tau_1,T).$$

Integrating equation (7), we get

$$U(t,\tau_1) = u_0(\tau_1-t)\Pi(\tau_1-t,\tau_1;\nu), \quad \tau_1 \in [T,T_1] \tag{21}$$

and

$$U(t,\tau_1) = \begin{cases} u_0(\tau_1-t)\Pi(\tau_1-t,\tau_1;\nu), & t \leq \tau_1 - T_4, \\ U(T_4+t-\tau_1,T_4)\Pi(T_4,\tau_1;\nu), & t > \tau_1 - T_4 \end{cases} \tag{22}$$

for $\tau_1 > T_4$. We write two last terms of the right hand side of equations (7) and sets $[0,\tau_1-T)\times[T_1,T_2]$, $[0,\tau_1-T)\times[T_2,T_3]$, and $[0,\tau_1-T)\times[T_3,T_4]$ in the form

$$\int_{\gamma_1(\tau_1)}^{\gamma_2(\tau_1)} \sum_{k=1}^n \nu_{k0}U_k\,\mathrm{d}\tau_2 = \begin{cases} \int_{\gamma_1(\tau_1)}^{\gamma_2(\tau_1)} B(t,\tau_1,\tau_2)\,\mathrm{d}\tau_2, & 0<t\leq\gamma_1(\tau_1), \\ \int_{\gamma_1(\tau_1)}^{t} U(t-\tau_2,\tau_1-\tau_2)A(\tau_1,\tau_2)\,\mathrm{d}\tau_2 & \\ \quad + \int_{t}^{\gamma_2(\tau_1)} B(t,\tau_1,\tau_2)\,\mathrm{d}\tau_2, & \gamma_1(\tau_1)<t\leq\gamma_2(\tau_1), \\ \int_{\gamma_1(\tau_1)}^{\gamma_2(\tau_1)} U(t-\tau_2,\tau_1-\tau_2)A(\tau_1,\tau_2)\,\mathrm{d}\tau_2, & t\geq\gamma_2(\tau_1), \end{cases}$$

$$\sum_{k=1}^{n} U_k|_{\tau_2=T} = \begin{cases} C(t,\tau_1), & 0 < t < T, \\ D(\tau_1)U(t-T,\tau_1-T), & t \geq T \end{cases}$$

$$\begin{aligned}[0,\tau_1-T)\times[T_1,T_2] = {} & \{0 \leq t \leq \tau_1 - T_1,\ \tau_1 \in [T_1,T_2]\} \\ & \cup \{\tau_1 - T_1 \leq t < \tau_1 - T,\ \tau_1 \in [T_1,T_2]\},\end{aligned}$$

$$\begin{aligned}[0,\tau_1-T)\times[T_2,T_3] = {} & \{0 \leq t \leq \min(\tau_1 - T_2, T),\ \tau_1 \in [T_2,T_3]\} \\ & \cup \{T \leq t \leq \tau_1 - T_2,\ \tau_1 \in [T_2+T,T_3]\} \\ & \cup \{\tau_1 - T_2 \leq t \leq T,\ \tau_1 \in [T_2,T_2+T]\} \\ & \cup \{\max(T,\tau_1-T_2) \leq t < \tau_1 - (T_2-T),\ \tau_1 \in [T_2,T_3]\} \\ & \cup \{\tau_1 - (T_2-T) \leq t < \tau_1 - T,\ \tau_1 \in [T_2,T_3]\},\end{aligned}$$

and

$$\begin{aligned}[0,\tau_1-T)\times[T_3,T_4] = {} & \{0 \leq t \leq \tau_1 - T_3,\ \tau_1 \in [T_3,T_4]\} \\ & \cup \{\tau_1 - T_3 \leq t \leq T,\ \tau_1 \in [T_3,T_4]\} \\ & \cup \{T \leq t \leq \tau_1 - (T_3-T),\ \tau_1 \in [T_3,T_4]\} \\ & \cup \{\tau_1 - (T_3-T) \leq t < \tau_1 - T,\ \tau_1 \in [T_3,T_4]\}.\end{aligned}$$

Then, by integrating, reduce equation (7) with conditions $(9)_{3,4}$ into the integral equations obtaining:

$$U(t,\tau_1) = \int_{\tau_1-t}^{\tau_1} \Pi(\xi,\tau_1;\nu+\alpha)\,\mathrm{d}\xi \int_{\tau_1-t}^{\xi} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta + f(t,\tau_1) \tag{23}$$

with

$$\begin{aligned}f(t,\tau_1) = {} & \int_{\tau_1-t}^{\tau_1} \Pi(\xi,\tau_1;\nu+\alpha)\,\mathrm{d}\xi \int_{\xi+t-\tau_1}^{\xi-T_1} B(\xi+t-\tau_1,\xi,\tau_2)\,\mathrm{d}\tau_2 \\ & + u_0(\tau_1-t)\Pi(\tau_1-t,\tau_1;\nu+\alpha)\end{aligned}$$

in $\{0 \leq t \leq \tau_1 - T_1,\ \text{ for } \tau_1 \in [T_1,T_2]\}$,

$$\begin{aligned}U(t,\tau_1) = {} & U(T_1+t-\tau_1,T_1)\Pi(T_1,\tau_1;\nu+\alpha) \\ & + \int_{T_1}^{\tau_1} \Pi(\xi,\tau_1;\nu+\alpha)\,\mathrm{d}\xi \int_{T_1}^{\xi} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta\end{aligned} \tag{24}$$

in $\{\tau_1 - T_1 \leq t < \tau_1 - T\ \text{ for } \tau_1 \in [T_1,T_2]\}$,

$$U(t,\tau_1) = \int_{\tau_1-t}^{\tau_1} \Pi(\xi,\tau_1;\nu+\alpha)\,\mathrm{d}\xi \int_{\tau_1-t}^{\xi} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta + f(t,\tau_1) \tag{25}$$

with

$$f(t,\tau_1) = u_0(\tau_1 - t)\Pi(\tau_1 - t, \tau_1; \nu + \alpha) + \int_{\tau_1 - t}^{\tau_1} \Pi(\xi, \tau_1; \nu + \alpha)\,\mathrm{d}\xi \int_{\xi + t - \tau_1}^{T} B(\xi + t - \tau_1, \xi, \tau_2)\,\mathrm{d}\tau_2 + \int_{\tau_1 - t}^{\tau_1} \Pi(\xi, \tau_1; \nu + \alpha) C(\xi + t - \tau_1, \xi)\,\mathrm{d}\xi$$

in $\{0 \le t \le \min(\tau_1 - T_2, T)$ for $\tau_1 \in [T_2, T_3]\}$,

$$U(t,\tau_1) = \int_{T+\tau_1-t}^{\tau_1} \Pi(\xi, \tau_1; \nu+\alpha)\,\mathrm{d}\xi \int_{\xi - T}^{\xi} U(\eta + t - \tau_1, \eta) A(\xi, \xi - \eta)\,\mathrm{d}\eta + f(t,\tau_1) \tag{26}$$

with

$$f(t,\tau_1) = u_0(\tau_1 - t)\Pi(\tau_1 - t, \tau_1; \nu + \alpha) + \int_{\tau_1 - t}^{T+\tau_1-t} \Pi(\xi, \tau_1; \nu+\alpha)\,\mathrm{d}\xi \left\{ \int_{\tau_1 - t}^{\xi} U(\eta + t - \tau_1, \eta) A(\xi, \xi - \eta)\,\mathrm{d}\eta + \int_{\xi + t - \tau_1}^{T} B(\xi + t - \tau_1, \xi, \tau_2)\,\mathrm{d}\tau_2 + C(\xi + t - \tau_1, \xi) \right\} + \int_{T+\tau_1-t}^{\tau_1} \Pi(\xi, \tau_1; \nu+\alpha) D(\xi) U(\xi + t - \tau_1 - T, \xi - T\}\,\mathrm{d}\xi$$

in $\{T \le t \le \tau_1 - T_2$ for $\tau_1 \in [T_2 + T, T_3]\}$,

$$U(t,\tau_1) = \int_{T_2}^{\tau_1} \Pi(\xi, \tau_1; \nu+\alpha)\,\mathrm{d}\xi \int_{\tau_1 - t}^{\xi} U(\eta + t - \tau_1, \eta) A(\xi, \xi - \eta)\,\mathrm{d}\eta + f(t,\tau_1) \tag{27}$$

with

$$f(t,\tau_1) = U(T_2 + t - \tau_1, T_2)\Pi(T_2, \tau_1; \nu+\alpha) + \int_{T_2}^{\tau_1} \Pi(\xi, \tau_1; \nu+\alpha)\,\mathrm{d}\xi \left\{ \int_{\xi + t - \tau_1}^{T} B(\xi + t - \tau_1, \xi, \tau_2) d\tau_2 + C(\xi + t - \tau_1, \xi) \right\}$$

in $\{\tau_1 - T_2 \le t \le T \ \text{ for } \ \tau_1 \in [T_2, T_2 + T]\}$,

$$U(t,\tau_1) = \int\limits_{T+\tau_1-t}^{\tau_1} \Pi(\xi,\tau_1;\nu+\alpha)\,\mathrm{d}\xi \int\limits_{\xi-T}^{\xi} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta + f(t,\tau_1) \tag{28}$$

with

$$\begin{aligned} f(t,\tau_1) = {} & U(T_2+t-\tau_1,T_2)\Pi(T_2,\tau_1;\nu+\alpha) \\ & + \int\limits_{T_2}^{T+\tau_1-t} \Pi(\xi,\tau_1;\nu+\alpha)\,\mathrm{d}\xi \Bigg\{ \int\limits_{\tau_1-t}^{\xi} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta \\ & \qquad + \int\limits_{\xi+t-\tau_1}^{T} B(\xi+t-\tau_1,\xi,\tau_2)\,\mathrm{d}\tau_2 + C(\xi+t-\tau_1,\xi) \Bigg\} \\ & + \int\limits_{T+\tau_1-t}^{\tau_1} \Pi(\xi,\tau_1;\nu+\alpha)D(\xi)U(\xi+t-\tau_1-T,\xi-T)\,\mathrm{d}\xi \end{aligned}$$

in $\{\max(T, \tau_1 - T_2) \le t \le \tau_1 - (T_2 - T) \ \text{ for } \ \tau_1 \in [T_2, T_3]\}$, and

$$U(t,\tau_1) = \int\limits_{T_2}^{\tau_1} \Pi(\xi,\tau_1;\nu+\alpha)\,\mathrm{d}\xi \int\limits_{\xi-T}^{\xi} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta + f(t,\tau_1) \tag{29}$$

with

$$\begin{aligned} f(t,\tau_1) = {} & U(T_2+t-\tau_1,T_2)\Pi(T_2,\tau_1;\nu+\alpha) \\ & + \int\limits_{T_2}^{\tau_1} \Pi(\xi,\tau_1;\nu+\alpha)D(\xi)U(\xi+t-\tau_1-T,\xi-T)\,\mathrm{d}\xi \end{aligned}$$

in $\{\tau_1 - (T_2 - T) \le t < \tau_1 - T \ \text{ for } \ \tau_1 \in [T_2, T_3]\}$,

$$\begin{aligned} U(t,\tau_1) = {} & u_0(\tau_1 - t)\Pi(\tau_1 - t,\tau_1;\nu) \\ & + \int\limits_{\tau_1-t}^{\tau_1} \Pi(\eta,\tau_1;\nu)\,\mathrm{d}\eta \Bigg\{ \int\limits_{\eta-T_3}^{T} B(\eta+t-\tau_1,\eta,\tau_2)\,\mathrm{d}\tau_2 + C(\eta+t-\tau_1,\eta) \Bigg\} \end{aligned} \tag{30}$$

in $\{0 \le t < \tau_1 - T_3 \text{ for } \tau_1 \in [T_3, T_4]\}$,

$$\begin{aligned} U(t,\tau_1) = {} & U(T_3+t-\tau_1, T_3)\Pi(T_3,\tau_1;\nu) \\ & + \int\limits_{T_3}^{\tau_1} \Pi(\xi,\tau_1;\nu)\,\mathrm{d}\xi \Bigg\{ \int\limits_{\tau_1-t}^{T_3} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta \\ & \qquad + \int\limits_{\xi+t-\tau_1}^{T} B(\xi+t-\tau_1,\xi,\tau_2)\,\mathrm{d}\tau_2 + C(\xi+t-\tau_1,\xi) \Bigg\} \end{aligned} \tag{31}$$

in $\{\tau_1 - T_3 < t \le T \text{ for } \tau_1 \in [T_3, T_4]\}$,

$$\begin{aligned} U(t,\tau_1) = {} & U(T_3+t-\tau_1, T_3)\Pi(T_3,\tau_1,\nu) \\ & + \int\limits_{T_3}^{T+\tau_1-t} \Pi(\xi,\tau_1;\nu)\,\mathrm{d}\xi \Bigg\{ \int\limits_{\tau_1-t}^{T_3} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta \\ & \qquad + \int\limits_{\xi+t-\tau_1}^{T} B(\xi+t-\tau_1,\xi,\tau_2)\,\mathrm{d}\tau_2 + C(\xi+t-\tau_1,\xi) \Bigg\} \\ & + \int\limits_{T+\tau_1-t}^{\tau_1} \Pi(\xi,\tau_1;\nu)\,\mathrm{d}\xi \Bigg\{ \int\limits_{\xi-T}^{T_3} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta \\ & \qquad + D(\xi)U(\xi+t-\tau_1-T,\xi-T) \Bigg\} \end{aligned} \tag{32}$$

in $\{T \le t \le \tau_1 - (T_3 - T) \text{ for } \tau_1 \in [T_3, T_4]\}$, and

$$\begin{aligned} U(t,\tau_1) = {} & U(T_3+t-\tau_1, T_3)\Pi(T_3,\tau_1;\nu) \\ & + \int\limits_{T_3}^{\tau_1} \Pi(\xi,\tau_1;\nu)\,\mathrm{d}\xi \Bigg\{ \int\limits_{\xi-T}^{T_3} U(\eta+t-\tau_1,\eta)A(\xi,\xi-\eta)\,\mathrm{d}\eta \\ & \qquad + D(\xi)U(\xi+t-\tau_1-T,\xi-T) \Bigg\} \end{aligned} \tag{33}$$

in $\{\tau_1 - (T_3 - T) \le t < \tau_1 - T \text{ for } \tau_1 \in [T_3, T_4]\}$.

By changing variables equations (23)–(29) can be written in a form of Volterra type integral equations with kernels independent of t and therefore have a unique positive C^0-solutions. Once equations (23)–(29) are solved, formulas (30)–(33), (21), and (22) determine function U which is continuous in $\{(t,\tau_1)\colon 0 \le t \le \tau_1 - T, \tau_1 \in [T, T_1] \cup [T_3, \infty)\}$. It is evident that function U is not differentiable at the points $\tau_1 = T_1, \dots, T_4$ and it is a C^1-function along the characteristic lines except the points $\tau_1 = T_1, \dots, T_4$.

If u_0 is a positive C^1-function, then under the conditions of Theorem 1 on differentiation equations (23)–(29) with respect to t, we derive integral equations of Volterra type for $\partial_t U$ written on the characteristic lines. These equations show that $\partial_t U$ is continuous function except lines $\tau_1 = T_2, t + T_s,\ s = 1, 2$. Thus U is a C^1-function for $t < \tau_1 - T,\ \tau_1 \in (T_1, T_3)$ except lines $\tau_1 = T_2, t + T_s,\ t > 0, s = 1, 2$. Similarly, by using (30)–(33) and (22) we prove that U is not differentiable at the lines $\tau_1 = T_4$ and $t = \tau_1 - T_s, \tau_1 \in (T_3, T_4),\ s = 1, \dots, 4$.

If $t > \tau_1 - T$, we have

$$U(t, \tau_1) = U(T + t - \tau_1, T) v^0(\tau_1) \tag{34}$$

with v^0 determined in Section 1. By definition (see $(9)_1$) we get the equation for $U(t, T)$,

$$U(t,T) = \begin{cases} \int\limits_{\sigma_3} \sum\limits_{k=1}^{n} kU_k|_{\tau_2=T}\, \mathrm{d}\tau_1, & 0 \le t \le T_1, \\ \int\limits_{T_2}^{t+T} U(T+t-\tau_1, T) v^0(\tau_1 - T) \sum\limits_{k=1}^{n} k v_k^0(\tau_1, T)\, \mathrm{d}\tau_1 & \\ \quad + \int\limits_{t+T}^{T_4} \sum\limits_{k=1}^{n} kU_k|_{\tau_2=T}\, \mathrm{d}\tau_1, & T_1 \le t \le T_3, \\ \int\limits_{\sigma_3} U(T+t-\tau_1, T) v^0(\tau_1 - T) \sum\limits_{k=1}^{n} k v_k^0(\tau_1, T)\, \mathrm{d}\tau_1, & t > T_3, \end{cases} \tag{35}$$

which has a retarded structure with the delay T_1 and has a unique positive solution. It is easy to see that $U(t,T) \in C^0([0,\infty)) \cap C^1((0,T) \cup (T,\infty))$. Thus, we have the following result:

Theorem 2. *Let u_0 and u_{k0} be positive, $u_0 \in C^0([T,\infty)) \cap C^1((T,\infty))$, $u_{k0} \in C^0(\bar{Q}) \cap C^1(Q)$, and $T_3 - T_1 > 2T$. Then under the conditions of Theorem* 1 *problem* (7)–(9) *has a unique positive solution with the properties*

$$\begin{aligned} U &\in C^0\big([0,\infty) \times [T,\infty)\big) \cap C^1\big(([0,\infty) \times [T,\infty)) \\ &\qquad \setminus \{\tau_1 = T_1, T_2, T_3, T_4; \tau_1 = t+T, t+T_1, t+T_2, t+T_3, t+T_4\}\big), \\ U_k &\in C^0\big([0,\infty) \times \bar{Q}\big) \cap C^1\big((0,\infty) \times Q) \\ &\qquad \setminus \{\tau_2 = t; \tau_1 = T_2, T_3, t+T, t+T_1, t+T_2, t+T_3\}\big). \end{aligned}$$

If in addition $u_0 \in L_1(T,\infty)$, then $\beta \in C^0([0,\infty)) \cap C^1(0,\infty)$.

The proof of the solvability of equation (10) is evident.

Note that the similar result can be obtained for the case $T_3 - T_1 \le 2T$, too.

As a result we formulate

Theorem 3. *Assume that $\rho \in C^1([0,\infty)), \rho(0) = 0$ and $\rho' > 0$. Then under the conditions of Theorem* 2 *equations* (10) *and* (12) *have a unique positive global solution such that f and $N \in C^1((0,\infty))$.*

3.3 The long time behavior of the solution to system (7)–(11)

In this section, we find the asymptotic behavior of the solution to system (7)–(11). We first find an upper bound for $U(t,T)$. It follows from equation (20) and (32) that

$$U(t,T) \leq \xi \int\limits_{t-T_3}^{t-T_1} u(x,t)\,\mathrm{d}x, \quad \xi = \max_{\bar{\sigma}_1} v^0(x) \sum_{k=1}^{n} k v_k^0(x+T,T), \quad t \geq T_3.$$

Now

$$U(t,T) \leq \eta\xi, \quad \eta = \int\limits_{0}^{T_3} U(x,T)\,\mathrm{d}x, \quad t \in [T_3, T_3+T_1],$$

then

$$U(t,T) \leq \xi \int\limits_{T_1}^{T_3+T_1} \leq \xi \int\limits_{T_1}^{T_3} U(x,T)\,\mathrm{d}x + \xi \int\limits_{T_3}^{T_3+T_1} U(x,T)\,\mathrm{d}x \leq \eta\xi(1+\xi T_1)$$

and

$$\int\limits_{T_1}^{T_3+T_1} U(x,T)\,\mathrm{d}x \leq \eta(1+\xi T_1), \quad t \in (T_3+T_1, T_3+2T_1],$$

and, by induction,

$$U(t,T) \leq \xi \int\limits_{mT_1}^{T_3+mT_1} U(x,T)\,\mathrm{d}x \leq \xi\eta(1+\xi T_1)^m, \quad t \in (T_3+mT_1, T_3+(m+1)T_1].$$

Therefore, there exists the Laplace transform $\widehat{U}(\lambda,T)$ of $U(t,T)$,

$$\begin{aligned}
\widehat{U}(\lambda,T) &= \int\limits_{\sigma_3} \mathrm{d}\tau_1 \int\limits_{0}^{\infty} \sum_{k=1}^{n} kU_k|_{\tau_2=T} \exp\{-t\lambda\}\,\mathrm{d}t \\
&= \int\limits_{\sigma_3} \mathrm{d}\tau_1 \int\limits_{0}^{\tau_1-T} \exp\{-t\lambda\} \sum_{k=1}^{n} kU_k|_{\tau_2=T}\,\mathrm{d}t \\
&\quad + \int\limits_{\sigma_3} v^0(\tau_1-T)\,\mathrm{d}\tau_1 \int\limits_{\tau_1-T}^{\infty} \exp\{-t\lambda\} \sum_{k=1}^{n} k v_k^0(\tau_1,T) U(T+t-\tau_1,T)\,\mathrm{d}t \\
&= I_1(\lambda) + \widehat{U}(\lambda,T) I(\lambda)
\end{aligned}$$

with

$$I_1(\lambda) = \int\limits_{\sigma_3} \mathrm{d}\tau_1 \int\limits_{0}^{\tau_1-T} \exp\{-t\lambda\} \sum_{k=1}^{n} kU_k|_{\tau_2=T}\,\mathrm{d}t$$

and $I(\lambda)$ defined by equation (18). Hence,

$$\widehat{U}(\lambda, T) = I_1(\lambda)/\bigl(1 - I(\lambda)\bigr).$$

Roots of $I(\lambda)$ are discussed in Section 1. Function $I_1(\lambda)$ is analytic and, using the method of a rectangle contour integral [22], we evaluate the inverse Laplace transform obtaining

$$U(t, T) = \eta \exp\{t\lambda_0\} + O(\exp\{t\mu\}), \quad \eta = -I_1(\lambda_0)/I'(\lambda_0) > 0 \tag{36}$$

where $\mu < \lambda_0$ is the real part of the first pair of conjugate complex roots. Then by equations (20) and (32), for large time ($t > \tau_1 - T$), we get the following formulas:

$$\begin{cases} U(t, \tau_1) = v^0(\tau_1) U(T + t - \tau_1, T), \\ U_k(t, \tau_1, \tau_2) = v_k^0(\tau_1, \tau_2) v^0(\tau_1 - \tau_2) U(T + t - \tau_1, T) \end{cases} \tag{37}$$

with $U(t, T)$ defined by equation (36).

The asymptotic behavior of β defined by equation (11) will now be studied. We assume that conditions of Theorem 2 for u_0 hold, while ν satisfies conditions of Theorem 1 and does not decrease as $\tau_1 \to \infty$. Function β can be written in the form $\beta = \sum\limits_{s=1}^{4} J_s$ where $J_1 = \int_T^{t+T} U \,\mathrm{d}\tau_1$, $J_2 = \int_{t+T}^{t+T_4} U \,\mathrm{d}\tau_1$, $J_3 = \int_{t+T_4}^{\infty} U \,\mathrm{d}\tau_1$, $J_4 = \int\limits_0^T \mathrm{d}\tau_2 \int_{T_1+\tau_2}^{T_3+\tau_2} \sum_{k=1}^{n} U_k \,\mathrm{d}\tau_1$.

By equation (36) we get $J_1 = J_{11} + J_{12}$ with

$$J_{11} = \eta \int\limits_T^{t+T} v^0(\tau_1) \exp\{\lambda_0(T + t - \tau_1)\} \,\mathrm{d}\tau_1$$

and

$$J_{12} = \int\limits_T^{t+T} v^0(\tau_1) O\bigl(\exp\{\mu(T + t - \tau_1)\}\bigr) \,\mathrm{d}\tau_1.$$

Now we get estimates of J_s for large time. Set $\nu_\infty = \lim \nu$ as $\tau_1 \to \infty$. We first consider the case $\nu_\infty < \infty$. From equations (14) and (15) it follows that $v^0 \le c_0 \exp\{-\int\limits_T^{\tau_1} \nu(x) dx\}$ where c_0 is a positive constant. Fix sufficiently large $t_1 > T_3$ and let $t > t_1$. Then

$$\begin{aligned} J_{11} \exp\{-t\lambda_0\} &= \eta \int\limits_T^{t+T} v^0(\tau_1) \exp\{\lambda_0(T - \tau_1)\} \,\mathrm{d}\tau_1 \\ &\le c_0 \int\limits_T^{t+T} \exp\{\lambda_0(T - \tau_1) - \int\limits_T^{\tau_1} \nu \,\mathrm{d}x\} \,\mathrm{d}\tau_1 = c_0 \int\limits_0^{t} \exp\{-\lambda_0 \xi - \int\limits_T^{t+\xi} \nu \,\mathrm{d}x\} \,\mathrm{d}\xi \\ &= c_0 \int\limits_0^{t_1} \exp\biggl\{ -\xi\lambda_0 - \int\limits_T^{T+\xi} \nu \,\mathrm{d}x \biggr\} \,\mathrm{d}\xi + \int\limits_{t_1}^{t} \exp\biggl\{ -\xi\lambda_0 - \int\limits_T^{T+\xi} \nu \,\mathrm{d}x \biggr\} \,\mathrm{d}\xi. \end{aligned}$$

When $\lambda_0 + \nu_\infty > \epsilon$ with a small $\epsilon > 0$ this integral converges as $t \to \infty$ since

$$\begin{aligned}
\int_{t_1}^{t} \exp\left\{ -\xi\lambda_0 - \int_{T}^{T+\xi} \nu \,\mathrm{d}x \right\} \mathrm{d}\xi &= \int_{t_1}^{t} \exp\left\{ -\xi\lambda_0 - \int_{t_1}^{T+\xi} \nu \,\mathrm{d}\xi - \int_{T}^{t_1} \nu \,\mathrm{d}x \right\} \mathrm{d}\xi \\
&\le \exp\left\{ - \int_{T}^{t_1} \nu \,\mathrm{d}x \right\} \int_{t_1}^{t} \exp\{-(\lambda_0 + \nu_\infty - \epsilon)\xi\} \,\mathrm{d}\xi < \infty
\end{aligned}$$

for all $t > t_1$ and tends to 0 as $t_1 \to \infty$. Similarly,

$$\begin{aligned}
J_{12} \exp\{-t\lambda_0\} &= \int_{T}^{t+T} v^0(\tau_1) O\big(\exp\{\mu(T + t - \tau_1)\}\big) \,\mathrm{d}\tau_1 \exp\{-t\lambda_0\} \\
&\le c_1 \int_{T}^{t+T} v^0(\tau_1) \exp\{\mu(T + t - \tau_1)\} \,\mathrm{d}\tau_1 \exp\{-t\lambda_0\} \\
&\le c_2 \exp\{-t(\lambda_0 - \mu)\} \int_{T}^{t+T} \exp\left\{ \mu(T - \tau_1) - \int_{T}^{\tau_1} \nu \,\mathrm{d}x \right\} \mathrm{d}\tau_1 \\
&= c_2 \exp\{-t(\lambda_0 - \mu)\} \int_{0}^{t} \exp\left\{ -\mu\xi - \int_{T}^{\xi+T} \nu \,\mathrm{d}x) \right\} \mathrm{d}\xi \\
&= c_2 \exp\{-t(\lambda_0 - \mu)\} \left\{ \int_{0}^{t_1} \exp\{-\mu\xi - \int_{T}^{\xi+T} \nu \,\mathrm{d}x) \right\} \mathrm{d}\xi \\
&\quad + \exp\left\{ - \int_{T}^{t_1} \nu \,\mathrm{d}x \right\} \int_{t_1}^{t} \exp\left\{ -\mu\xi - \int_{t_1}^{T+\xi} \nu \,\mathrm{d}x \right\} \mathrm{d}\xi
\end{aligned}$$

where

$$\begin{aligned}
&\exp\{-t(\lambda_0 - \mu)\} \int_{t_1}^{t} \exp\left\{ -\mu\xi - \int_{t_1}^{\xi+T} \nu \,\mathrm{d}x \right\} \\
&\quad \le \exp\{-t(\lambda_0 - \mu)\} \int_{t_1}^{t} \exp\{-(\mu + \nu_\infty - \epsilon)\xi\} \,\mathrm{d}\xi \\
&\quad \le \begin{cases} c_3 \exp\{-t(\lambda_0 - \mu)\}, & \mu + \nu_\infty - \epsilon > 0, \\ t \exp\{-t(\lambda_0 + \nu_\infty - \epsilon)\}, & \mu + \nu_\infty - \epsilon = 0, \\ c_4 \exp\{-t(\lambda_0 + \nu_\infty - \epsilon)\}, & \mu + \nu_\infty - \epsilon < 0 \end{cases}
\end{aligned}$$

and the integral

$$\exp\{-t(\lambda_0-\mu)\}\int_0^{t_1}\exp\left\{-\mu\xi-\int_T^{\xi+T}\nu\,\mathrm{d}x\right\}\mathrm{d}\xi$$

tends to 0 as $t\to\infty$ since, for negative μ, it can be written as

$$\exp\{-t(\lambda_0-\mu+\mu t_1/t)\}\int_0^{t_1}\exp\left\{\mu(t_1-\xi)-\int_T^{\xi+T}\nu\,\mathrm{d}x\right\}$$

and tends to 0 if $-\mu t_1/(\lambda_0-\mu)<t\to\infty$, while, for $\mu\le 0$, this assertion is evident;

$$\begin{aligned}
J_3\exp\{-t\lambda_0\}&=\exp\{-t\lambda_0\}\int_{t+T_4}^{\infty}u_0(\tau_1-t)\exp\left\{-\int_{\tau_1-t}^{\tau_1}\nu\,\mathrm{d}x\right\}\mathrm{d}\tau_1\\
&=\exp\{-t\lambda_0\}\int_{T_4}^{\infty}u_0(\xi)\exp\left\{-\int_{\xi}^{t+\xi}\nu\,\mathrm{d}x\right\}\mathrm{d}\xi\\
&=\exp\{-t\lambda_0\}\left\{\int_{T_4}^{t_1}u_0(x)\exp\{-\int_{\xi}^{t_1}\nu\,\mathrm{d}x-\int_{t_1}^{t+\xi}\nu\,\mathrm{d}x\right\}\mathrm{d}\xi\\
&\quad+\int_{t_1}^{\infty}u_0(\xi)\exp\left\{-\int_{\xi}^{t+\xi}\nu\,\mathrm{d}x\,\mathrm{d}\xi\right\}\\
&\le\left\{\int_{T_4}^{t_1}u_0(\xi)\exp\left\{-\int_{\xi}^{t_1}\nu\,\mathrm{d}x\right\}\mathrm{d}\xi+\int_{t_1}^{\infty}u_0(\xi)\,\mathrm{d}\xi\right\}\exp\{-t(\lambda_0+\nu_\infty-\epsilon)\}\\
&\le\int_{T_4}^{\infty}u_0(\xi)\,\mathrm{d}\xi\exp\{-(\lambda_0+\nu_\infty-\epsilon)\};
\end{aligned}$$

and

$$J_4\exp\{-t\lambda_0\}=\eta\int_0^T\mathrm{d}\tau_2\int_{T_1+\tau_2}^{T_3+\tau_2}\sum_{k=1}^{n}v_k^0(\tau_1,\tau_2)v^0(\tau_1-\tau_2)\exp\{\lambda_0(T-\tau_1)\}\,\mathrm{d}\tau_1.$$

Here $c_1,\dots,c_4$ are some positive constants. From equations (21) and (30) it follows that $U\le c_5\exp\{-\int_{\xi}^{\tau_1}\nu dx\}$ with a constant $c_5>0$ for $t\le\tau_1-T$, $T\le\tau_1\le T_4$. Hence,

$$J_2\exp\{-t\lambda_0\}=\exp\{-t\lambda_0\}\int_{t+T}^{t+T_4}U(T_4+t-\tau_1,T_4)\exp\left\{-\int_{T_4}^{\tau_1}\nu\,\mathrm{d}x\right\}\mathrm{d}\tau_1$$

$$
\begin{aligned}
&\le c_5 \exp\{-t\lambda_0\} \int\limits_{t+T}^{t+T_4} \exp\left\{ - \int\limits_{\tau_1 - t}^{T_4} \nu \, \mathrm{d}x - \int\limits_{T_4}^{\tau_1} \nu \, \mathrm{d}x \right\} \mathrm{d}\tau_1 \\
&= c_5 \exp\{-t\lambda_0\} \int\limits_{t+T}^{t+T_4} \exp\left\{ - \int\limits_{\tau_1 - t}^{\tau_1} \nu \, \mathrm{d}x \right\} \mathrm{d}\tau_1 \\
&= c_5 \exp\{-t\lambda_0\} \int\limits_{T}^{T_4} \exp\left\{ - \int\limits_{\xi}^{t+\xi} \nu \, \mathrm{d}x \right\} \mathrm{d}\xi \\
&= c_5 \exp\{-t\lambda_0\} \int\limits_{T}^{T_4} \exp\left\{ - \int\limits_{\xi}^{t_1} \nu \, \mathrm{d}x - \int\limits_{t_1}^{t+\xi} \nu \, \mathrm{d}x \right\} \mathrm{d}\xi \\
&\le c_5 \exp\{-t(\lambda_0 + \nu_\infty - \epsilon)\} \int\limits_{T}^{T_4} \exp\left\{ - \int\limits_{\xi}^{T_4} \nu \, \mathrm{d}x \right\} \mathrm{d}\xi.
\end{aligned}
$$

Since these estimates for J_{11}, J_{12}, J_2, and J_3 are valid for every small $\epsilon > 0$, we conclude that, for large time and $\nu_\infty < \infty$,

$$
\beta \sim \bar{\beta}(\lambda_0) \exp\{t\lambda_0\}, \quad \bar{\beta}(\lambda_0) = \eta(\lambda_0)\tilde{\beta}(\lambda_0), \tag{38}
$$

$$
\begin{aligned}
\tilde{\beta}(\lambda_0) = &\int\limits_0^\infty v^0(x+T) \exp\{-x\lambda_0\} \, \mathrm{d}x \\
&+ \int\limits_0^T \mathrm{d}\tau_2 \int\limits_{T_1+\tau_2}^{T_3+\tau_2} \sum_{k=1}^n v_k^0(\tau_1, \tau_2) v^0(\tau_1 - \tau_2) \exp\{\lambda_0(T - \tau_1)\} \, \mathrm{d}\tau_1
\end{aligned} \tag{39}
$$

if $\lambda_0 + \nu_\infty > 0$. It is evident that $(J_{12} + J_2 + J_3)\exp\{-t\lambda_0\}$ for $\nu_\infty = \infty$ is less than that given above for $\nu_\infty < \infty$. Therefore formula (38) remains valid for the case $\nu_\infty = \infty$, too.

It remains to find the asymptotic behavior of N defined by equation (12). Put $f(t) = F(t)\exp\{-t\lambda_0\}$ in equation (10) to get

$$
F' = \big(\lambda_0 - \rho(F\beta \exp\{-t\lambda_0\})\big)F, \quad F(0) = 1.
$$

The asymptotic behavior of F and N can be described by the unique solutions of the equations

$$
\tilde{F}' = \big(\lambda_0 - \rho\big(\tilde{F}\bar{\beta}(\lambda_0)\big)\big)\tilde{F}, \quad \tilde{F}(0) = 1
$$

and

$$
\tilde{N}' = \big(\lambda_0 - \rho\big(\tilde{N}\big)\big)\tilde{N}, \quad \tilde{N}(0) = \bar{\beta}(\lambda_0),
$$

respectively. Hence,

$$\begin{cases} \tilde{F},\ \tilde{N} \to 0 \text{ as } t \to \infty & \text{if } \lambda_0 \le 0, \\ \tilde{F},\ \tilde{N} \to \infty \text{ as } t \to \infty & \text{if } \sup\limits_{N \ge 0} \rho(N) \le \lambda_0 < \infty, \\ \tilde{F} \to N^*/\bar{\beta}(\lambda_0) \text{ and } \tilde{N} \to N^* \text{ as } t \to \infty & \text{if } \lambda_0 \in \big(0, \sup\limits_{N \ge 0} \rho(N)\big), \\ & \quad \bar{\beta}(\lambda_0) < \infty, \text{ and } \lambda_0 = \rho(N^*). \end{cases} \tag{40}$$

This enables us to formulate

Theorem 4. *Let conditions of Theorem* 3 *be satisfied,* ν *is non-decreasing, and* $\bar{\beta}(\lambda_0) < \infty$ *where* λ_0 *is a unique real root of equation* (18)*. Then the solution of problem* (6)–(11) *for large time behaves as follows:*

$$\begin{cases} N \sim \tilde{N}, \\ u \sim v^0(\tau_1) \exp\{\lambda_0(T - \tau_1)\} \tilde{N}/\tilde{\beta}(\lambda_0), \\ u_k \sim v_k^0(\tau_1, \tau_2) v^0(\tau_1 - \tau_2) \exp\{\lambda_0(T - \tau_1)\} \tilde{N}/\tilde{\beta}(\lambda_0) \end{cases} \tag{41}$$

where asymptotic behavior of $\tilde{N}$ *is given by* (40)*.*

4 A population dynamics model with spatial diffusion

In this section we generalize the model in Section 3 by including the random spatial diffusion in an open bounded domain $\Omega \subset \mathbb{R}^m$ with the extremely inhospitable boundary $\partial\Omega$ and examine two special and steady state solutions in the case of constant diffusion modulus κ and time-space-independent vital rates. The model reads as follows:

$$\begin{cases} \partial_t u + \partial_{\tau_1} u + \big(\nu + \rho(N)\big) u - \kappa \Delta u \\ \qquad = -\begin{cases} 0, & \tau_1 \in \sigma_1^*, \\ \alpha u, & \tau_1 \in \sigma_1 \end{cases} + \begin{cases} 0, & \tau_1 \in \sigma_2^*, \\ \int\limits_{\gamma_1(\tau_1)}^{\gamma_2(\tau_1)} \sum\limits_{k=1}^{n} \nu_{k0} u_k \, \mathrm{d}\tau_2, & \tau_1 \in \sigma_2 \end{cases} \\ \qquad + \begin{cases} 0, & \tau_1 \in \sigma_3^*, \\ \sum\limits_{k=1}^{n} u_k|_{\tau_2 = T}, & \tau_1 \in \sigma_3, \end{cases} \quad t > 0, \ \ x \in \Omega, \\ u|_{\tau_1 = T} = \int\limits_{\sigma_3} \sum\limits_{k=1}^{n} k u_k|_{\tau_2 = T} \, \mathrm{d}\tau_1, \\ u|_{t=0} = u_0, \ \ u|_{\partial\Omega} = 0, [u|_{\tau_1 = \tau}] = 0, \ \ \tau = T_1, T_2, T_3, T_4, \end{cases} \tag{42}$$

$$\begin{cases} \partial_t u_k + \partial_{\tau_1} u_k + \partial_{\tau_2} u_k + \big(\tilde{\nu}_k + \rho(N)\big) u_k - \kappa \Delta u_k \\ \qquad = \begin{cases} 0, & k = n, \\ \sum\limits_{s=k+1}^{n} \nu_{sk} u_s, & 1 \le k \le n-1, \end{cases} \ (\tau_1, \tau_2) \in Q, \ \ t > 0, \ \ x \in \Omega, \\ u_k|_{\tau_2 = 0} = \alpha_k u, \ \ u_k|_{t=0} = u_{k0}, \ \ u_k|_{\partial\Omega} = 0, \end{cases} \tag{43}$$

$$N = \int_T^\infty u \, \mathrm{d}\tau_1 + \int_0^T \mathrm{d}\tau_2 \int_{T_1+\tau_2}^{T_3+\tau_2} \sum_{k=1}^n u_k \, \mathrm{d}\tau_1. \tag{44}$$

Here Δ signifies the Laplace operator in $\mathbb{R}^m$. We examine the case where u_0 and u_{k0} depend on (τ_1, x) and (τ_1, τ_2, x), respectively, ν, ν_k, α_k, and ν_{sk} do not depend on t and x, and add the following compatibility conditions:

$$u_0|_{\tau_1=T} = \int_{\sigma_3} \sum_{k=1}^n k u_{k0}|_{\tau_2=T} \, \mathrm{d}\tau_1, \;\; u_0|_{\partial\Omega} = 0,$$
$$[u_0|_{\tau_1=\tau}] = 0, \;\; \tau = T_1, T_2, T_3, T_4;$$
$$u_{k0}|_{\tau_2=0} = (\alpha_k)|_{t=0} u_0, \;\; u_{k0}|_{\partial\Omega} = 0.$$

4.1 A case of product initial distributions

In this section we study a special case of initial functions and look for solutions to equations (42)–(44) of the form

$$\begin{cases} u(t, \tau_1, x) = U(t, \tau_1) f(t, x), \;\; u_0(\tau_1, x) = U_0(\tau_1) f_0(x), \;\; f_0|_{\partial\Omega} = 0, \\ u_k(t, \tau_1, \tau_2, x) = U_k(t, \tau_1, \tau_2) f(t, x), \;\; u_{k0}(\tau_1, \tau_2, x) = U_{k0}(\tau_1, \tau_2) f_0(x) \end{cases} \tag{45}$$

where $f_0(x) > 0$ in Ω while U and U_k are unique solutions of problem (7)–(9) and (5) with u_0 and u_{k0} replaced by U_0 and U_{k0}, respectively. Substituting (45) into equations (42)–(44), we get the problem for f and N,

$$\begin{cases} \partial_t f = -\rho(N) f + \kappa \Delta f, \;\; f(0, x) = f_0(x), \;\; f|_{\partial\Omega} = 0, \\ N = f\beta \end{cases} \tag{46}$$

with $\beta(t)$ defined by equation (11). By substitution $f(t, x) = F(t, x) \exp\{-t\lambda_0\}$ we reduce this equation into the problem

$$\begin{cases} \partial_t F = \big(\lambda_0 - \rho(aF)\big) F + \kappa \Delta F, \;\; F(0, x) = f_0(x), \;\; F|_{\partial\Omega} = 0, \\ N(t, x) = F(t, x) a(t), \;\; a(t) = \beta(t) \exp\{-t\lambda_0\}. \end{cases} \tag{47}$$

Theorem 5. *Let conditions of Theorem* 2 *with* u_0 *and* u_{k0} *replaced by* U_0 *and* U_{k0} *hold. Assume that* $0 < f_0 \in C^{2+\delta}(\bar{\Omega})$ *with* $\delta \in (0, 1)$, $f_0|_{\partial\Omega} = 0$, *and* $\partial\Omega \in C^{2+\delta}$. *Let* λ_0 *be as in Theorem* 4. *Then problem* (42)–(44) *has a unique solution of type* (45) *which for large* t $(t > \tau_1 - T)$ *behaves as follows:*

$$\text{(i)} \quad \begin{cases} u(t, \cdot) \to 0 & \textit{uniformly in } [T, \infty) \times \Omega, \\ u_k(t, \cdot) \to 0 & \textit{uniformly in } [T, \infty) \times (0, T] \times \Omega \end{cases} \tag{48}$$

if $\lambda_0 \le \kappa\Lambda_1$ *and* $t \to \infty$*,*

$$\text{(ii)}\quad \begin{cases} u(t,\cdot) \to (N^*(x)/\tilde\beta(\lambda_0))v^0(\tau_1)\exp\{\lambda_0(T-\tau_1)\} \\ \quad \textit{uniformly in } [T,\infty)\times\Omega, \\ u_k(t,\cdot) \to (N^*(x)/\tilde\beta(\lambda_0))v_k^0(\tau_1,\tau_2)v^0(\tau_1-\tau_2)\exp\{\lambda_0(T-\tau_1)\} \\ \quad \textit{uniformly in } [T,\infty)\times(0,T]\times\Omega \end{cases} \tag{49}$$

if $\lambda_0 > \kappa\Lambda_1$ *and* $t \to \infty$ *where* v^0 *and* v_k^0 *are defined in Section* 3.1*,* Λ_1 *is the first eigenvalue of the Dirichlet problem to the operator* $-\Delta$ *in* Ω*,* N^* *is a unique positive in* Ω *solution of the problem*

$$\big(\lambda_0 - \rho(N^*)\big)N^* + \kappa\Delta N^* = 0 \quad \textit{in } \Omega, N^*|_{\partial\Omega} = 0, \tag{50}$$

and $\tilde\beta(\lambda_0)$ *is defined by equation* (39)*.*

Proof. We use the upper and lower solutions technique. By [23, Chapters 5 and 6], 0 and a constant $b \ge \max\big(\gamma(\lambda_0)/\inf a, \max f_0\big)$ with $\inf a > 0$ and $\gamma(\lambda_0)$ a unique positive root of $\rho(\gamma) = \lambda_0$ are lower and upper solutions of time-dependent problem (47) and its steady-state analogue

$$\big(\lambda_0 - \rho\big(\bar\beta(\lambda_0)\tilde F\big)\big)\tilde F + \kappa\Delta\tilde F = 0 \quad \text{in } \Omega, \tilde F|_{\partial\Omega} = 0. \tag{51}$$

Here $\bar\beta(\lambda_0) = \eta(\lambda_0)\tilde\beta(\lambda_0)$ where $\eta(\lambda_0)$ is defined by equation (36).

Let $\Phi_1 > 0$ in Ω and Λ_1 be the normalized principle eigenfunction ($\max_\Omega \Phi_1 = 1$) and corresponding eigenvalue of the Dirichlet problem to the operator $-\Delta$ in Ω. Function $\xi\Phi_1$ with $\xi \le \gamma(\lambda_0 - \kappa\Lambda_1)/\bar\beta(\lambda_0)$ is a lower solution to problem (50) if $\lambda_0 > \kappa\Lambda_1$ and $\xi\Phi_1$ with a positive ξ is an upper solution to the same problem if $\lambda_0 \le \kappa\Lambda_1$. The lower solution to problem (51) is 0 if $\lambda_0 \le \kappa\Lambda_1$. By Theorem 4.4 of Chapter 3 in [23], equation (51) has only zero solution if $\lambda_0 \le \kappa\Lambda_1$, and a unique positive in Ω solution $\tilde F(x;\bar\beta(\lambda_0))$ if $\lambda_0 > \kappa\Lambda_1$. By Theorem 4.1 of Chapter 2 in [23], problem (47) has a unique global solution $F(t,x) \in [0,b]$.

Now we prove that $F(t,x)$ has a nonnegative limit as $t \to \infty$. Let us consider problem $(47)_1$ for large time $t > t_0 > 0$ with the initial condition $F(0,x) = f_0(x)$ replaced by the $F|_{t=t_0} = F(t_0,x)$. We denote this problem by $P(t_0)$. Since, by equation (38), $a \to \bar\beta(\lambda_0)$ as $t \to \infty$, we have $0 < a_-(t) := \bar\beta(\lambda_0) - \epsilon(t) < a(t) < a_+(t) := \bar\beta(\lambda_0) + \epsilon(t)$ for $t \ge t_0$, where $\epsilon(t) > 0$ monotonically tends to 0 as $t \to \infty$. Denote by $P_\pm(t_0)$ the problem $P(t_0)$ with $a(t)$ replaced by $a_\pm(t_0)$, respectively. Let $\tilde F(x;a_\pm(t_0))$ be the unique solutions of the steady-state analogue of problem $P_\pm(t_0))$. Then functions $\xi_\pm\tilde F(x;a_\pm(t_0))$ with sufficiently large ξ_- and small $\xi_+ > 0$ represent the lower and upper solutions to problems $P_\pm(t_0)$ and their steady-state analogues, respectively. Because of the uniqueness of the solution to problem (51) and by Theorem 7.3 of Chapter 10 in [23] problem $(47)_1$ has a unique solution which tends to the unique solution of Problem (51). Hence, $N \to N^* = \bar\beta(\lambda_0)\tilde F(x;\bar\beta(\lambda_0))$ as $t \to \infty$. The proof is complete.

4.2 A case of the linear combination of the product initial distributions

In this section we examine the case of initial functions

$$\begin{cases} u_0(\tau_1, x) = \sum\limits_{i=1}^{s} U_0^i(\tau_1) f_0^i(x), \quad f_0^i|_{\partial\Omega} = 0, \\ u_{k0}(\tau_1, \tau_2, x) = \sum\limits_{i=1}^{s} U_{k0}^i(\tau_1, \tau_2) f_0^i(x) \end{cases} \tag{52}$$

and look for the solution of problem (42)–(44) in the form

$$\begin{cases} u(t, \tau_1, x) = \sum\limits_{i=1}^{s} U^i(t, \tau_1) f^i(t, x), \\ u_k(t, \tau_1, \tau_2, x) = \sum\limits_{i=1}^{s} U_k^i(t, \tau_1, \tau_2) f^i(t, x) \end{cases} \tag{53}$$

where U^i, U_k^i represent the unique solution (7)–(9) and (5) with u_0, u_{k0} in (9) and (5) replaced by U_0^i, U_{k0}^i, respectively. From (42)–(44), by using equation (52), (53), and (7)–(9) we get the system

$$\begin{cases} \partial_t f^i = -\rho(N) f^i + \kappa \Delta f^i, \quad t > 0, \ x \in \Omega, \\ N = \sum\limits_{i=1}^{s} f^i \beta^i(t), \\ f^i|_{t=0} = f_0^i, \quad x \in \Omega, \\ f^i|_{\partial\Omega} = 0, \quad t > 0 \end{cases}$$

or

$$\begin{cases} f^i = F^i \exp\{-t\lambda_0\}, \\ \partial_t F^i = \big(\lambda_0 - \rho(N)\big) F^i + \kappa \Delta F^i, \quad t > 0, \ x \in \Omega, \\ N = \sum\limits_{i=1}^{s} a^i(t) F^i, \ a^i(t) = \beta^i(t) \exp\{-t\lambda_0\}, \\ F^i|_{t=0} = f_0^i, \quad x \in \Omega, \\ F^i|_{\partial\Omega} = 0, \quad t > 0 \end{cases} \tag{54}$$

where $\beta^i(t)$ is defined by equation (11) with U and U_k replaced by U^i and U_k^i, respectively.

Theorem 6. *Assume that conditions of Theorem* 2 *with u_0 and u_{k0} replaced by U_0^i and U_{k0}^i hold and that $0 < f_0^i \in C^{2+\delta}(\bar{\Omega})$, $f_0^i|_{\partial\Omega} = 0$, and $\partial\Omega \in C^{2+\delta}$ with $\delta \in (0,1)$. Let λ_0 be as in Theorem* 4 *and let $\rho \in C^{1+\delta}(\mathbb{R}_1^+)$, $\rho(0) = 0$, $\rho' > 0$. Then problem* (42)–(44) *has a unique solution of type* (52), (53)*, the large time behavior of which is described by formulas* (48) *and* (49)*.*

Proof. By equation (38), $a^i \to \eta^i(\lambda_0)\tilde{\beta}(\lambda_0)$ as $t \to \infty$ where $\tilde{\beta}(\lambda_0)$ is given by (39), while $\eta^i(\lambda_0)$ is defined in (36) and depends on U_0^i and U_{k0}^i. It is evident that 0 is a lower solution of problem (54) and its steady-state analogue. The constant $b \geq \max(\max_{\Omega} f_0^i, \gamma(\lambda_0)/\min_i \inf_t a^i)$ with $\gamma(\lambda_0)$ a unique solution of $\rho(\gamma) = \lambda_0$ is an upper solution of problem (54) and its steady-state analogue. Then Theorem 8.1 of Chapter 8 in [23] ensures the existence and uniqueness of the global solution $F^i \in [0, b]$, $i = 1, \dots, s$ to problem (54).

Now we examine the large time behavior of F^i. Let t_0 be sufficiently large. We rewrite system (54) in the form

$$\begin{cases} \partial_t F^i = \big(\lambda_0 + q - \rho(\tilde{N})\big)F^i + \kappa \Delta F^i, \quad t > t_0, \ \ x \in \Omega, \\ F^i|_{\partial\Omega} = 0, \quad t > t_0, \\ F^i|_{t=t_0} = F^i(t_0, x), \quad x \in \Omega \\ \tilde{N} = \tilde{\beta}(\lambda_0) \sum\limits_{i=1}^{s} \eta^i(\lambda_0) F^i \end{cases} \tag{55}$$

with known

$$q(t, x) = -\rho'\big(\tilde{N} + \xi\big(N - \tilde{N}\big)\big) \sum_{i=1}^{s} \big(a^i - \eta^i(\lambda_0)\tilde{\beta}(\lambda_0)\big)F^i, \quad \xi(t, x) \in (0, 1)$$

and then get

$$\begin{cases} \partial_t \tilde{N} = \big(\lambda_0 + q - \rho\big(\tilde{N}\big)\big)\tilde{N} + \kappa \Delta \tilde{N}, \quad t > t_0, \ \ x \in \Omega, \\ \tilde{N}|_{\partial\Omega} = 0, \quad t > t_0, \\ \tilde{N}|_{t=t_0} = \tilde{\beta}(\lambda_0) \sum\limits_{i=1}^{s} \eta^i(\lambda_0) F^i(t_0, x), \quad x \in \Omega. \end{cases} \tag{56}$$

Note that $q \to 0$ as $t \to \infty$ and $q^* = \sup_{t,x} |q| < \infty$ since $F^i \in [0, b]$. Let $\gamma(\lambda_0 + q^*)$ be a solution of $\rho(\gamma) = \lambda_0 + q^*$. The constants 0 and $\gamma(\lambda_0 + q^*)$ are the lower and upper solutions of problem (56) and of the problem $(\lambda_0 + q^* - \rho(\bar{N}))\bar{N} + \kappa \Delta \bar{N} = 0$ in Ω, $\bar{N}|_{\partial\Omega} = 0$. Since the steady-state analogue of problem (56), $(\lambda_0 - \rho(N^*))N^* + \kappa \Delta N^* = 0$ in Ω, $N^*|_{\partial\Omega} = 0$, has a unique solution ($N^* = 0$ if $\lambda_0 \leq \kappa\Lambda_1$ and $N^* > 0$ in Ω if $\lambda_0 > \kappa\Lambda_1$, where Λ_1 is defined in Section 4.1) Theorem 7.3 of Chapter 10 in [23] shows that $\tilde{N}(t, x) \to N^*(x)$ uniformly in Ω as $t \to \infty$. Obviously, $F^j \to 0$ as $t \to \infty$ if $\lambda_0 \leq \kappa\Lambda_1$.

Consider the case $\lambda_0 > \kappa\Lambda_1$. Let $\tilde{\Lambda}_k$ and ω_k be the eigenvalue and corresponding eigenfunction of the Dirichlet problem to the operator $-\kappa\Delta + \rho\big(N^*(x)\big)I$ in Ω, where I is the identity operator. Then $\tilde{\Lambda}_1 = \lambda_0$, $\omega_1 = N^* > 0$ in Ω, and $\tilde{\Lambda}_k > \tilde{\Lambda}_1$ for $k \geq 2$. We rewrite system (56) in the form

$$\begin{cases} \partial_t \tilde{N} = \big(\lambda_0 - \rho\big(N^*(x)\big)\big)\tilde{N} + \kappa \Delta \tilde{N} + (q + g)\tilde{N}, \quad t > t_0, \ \ x \in \Omega, \\ \tilde{N}|_{\partial\Omega} = 0, \quad t > t_0, \\ \tilde{N}|_{t=t_0} = \tilde{\beta}(\lambda_0) \sum\limits_{i=1}^{s} \eta^i(\lambda_0) F^i(t_0, x), \quad x \in \Omega \end{cases}$$

with known

$$g(t,x) = -\rho'\big(N^*(x) + \xi\big(\tilde{N} - N^*\big)\big)\big(\tilde{N} - N^*\big), \quad \xi(t,x) \in (0,1).$$

Obviously, $g \to 0$ as $t \to \infty$. We seek now its solution in the form

$$\tilde{N} = \sum_{j=1}^{\infty} p_j(t)\omega_j(x), \quad q\tilde{N} = \sum_{j=1}^{\infty} q_j(t)\omega_j(x), \quad g\tilde{N} = \sum_{j=1}^{\infty} q_j(t)\omega_j(x)$$

and obtain

$$p_j' = \big(\lambda_0 - \tilde{\Lambda}_k\big)p_j + q_j + r_j, \quad p_j(t_0) = \int_\Omega \omega_j(x)\tilde{N}(t_0,x)\,\mathrm{d}x \Big/ \int_\Omega \omega_j^2\,\mathrm{d}x.$$

Hence, $p_j \to 0$ for $j \geq 2$ as $t \to \infty$ and $p_1 = p_1(t_0) + \int_0^t (q_1(\tau) + r_1(\tau))d\tau \to 1$ as $t \to \infty$ since $N^* = \lim_{t\to\infty} \tilde{N} = \lim_{t\to\infty} \sum_{j=1}^{s} p_j\omega_j = \lim_{t\to\infty} p_1 N^*$. Similarly, we get

$$\begin{cases} \partial_t F^i = \big(\lambda_0 - \rho\big(N^*(x)\big)\big)N^i + \kappa\Delta F^i + \big(q + g^i\big)F^i, \quad t > t_0,\ \ x \in \Omega, \\ F^i|_{\partial\Omega} = 0, \quad t > t_0, \\ F^i|_{t=t_0} = F^i(t_0,x), \quad x \in \Omega \end{cases}$$

with known

$$g^i(t,x) = -\rho'\big(N^*(x) + \xi(\tilde{N} - N^*)\big)\big(\tilde{N} - N^*\big)F^i \quad \text{and} \quad \xi(t,x) \in (0,1)$$

where $g^i(t,x) \to 0$ as $t \to \infty$. Then

$$F^i = \sum_{j=1}^{s} p_j^i\omega_j, \quad qF^i = \sum_{j=1}^{s} q_j^i\omega_j, \quad g^iF^i = \sum_{j=1}^{s} g_j^i\omega_j,$$

and finally

$$\begin{aligned} &{p^i}'_j = \big(\lambda_0 - \tilde{\Lambda}_1\big){p^i}_j + {q^i}_j + {g^i}_j, \\ &p_j^i(t_0) = \int_\Omega \omega_j(x)F^i(t_0,x)\,\mathrm{d}x \Big/ \int_\Omega \omega_j^2\,\mathrm{d}x. \end{aligned}$$

Obviously, ${p^i}_j \to 0$ as $t \to \infty$ if $j \geq 2$ and ${p^i}_1 = {p^i}_1(t_0) + \int_0^t (q_1^i(\tau) + g_1^i(\tau))\,\mathrm{d}\tau$ which because of the boundedness of F^i is bounded, too. Since ???? Then, for large time, by Equations (53), (36), and (37) we get

$$\begin{aligned} u(t,\tau_1,x) &\sim v^0(\tau_1)\sum_{i=1}^{s} \eta^i p_1^i \exp\{\lambda_0(T-\tau_1)\}N^*(x) \\ &\to N^*(x)v^0(\tau_1)\exp\{\lambda_0(T-\tau_1)\}/\tilde{\beta}(\lambda_0) \end{aligned}$$

and similarly

$$u_k(t,\tau_1,\tau_2,x) \sim N^*(x)v_k^0(\tau_1,\tau_2)v^0(\tau_1-\tau_2)\exp\{\lambda_0(T-\tau_1)\}/\tilde{\beta}(\lambda_0).$$

The proof is complete. □

4.3 Steady-state solutions

We consider the steady-state problem. In this case all functions in model (42)–(44) do not depend on time t. Assume that it has a positive solution.

Theorem 7. *Let $\kappa, T, T_1, \dots, T_4$ be positive constants and functions ν, ν_k, ν_{ks}, and α_k satisfy conditions of Theorem* 1*. Then any positive steady-state solution of problem* (42)–(44) *is separable, i. e. any nontrivial separable solution con be written in the form*

$$u(\tau_1, x) = v^0(\tau_1) \exp\{\lambda_0(T - \tau_1)\} N(x)/\tilde{\beta}(\lambda_0),$$
$$u_k(\tau_1, \tau_2, x) = v_k^0(\tau_1, \tau_2) v^0(\tau_1 - \tau_2) \exp\{\lambda_0(T - \tau_1)\} N(x)/\tilde{\beta}(\lambda_0)$$

where v^0 and v_k^0 are defined in Section 3, λ_0 is as in Theorem 4*, and $N(x)$ is a unique positive in Ω solution of equation* (48)*.*

Proof. We use the Langlais [24] argument. Let the steady-state problem has a positive supported solution. Then $N(x)$ defined by formula (44) is known. Let $\tilde{\Lambda}_j$ and $\omega_j(x)$, $j \geq 1$ be as in Section 4.2. Then, for u and $u_k \in L_2(\Omega)$, we have

$$\begin{cases} u = \sum\limits_{s=1}^{\infty} U^s(T) z^s(\tau_1) \omega_s(x), \quad z^s(T) = 1, \\ u_k = \sum\limits_{s=1}^{\infty} U^s(T) z^s(\tau_1 - \tau_2) z_k^s(\tau_1, \tau_2) \omega_s(x). \end{cases} \tag{57}$$

Substituting functions (57) into the steady version of equations (42)–(44), we get equations 14 and (15) with λ, v^λ and v_k^λ replaced by $\tilde{\Lambda}_s$, z^s and z_k^s, respectively. Obviously,

$$z^s(\tau_1) = v^0(\tau_1) \exp\{-\tilde{\Lambda}_s(\tau_1 - T)\}, \quad z_k^s(\tau_1, \tau_2) = v_k^0(\tau_1, \tau_2) \exp\{-\tilde{\Lambda}_s \tau_2\}. \tag{58}$$

For $\tilde{\Lambda}_s$ we get the equations $U^s(T)(1 - I(\tilde{\Lambda}_s)) = 0$ with $I(\tilde{\Lambda}_s)$ defined by equation (18). Since $I(\tilde{\Lambda}_s) = 1$ only for $\tilde{\Lambda}_s = \lambda_0$, only one of $U^s(T)$ is not zero. Denote this U^s by $\tilde{U}$ and the corresponding $\omega^s(x)$ by $\tilde{\omega}(x)$. Then, by definition, we get $\tilde{U}\tilde{\omega}(x) = N(x)/\tilde{\beta}(\lambda_0) > 0$ in Ω. Finally, from Equations (57) and (58) the result of theorem follows.

5 Concluding remarks

A discrete newborns set-based deterministic model of one-sex age-structured and density-dependent population dynamics both with and without spatial diffusion has been proposed and investigated. The model consists of a system of $n + 1$ integro-partial differential equations subject to conditions of an integral type. The number n is a biologically possible maximal number of newborns of the same generation produced by an individual. Dynamics of young individuals in models given in [12–16] is described by differential equations for densities. In [17] and in the present model equations for offsprings under maternal care are not used in all. The spatial density $Y(t, \tau_2, x)$ of young offsprings aged

τ_2 at time t at the position x is determined in this model by the formula $Y(t, \tau_2, x) = \int_{T_1+\tau_2}^{T_3+\tau_2} \sum_{k=1}^{n} k u_k \, \mathrm{d}\tau_1$.

When $\lambda_0 < \kappa\Lambda_1$ then there exists no nontrivial steady-state solution of model (42)–(44).

Under the conditions of Theorem 6 the limit functions given by equation (49) represent a unique nontrivial separable solution to the steady-state analogue of problem (42)–(44).

The nontrivial asymptotic behavior of the solution to the model given above both with (at least for the (52) initial distributions) and without spatial diffusion is described by product of spatial density N^* and the same age profiles (see equations (40), (41), and (49)), where N^* is a constant for the non-dispersing population and it is a function of the spatial position x in the opposite case.

It is well known that the Sharpe-Lotka-McKendrick-von Förster or Gurtin-MacCamy models, that can be applied only for the population which does not take child care, under some restrictions on the vital rates have a class of product solutions. Such the populations, e.g. fishes, reptilia, and amphibia, produces very large number of newborns and a large part of them dies because of predators. Usually populations taking care of offsprings produce a small number of newborns and only due to child care the model of the such populations, (1)–(4), under suitable restrictions on the vital rates has a class of product solutions, too.

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