MATHEMATICAL BIOSCIENCES
AND ENGINEERING
Volume **13**, Number **2**, April **2016**

doi:10.3934/mbe.2015002

pp. **261–279**

STRUCTURED POPULATIONS WITH DIFFUSION AND FELLER CONDITIONS

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(Communicated by Xingfu Zou)

Abstract. We prove a weak maximum principle for structured population models with dynamic boundary conditions. We establish existence and positivity of solutions of these models and investigate the asymptotic behaviour of solutions. In particular, we analyse so called *size profile*.

1. Introduction.

Physiologically structured population models are widely discussed in the literature which concerns the modeling of population dynamics. Structured population models distinguish between individuals, depending on characteristics such as age, size, location, status, movement or any variable that reflects it and has a real effect on the population dynamics, see [7, 13, 18, 19]. Studies using these models show how the above characteristics influence the population dynamics. Thus our attention will be focused on structured variables related to physiological characteristics. A physiologically structured population equation is used, for example, to describe algae as food for small aquatic insects Daphnia (where the size x means the length), *e.g.* [20], § 4.3. Other examples are models of populations structured by an infection level or parasite load, see [22]. The resulting mathematical model is given by a first order partial differential equation with an initial condition and a boundary condition with diffusion.

Differential operators with boundary conditions containing diffusion terms were introduced by Feller and Wentzell in the context of stochastic diffusion processes, see [11, 24]. More precisely, boundary conditions for one dimensional diffusion processes were proposed by Feller [11], whereas multi-dimensional processes were studied by Wentzell, [24]. It turns out that Feller or Wentzell conditions are applicable to population dynamics models, because they are responsible for diffusive effects during migrations through the boundary. These conditions are more general

2010 *Mathematics Subject Classification.* Primary: 35Q92, 92D25; Secondary: 47N60, 35B35.
Key words and phrases. Size-structured model, Feller boundary condition, diffusion, size profile, maximum principle, Fourier analysis.

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than Dirichlet, Neumann and Robin conditions, see [1]. For example, Hadeler [14] proposes a mathematical model with Robin boundary conditions.

The present paper raises and develops the ideas of [10]. We study a size-structured model which describes the dynamics of one population with growth, diffusion, reproduction and mortality rates. We add an immigration term to the model, having in mind possible questions concerning open models, where individuals can be transported from other regions. The authors of [10] assign the name of Wentzell to the boundary conditions introduced by Feller, but in our paper, like in [5], we return to the name of Feller boundary conditions. They show that the size structured model with certain boundary conditions is governed by a positive quasicontractive semigroup on a biologically relevant state space. Furthermore, they characterize the asymptotic behaviour of solutions via balanced exponential growth of the governing semigroup. The advantage of the semigroup approach is that it enables the description of population processes as dynamical systems in the state space. It seems that positivity of solutions is technical and tedious in their semigroup setting, whereas our approach is straightforward. By the maximum principle we know that the asynchronous exponential growth is possible, compare [10]. The aim of our article is to provide more precise attempts to asymptotic analysis in a Hilbert space where one can recognize a finite dimensional subspace attracting some solutions. In [10] it is proven the existence and positivity of solutions by showing that solutions are governed by a positive quasicontractive semigroup of linear operators on the biologically relevant state space. We observe that if the initial function is of class L^1 and the data are regular, then the solution is of class C^2 for any $t > 0$ and satisfies the Feller conditions. Finding a suitable Hilbert space allows to analyse not only the solutions but also the size profile. Since our Hilbert space contains continuous functions, one has to solve complicated systems of ODE's on Fourier coefficients in l^2. The main difficulty is caused by the nonlocal birth operator. Our main achievement is to recognize these l^2-structures and derive some conclusions.

The paper is organised as follows: we formulate the problem, prove the maximum principle, analyse so called *size profile* and the asymptotic behaviour of solutions for specific mortality and reproduction rates. Finally, we present examples and conclusions.

2. **Formulation of the problem.** Suppose that $\mu \in C[0,m]$, $\beta \in C\left([0,m]\times[0,m]\right)$, $d,\gamma \in C^1[0,m]$, $\mu,\beta \geq 0$, $d > 0$, $\gamma \geq 0$ and $g : \mathbb{R}_+ \times [0,m] \to \mathbb{R}_+$ is measurable, where $\mathbb{R}_+ = [0,+\infty)$. Let $b_0, b_m > 0$ and $c_0, c_m \geq 0$. If we denote by $u(t,s)$ the density of individuals of size s at time t, then a general size-structured model for the evolution of u is written as

$$\begin{aligned} u_t(t,s) = {} & \left(d(s)u_s(t,s)\right)_s - \left(\gamma(s)u(t,s)\right)_s - \mu(s)u(t,s) \\ & + \int_0^m \beta(s,y)u(t,y)\,dy + g(t,s), \quad s \in (0,m) \end{aligned} \tag{1}$$

with linear Feller's boundary conditions

$$\begin{aligned} \left[\left(d(s)u_s(t,s)\right)_s\right]_{s=0} - b_0 u_s(t,0) + c_0 u(t,0) = 0 \\ \left[\left(d(s)u_s(t,s)\right)_s\right]_{s=m} + b_m u_s(t,m) + c_m u(t,m) = 0 \end{aligned} \tag{2}$$

and the initial condition

$$u(0,s) = \omega(s), \quad \omega(s) \geq 0. \tag{3}$$

The biological interpretation of the coefficients of this model is as follows: d is the diffusion coefficient, μ – the mortality rate, γ – the growth rate, the function β – the reproduction rate of individuals and g – immigration. The addition of the migration is important in the construction of theoretical biological models. There is rich literature which include some immigration, see [2, 18].

In the same way as in [10] condition (2) can be replaced by the condition in the dynamic form

$$\begin{aligned} u_t(t,0) = &\left(-\gamma'(0) - \mu(0) - c_0\right) u(t,0) + \left(b_0 - \gamma(0)\right) u_s(t,0) \\ &+ \int_0^m \beta(0,y) u(t,y)\, dy + g(t,0) \end{aligned} \tag{4}$$

and

$$\begin{aligned} u_t(t,m) = &\left(-\gamma'(m) - \mu(m) - c_m\right) u(t,m) - \left(b_m + \gamma(m)\right) u_s(t,m) \\ &+ \int_0^m \beta(m,y) u(t,y)\, dy + g(t,m). \end{aligned} \tag{5}$$

The dynamic boundary conditions have the following natural interpretation. Individuals in a population that are very small size can be absorbed in the states $s = 0$, which means inactivity. Then, after a time of rest, these individuals are leaving this state due to diffusion and become active. A similar behaviour is observed at the edge $s = m$, see [9].

The boundary value problem (1)–(3) is equivalent to (1) and (3) with these nonlocal conditions (4), (5). In [6], the spread of infection of a vertically transmitted disease is described using a model with diffusion in the state space and dynamic boundary conditions.

3. **Maximum principle.** We consider differential inequalities generated by problem (1)–(3). We are interested in seeing whether the implication holds: if $\omega \geq 0$ and $g \geq 0$, then the solution of (1)–(3) satisfies $u \geq 0$. In fact, we prove a weak maximum principle for (1), (3) with the dynamic conditions (4), (5), which is based on the respective strong maximum principle, [4, 23].

Theorem 3.1. *Suppose that*

1. $\mu \in C[0,m]$, $\beta \in C\left([0,m] \times [0,m]\right)$, $d, \gamma \in C^1[0,m]$,
2. $\mu(s), \beta(s,y) \geq 0$, $d(s) > 0$, b_0, $b_m > 0$, $c_0, c_m \geq 0$ *and* $b_0 - \gamma(0) \geq 0$, $b_m + \gamma(m) \geq 0$,
3. *the differential inequality is satisfied*

$$\begin{aligned} u_t(t,s) \geq &\left(d(s) u_s(t,s)\right)_s - \left(\gamma(s) u(t,s)\right)_s - \mu(s) u(t,s) \\ &+ \int_0^m \beta(s,y) u(t,y)\, dy \quad \textit{for} \quad t > 0,\ s \in (0,m), \end{aligned}$$

4. *the initial and the dynamic boundary inequalities are satisfied*

$$\begin{aligned} u(0,s) \geq &0 \quad s \in [0,m], \\ u_t(t,0) \geq &\left(-\gamma'(0) - \mu(0) - c_0\right) u(t,0) + \left(b_0 - \gamma(0)\right) u_s(t,0) \\ &+ \int_0^m \beta(0,y) u(t,y)\, dy \quad t > 0, \\ u_t(t,m) \geq &\left(-\gamma'(m) - \mu(m) - c_m\right) u(t,m) - \left(b_m + \gamma(m)\right) u_s(t,m) \end{aligned}$$

$$+\int_0^m \beta(m,y)u(t,y)\,dy \quad t>0.$$

Then $u(t,s)\geq 0$ *for* $t\geq 0,\ s\in[0,m]$.

Proof. Define $\tilde u(t,s)=u(t,s)+\varepsilon e^{\lambda t}$, where $\varepsilon>0$ and $\lambda\in\mathbb{R}$. The function $\tilde u$ satisfies the assumptions of the strong maximum principle if λ is sufficiently large. It is clear that $\tilde u(0,s)>0$. If

$$\lambda > -\gamma'(s)-\mu(s)+\int_0^m \beta(s,y)\,dy,$$

then the function $\tilde u$ satisfies the inequality

$$\begin{aligned}\tilde u_t(t,s) > &\left(d(s)\tilde u_s(t,s)\right)_s-\left(\gamma(s)\tilde u(t,s)\right)_s-\mu(s)\tilde u(t,s)\\ &+\int_0^m \beta(s,y)\tilde u(t,y)\,dy\end{aligned}$$

for $t>0,\ s\in(0,m)$. Similarly, we check the strong dynamic boundary conditions for $\tilde u$, when

$$\begin{aligned}\lambda >& -\gamma'(0)-\mu(0)-c_0+\int_0^m \beta(0,y)\,dy,\\ \lambda >& -\gamma'(m)-\mu(m)-c_m+\int_0^m \beta(m,y)\,dy.\end{aligned}$$

Let λ fulfills the above inequalities. We prove that the function $\tilde u$ satisfies the inequality $\tilde u(t,s)>0$ for $t\geq 0,\ s\in[0,m]$. Suppose, on the contrary, that this inequality does not occur. Then we can find a Nagumo point (t^*,s^*), which satisfies the conditions

$$\tilde u(t^*,s^*)=0 \quad \text{and} \quad \forall_{t\in[0,t^*)}\forall_{s\in[0,m]}\,\tilde u(t,s)>0.$$

It is obvious that $t^*>0$. First, we consider the case $s^*\in(0,m)$. Since $\tilde u(t,s)>0$ for $t<t^*$, we have $\tilde u_t(t^*,s^*)\leq 0$ and

$$\tilde u(t^*,s^*)=\tilde u_s(t^*,s^*)=0, \quad \tilde u_{ss}(t^*,s^*)\geq 0.$$

Hence, at the point (t^*,s^*) we obtain the inequalities

$$\begin{aligned}\tilde u_t(t^*,s^*) > &\left(d(s^*)\tilde u_s(t^*,s^*)\right)_s-\left(\gamma(s^*)\tilde u(t^*,s^*)\right)_s-\mu(s^*)\tilde u(t^*,s^*)\\ &+\int_0^m \beta(s^*,y)\tilde u(t^*,y)\,dy\geq 0.\end{aligned}$$

This leads to the contradiction with $\tilde u_t(t^*,s^*)\leq 0$. Consider the case $s^*=0$. Then we derive the inequalities

$$0\geq \tilde u_t(t^*,0) > (b_0-\gamma(0))\tilde u_s(t^*,0)+\int_0^m \beta(s^*,0)\tilde u(t^*,y)\,dy\geq 0,$$

which contradict the strong dynamic inequality. A similar treatment can be performed for $s^*=m$. Since $\tilde u(t,s)=u(t,s)+\varepsilon e^{\lambda t}>0$, letting $\varepsilon\to 0^+$, we get $u(t,s)\geq 0$ for $t\geq 0,\ s\in[0,m]$. This completes the proof. □

Note that if we apply Theorem 3.1 to the problem (1)–(3), then the assumption 3 of this theorem means that the migration g is nonnegative. Furthermore, the condition 4 implies that $\omega\geq 0$ and the migration g is nonnegative on the boundary, *i.e.* for $p=0$ and $s=m$. This implication holds true due to the dynamic version of the Feller boundary conditions (2). The inequalities in the condition 4 have the following biological interpretation: the nonnegative migration g at the lateral boundary forces the dynamics of $u_t(t,0)$ and $u_t(t,m)$.

Corollary 1. *Suppose that the assumptions 1 and 2 of Theorem 3.1 are satisfied. If* $0 \le \omega(s) \le K$ *and* $g \equiv 0$, *then the solution* u *of problem* (1)–(3) *satisfies the following inequalities*

$$0 \le u(t,s) \le Ke^{\lambda t},$$

where

$$\lambda \ge -\gamma'(s) - \mu(s) + \int_0^m \beta(s,y)\,dy. \tag{6}$$

Proof. Since problem (1)–(3) is equivalent to the problem with the dynamic conditions, we conclude that $u(t,s) \ge 0$ for $t \ge 0$ and $s \in [0,m]$. This follows from the maximum principle, *i.e.* Theorem 3.1. In order to get the inequality $u(t,s) \le Ke^{\lambda t}$ it is sufficient to show that the function $Ke^{\lambda t} - u(t,s)$ satisfies the maximum principle for the problem with dynamic conditions. This follows immediately from inequality (6). □

Corollary 2. *Suppose that the assumptions 1 and 2 of Theorem 3.1 are satisfied. If* ω *is nonnegative and integrable,* $g \in C(\mathbb{R}_+, L^1[0,m])$ *is nonnegative, then there is a unique solution* $u \ge 0$ *and*

$$u(t,s) = \int_0^m G(t,s,y)\,\omega(y)\,dy + \int_0^t \int_0^m G(t-\tau,s,y)\,g(\tau,y)\,dy\,d\tau, \tag{7}$$

where G *is the Green function of problem* (1)–(3). *Moreover, if* ω *and* g *are continuous, then the solution of* (7) *is of the class* $C^{1,2}$ *in the interior of the domain.*

Proof. Note first that it is sufficient to consider (7) with $g \equiv 0$ because the second term in the expression (7) can be derived from the Duhamel principle. The Green function can be defined as follows

$$G(t,s,r) := \lim_{n\to\infty} u_n(t,s;r),$$

where $u_n(t,s;r)$ are the solutions of the homogeneous partial differential equation with the initial condition $u_n(0,s;r) = \omega_n(s;r)$, $\omega_n(\cdot;r)$ are nonnegative C^∞ functions which approximate the Dirac delta function δ_r. The Green function G is a distributional object, but one can see that it is a regular function. The proof of (7) is divided into two steps: 1. $\mu \equiv 0$ and $\beta \equiv 0$; 2. general case.

Step 1. Applying Corollary 1, being a consequence of the maximum principle, we obtain a priori estimate

$$0 \le \omega(s) \le K \quad \Rightarrow \quad 0 \le u(t,s) \le K,$$

which means that $\omega \longmapsto u$ is a contraction with respect to the uniform norm. Suppose that equation (7) holds for continuous functions ω. Using the maximum principle one can easily prove that

$$G(t,s,y) \ge 0 \quad \text{and} \quad 0 \le \int_0^{\mathrm{m}} \mathrm{G(t,s,y)\,dy} \le 1.$$

Since $(d\xi_s)_s$ is a self-adjoint operator with respect to the usual L^2 inner scalar product on $[0,m]$ in a subspace of smooth functions vanishing at the boundary, we get the symmetry condition

$$G(t,s,y) = G(t,y,s) \quad \text{for} \quad \mathrm{y \ne s}.$$

This means that the function $G(t,\cdot,y)$ is integrable and $G(t,s,\cdot)$ is continuous. Let $C[0,m] \ni \omega_n \xrightarrow{L^1} \omega \in L^1[0,m]$, $\omega_n \geq 0$. By (7) we have a sequence of continuous functions

$$u_n(t,s) = \int_0^m G(t,s,y)\,\omega_n(y)\,dy, \quad n = 1,2,\ldots$$

Note that for any continuous function $\eta : [0,m] \to \mathbb{R}$, $0 \leq \eta \leq 1$ the following relations hold

$$\begin{aligned} 0 &\leq \int_0^m \eta(s)\,u_n(t,s)\,ds = \int_0^m \eta(s) \int_0^m G(t,s,y)\,\omega_n(y)\,dy\,ds \\ &= \int_0^m \omega_n(y) \int_0^m G(t,s,y)\,\eta(s)\,ds\,dy \leq \int_0^m \omega_n(y)\,dy \to \int_0^m \omega(y)\,dy. \end{aligned}$$

Therefore

$$u_n(t,s) \xrightarrow{L^1} \int_0^m G(t,s,y)\,\omega(y)\,dy$$

and

$$0 \leq \int_0^m u(t,s)\,ds = \int_0^m \omega(y) \int_0^m G(t,s,y)\,ds\,dy \leq \int_0^m \omega(y)\,dy,$$

i.e. $\omega \longmapsto u(t,\cdot)$ is a contraction in $L^1[0,m]$ for all $t \geq 0$. Recall that the Duhamel principle yields the general version of (7) with $g \in C(R_+, L^1[0,m])$, and one has the estimate

$$\|u(t,\cdot)\|_{L^1[0,m]} \leq \|\omega\|_{L^1[0,m]} + \int_0^t \|g(\tau,\cdot)\|_{L^1[0,m]}\,d\tau.$$

Step 2. Having in mind the Duhamel principle we assume that $g \equiv 0$. We apply the representation (7) from step 1 where we regard $\mu u + \int \beta u$ as a 'migration' term, say $\bar{g}$. Thus we get the integral equation

$$\begin{aligned} u(t,s) &= \int_0^m G(t,s,y)\,\omega(y)\,dy \\ &\quad + \int_0^t \int_0^m G(t-\tau,s,y) \Big\{ \underbrace{\mu(y)\,u(t,y) + \int_0^m \beta(y,y')\,u(t,y)\,dy'}_{\tilde{g}} \Big\}\,dy\,d\tau. \end{aligned}$$

According to formula (7) with G replaced by H, we are looking for solutions in the form

$$u(t,s) = \int_0^m H(t,s,y)\,\omega(y)\,dy.$$

Comparing the last two formulas leads to the integral equation (see [12, 17])

$$\begin{aligned} H(t,s,y) = G(t,s,y) &- \int_0^t \int_0^m G(t-\tau,s,y')\,\mu(y')\,H(\tau,y',y)\,dy'\,d\tau \\ &+ \int_0^t \int_0^m \int_0^m G(t-\tau,s,y')\,\beta(y',y)\,H(\tau,y',y)\,dy\,dy'\,d\tau. \end{aligned}$$

By the maximum principle we have $H \geq 0$. It follows from the continuity of G that H is also continuous. From the integrability of the function $G(t,s,\cdot)$, we deduce that $H(t,s,\cdot)$ is integrable and derive the estimate

$$0 \leq \int_0^m H(t,s,y)\,dy \leq c_T \quad \text{for t} \in [0,\text{T}].$$

We conclude from this estimate and the Duhamel principle for the kernel H that formula (7) is valid for H and (similarly as in step 1) we can derive an L^1 estimate

$$\|u(t,\cdot)\|_{L^1[0,m]} \le c_T \left(\|\omega\|_{L^1[0,m]} + \int_0^t \|g(\tau,\cdot)\|_{L^1[0,m]} \right).$$

□

Remark 1. The proof of Corollary 2 shows that the assertion is true for the migration term g which is nonnegative and locally integrable on $\mathbb{R}_+ \times [0,m]$.

Remark 2. Corollary 1 shows that, if the coefficients γ, β and μ allow inequality (6) with some $\lambda < 0$, then the solutions are exponentially stable, *i.e.* the population dies out. This means that the mortality rate μ is sufficiently large compared with the birth and growth terms.

4. **Size profile.** It is obvious that even if the initial function $u(0,\cdot)$ is taken from the space $L^1[0,m]$, then the parabolic operator regularizes the solution u, and the functions $u(t,\cdot)$ are $C^2[0,m]$ for all $t>0$. Hence we can study continuous solutions, because the initial condition at $t_0 = 0$ can be replaced by an initial value problem at some $t_0 > 0$, where the solution is regular. Let $U(t) = \int_0^m u(t,s)\,ds$ be the total number of individuals at time t, then $v(t,s) = u(t,s)/U(t)$ is the normalized size distribution at time t, provided that $U(t) \neq 0$. In this case the integral $\int_0^m v(t,s)\,ds$ is equal to 1 for all $t \ge 0$. The function v is called *the size profile*, see [10]. If $u \equiv 0$, then we put $v \equiv 0$. Integrating equation (1) with respect to s over the interval $[0,m]$ we obtain

$$\begin{aligned}\frac{dU(t)}{dt} &= \left(d(\cdot)u_s(t,\cdot)\right)\Big|_0^m - \left(\gamma(\cdot)u(t,\cdot)\right)\Big|_0^m - \int_0^m \mu(s)u(t,s)\,ds \\ &\quad + \int_0^m \int_0^m \beta(s,y)u(t,y)\,dy\,ds + \int_0^m g(t,s)\,ds.\end{aligned}$$

Taking into account equation (1) and the derivatives

$$v_s = \frac{u_s}{U}, \quad (dv_s)_s = \frac{(du_s)_s}{U} \quad \text{and} \quad v_t = \frac{u_t}{U} - \frac{uU_t}{U^2},$$

we note that the equation for the size profile function is as follows

$$\begin{aligned} v_t(t,s) &= \left(d(s)v_s(t,s)\right)_s - \left(\gamma(s)v(t,s)\right)_s - \mu(s)v(t,s) + \int_0^m \beta(s,y)v(t,y)\,dy \\ &\quad - v(t,s)\left[\left(d(\cdot)v_s(t,\cdot)\right)\Big|_0^m - \left(\gamma(\cdot)v(t,\cdot)\right)\Big|_0^m - \int_0^m \mu(y)v(t,y)dy \right. \\ &\quad \left. + \int_0^m\int_0^m \beta(x,y)v(t,y)\,dy\,dx \right] + \frac{1}{U(t)}\int_0^m g(t,s)\,ds \end{aligned} \tag{8}$$

for $s \in (0,m)$. The function v satisfies Feller's boundary conditions (2). In the sequel we consider a closed population with no immigration.

4.1. **Self-adjoint operator.** Let $\gamma = 0$. If $\gamma \neq 0$, then we reduce the leading operator to a self-adjoint form by replacing $u(t,s)$ by $u(t,s)\exp\left(-\int_0^s \frac{\gamma(y)}{2d(y)}\,dy\right)$. This substitution preserves fundamental features of the model under mild assumptions on γ. Define a functional space generated by the Feller conditions (2)

$$\mathcal{X} = \left\{ \xi \in C^2[0,m] : \begin{array}{r} (d\,\xi')'(0) - b_0\,\xi'(0) + c_0\,\xi(0) = 0 \\ (d\,\xi')'(m) + b_m\,\xi'(m) + c_m\,\xi(m) = 0 \end{array} \right\}$$

with the inner scalar product for $\xi, \eta \in \mathcal{X}$:

$$\langle \xi, \eta \rangle = \int_0^m \xi(s)\,\eta(s)\,ds + \frac{d(0)}{b_0}\,\xi(0)\eta(0) + \frac{d(m)}{b_m}\xi(m)\eta(m).$$

L^p-type norms generated by this type of inner scalar product have been applied in [16] (the multidimensional case). Then problem (1)–(3) can be written as an abstract evolution equation in $\bar{\mathcal{X}}$, *i.e.* a completion of $\mathcal{X}$ with respect to the inner scalar product $\langle \cdot, \cdot \rangle$:

$$\frac{du}{dt} + \mathcal{L}u = -\mathcal{M}u + \mathcal{B}u + g, \quad u_0 \in \bar{\mathcal{X}},$$

where $\mathcal{L}$ is the leading operator, $\mathcal{M}$ – mortality, $\mathcal{B}$ – birth, namely:

$$(\mathcal{L}\eta)(s) = -(d(s)\eta'(s))',\ (\mathcal{M}\eta)(s) = \mu(s)\eta(s),\ (\mathcal{B}\eta)(s) = \int_0^m \beta(s,y)\eta(y)\,dy.$$

Note that $\mathcal{L}$ is a nonnegative and self-adjoint operator with respect to the inner scalar product $\langle \cdot, \cdot \rangle$. The positive semi-definiteness of the operator $\mathcal{L}$ follows from the maximum principle. Had the operator $\mathcal{L}$ a negative eigenvalue we would get an unbounded solution (like $e^{-\lambda t}$) of the homogeneous equation $du/dt + \mathcal{L}u = 0$, which contradicts the maximum principle. Suppose that $e_1, e_2, \ldots$ is a complete system of eigenvectors of $\mathcal{L}$, orthonormal with respect to $\langle \cdot, \cdot \rangle$ with the respective eigenvalues $\lambda_1 \le \lambda_2 \le \ldots$. Moreover, assume that $e_1 \ge 0$. This assumption is possible to be realised by virtue of the maximum principle as follows. Take any positive function $\eta \in \mathcal{X}$ and consider the differential problem

$$\frac{du}{dt} + \mathcal{L}u = 0, \quad u(0,\cdot) = \eta$$

with Feller conditions. By the maximum principle the solution u is positive. If we normalize $u(t,\cdot)$ we have that

$$\frac{u(t,\cdot)}{\sqrt{\langle u(t,\cdot), u(t,\cdot) \rangle}}$$

tends to an eigenvector in $\mathcal{X}$ corresponding to the first eigenvalue λ_1 as $t \to \infty$. Thus we can choose this limit as e_1. In practice, this can be also done by minimizing of the Rayleigh quotient $\langle \mathcal{L}\eta, \eta \rangle \,/\, \langle \eta, \eta \rangle$ by means of the steepest descent method starting from any positive function $\eta \in \mathcal{X}$. In the case $\mathcal{M} = 0$, $\mathcal{B} = 0$ and $g = 0$ the size profile equation has the form

$$\frac{dv}{dt} + \mathcal{L}v = -\mathcal{A}_v v,$$

where $\mathcal{A}_v = (dv_s)\Big|_0^m$, $v(0,s) \ge 0$, $\int_0^m v(0,s)ds = 1$.

Lemma 4.1. *If* $\mathcal{M} = 0$, $\mathcal{B} = 0$, $g = 0$, $v(0,s) \ge 0$, $\int_0^m v(0,s)ds = 1$ *and* $\lambda_1 = \ldots = \lambda_k < \lambda_{k+1}$, *then* $v(t,s)$ *tends to* $v^*(s) = C_1 e_1(s) + \ldots + C_k e_k(s)$ *as* $t \to +\infty$.

Proof. Since $v(t,s) = u(t,s)/U(t)$, it is sufficient to study the solution of $du/dt + \mathcal{L}u = 0$, $u(0,\cdot) = v(0,\cdot)$. This function has the expansion

$$u(t,s) = \sum_{i=1}^{\infty} \phi_i(t) e_i(s),$$

where $\phi_i(t) = \phi_i(0) \cdot e^{-\lambda_i t}$. Hence $u(t,s) \cdot e^{\lambda_1 t}$ tends to a linear combination of $e_1(s), \ldots, e_k(s)$. □

In fact the eigenfunctions $e_1, e_2, \ldots$ admit distinct eigenvalues $\lambda_1 < \lambda_2 < \ldots$, hence we have $k = 1$ in Lemma 4.1, which means that the size profile is determined by e_1 in absence of birth, migration. Furthermore, this basis fulfills the assumption of the Stone–Weierstrass Theorem (it separates points), hence the space $\bar{\mathcal{X}}$ contains all continuous functions. If one finds expressions of Fourier coefficients this will lead to some complete picture of solutions to nonlocal PDE's. With this tool, we consider the more general model with nontrivial mortality and reproduction rates

$$\frac{du}{dt} + \mathcal{L}u = -\mathcal{M}u + \mathcal{B}u, \quad u_0 \in \bar{\mathcal{X}}. \tag{9}$$

Suppose that $\mu(s) = \mu = const. \geq 0$ and $\beta(\cdot, y)$ admits the following expansion

$$\beta(s,y) = \sum_{j=1}^{\infty} \beta_j(y) e_j(s),$$

where $\beta_j(y) = \langle e_j, \beta(\cdot, y) \rangle$. We are looking for the solution to problem (9) in the form

$$u(t,s) = \sum_{j=1}^{\infty} \phi_j(t) e_j(s). \tag{10}$$

Substituting solution (10) into equation (9) we get the following equation

$$\sum_{j=1}^{\infty} \phi_j'(t) e_j(s) + \sum_{j=1}^{\infty} \lambda_j \phi_j(t) e_j(s) = -\mu \sum_{j=1}^{\infty} \phi_j(t) e_j(s) + \sum_{j=1}^{\infty} \int_0^m \beta_j(y) u(t,y)\, dy \cdot e_j(s).$$

The comparison of corresponding Fourier coefficients gives the following system of ODE's

$$\phi_j'(t) + (\lambda_j + \mu)\, \phi_j(t) = \int_0^m \beta_j(y) u(t,y)\, dy,$$

whose solution is of the form

$$\phi_j(t) = \phi_j(0) e^{-t(\lambda_j + \mu)} + \int_0^t e^{-(t-\tau)(\lambda_j+\mu)} \int_0^m \beta_j(y) u(\tau, y)\, dy\, d\tau \tag{11}$$

for $j = 1, 2, \ldots$ Substituting (11) into (10), we get the integral equation for u

$$u(t,s) = \sum_{j=1}^{\infty} \phi_j(0) e^{-t(\lambda_j+\mu)} e_j(s) + \int_0^t \sum_{j=1}^{\infty} e^{-(t-\tau)(\lambda_j+\mu)} \int_0^m \beta_j(y) e_j(s) u(\tau, y)\, dy\, d\tau. \tag{12}$$

We use this representation to study the size profile.

4.2. **Fourier analysis.** Denote $\boldsymbol{\Lambda} = \operatorname{diag}(\lambda_1, \lambda_2, \ldots)$, $\boldsymbol{L} = [L_{ij}]_{i,j=1,\ldots}$ and

$$L_{ij} = \int_0^m \beta_i(y)\, e_j(y)\, dy \quad \text{for} \quad i,j = 1, 2, \ldots$$

First, we formulate the following lemma which makes easier the calculus of Fourier coefficients with respect to the Hilbert space $\bar{\mathcal{X}}$.

Lemma 4.2. *Assume that* $(\beta_i(y))_{i\in Z} \in l^2$ *and* $\boldsymbol{L} : l^2 \to l^2$. *Let* $Z(t) = e^{t\boldsymbol{\Lambda}} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})}$ *and* $Y(t) = \exp\left(\int_0^t e^{\tau\boldsymbol{\Lambda}} \boldsymbol{L} e^{-\tau\boldsymbol{\Lambda}}\, d\tau\right)$ *be two families of operators acting on a dense subspace of* l^2. *Then*

$$\exp\left(\int_0^t e^{\tau\boldsymbol{\Lambda}} \boldsymbol{L} e^{-\tau\boldsymbol{\Lambda}}\, d\tau\right) = e^{t\boldsymbol{\Lambda}} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})}$$

on a dense subspace of l^2.

Proof. Consider the abstract problem on a dense subspace of l^2, *e.g.* finite sequences

$$Y'(t) = e^{t\boldsymbol{\Lambda}} \boldsymbol{L} e^{-t\boldsymbol{\Lambda}} Y(t), \quad Y(0) = I. \tag{13}$$

We need to show that $Z(t)$ is also the solution of (13). It is clear that

$$\begin{aligned}
Z'(t) =& \boldsymbol{\Lambda} e^{t\boldsymbol{\Lambda}} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} + e^{t\boldsymbol{\Lambda}} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})}(\boldsymbol{L}-\boldsymbol{\Lambda}) \\
=& \boldsymbol{\Lambda} e^{t\boldsymbol{\Lambda}} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} + e^{t\boldsymbol{\Lambda}} (\boldsymbol{L}-\boldsymbol{\Lambda}) e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} \\
=& \boldsymbol{\Lambda} e^{t\boldsymbol{\Lambda}} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} + e^{t\boldsymbol{\Lambda}} \boldsymbol{L} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} - e^{t\boldsymbol{\Lambda}} \boldsymbol{\Lambda} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} \\
=& e^{t\boldsymbol{\Lambda}} \boldsymbol{L} e^{-t\boldsymbol{\Lambda}} e^{t\boldsymbol{\Lambda}} e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} \\
=& e^{t\boldsymbol{\Lambda}} \boldsymbol{L} e^{-t\boldsymbol{\Lambda}} Z(t).
\end{aligned}$$

Proceeding as in the theory of semigroups (*cf.* [8]), we obtain that $Y = Z$ on the dense subspace of l^2. □

We use the assertion of Lemma 4.2 to derive the Fourier expansion of the solution of (9).

Theorem 4.3. *Assume that* $(\beta_i(y))_{i\in Z} \in l^2$ *and* $\boldsymbol{L} : l^2 \to l^2$. *Let* $u(0,\cdot) \geq 0$, $\mu(s) = \mu = const. \geq 0$,

$$\beta(s,y) = \sum_{j=1}^{\infty} e_j(s)\beta_j(y) \geq 0$$

and the semigroup $e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})}$ *maps* l^2 *into* l^2. *If* $u(0,\cdot) \in \bar{\mathcal{X}}$ *and* u *satisfies* (9), *then the solution of* (12) *has the form*

$$u(t,s) = e^{-t\mu} \sum_{j=1}^{\infty} e_j(s) \boldsymbol{e}_j^T e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} \boldsymbol{\phi}(0), \tag{14}$$

where $\boldsymbol{e}_j^T$ *is the transpose of the* j*-th vector of the standard basis in* $\mathbb{R}^N$ *and* $\phi_j(0)$ *are Fourier coefficients of* $u(0,\cdot)$ *in the Hilbert space* $\bar{\mathcal{X}}$.

Proof. Multiplying (12) by $e^{t(\lambda_i+\mu)}$ gives

$$\begin{aligned}
u(t,s)e^{t(\lambda_i+\mu)} =& \sum_{j=1}^{\infty} \phi_j(0) e^{-t(\lambda_j-\lambda_i)} e_j(s) \\
&+ \int_0^t \sum_{j=1}^{\infty} e_j(s) e^{-t(\lambda_j-\lambda_i)} \int_0^m e^{\tau(\lambda_j+\mu)} \beta_j(y) u(\tau,y)\, dy\, d\tau.
\end{aligned}$$

Before multiplying this expression by $\beta_i(s)$ and integrating over $[0,m]$, we denote

$$w_j(t) = e^{t(\lambda_j+\mu)} \int_0^m \beta_j(y) u(t,y)\, dy, \quad j = 1,2,\ldots \tag{15}$$

Then we obtain integral equations for the variables given by (15) as follows

$$w_i(t) = \sum_{j=1}^{\infty} \phi_j(0) e^{-t(\lambda_j - \lambda_i)} L_{ij} + \int_0^t \sum_{j=1}^{\infty} e^{-t(\lambda_j-\lambda_i)} L_{ij} w_j(\tau)\, d\tau \tag{16}$$

and we get from (12) the following representation of u

$$u(t,s) = \sum_{j=1}^{\infty} \phi_j(0) e^{-t(\lambda_j+\mu)} e_j(s) + \int_0^t \sum_{j=1}^{\infty} e_j(s) e^{-t(\lambda_j+\mu)} w_j(\tau)\, d\tau. \tag{17}$$

Formula (16) can be written as the infinite system in l^2

$$w(t) = e^{t\boldsymbol{\Lambda}} \boldsymbol{L} e^{-t\boldsymbol{\Lambda}} \phi(0) + \int_0^t e^{t\boldsymbol{\Lambda}} \boldsymbol{L} e^{-t\boldsymbol{\Lambda}} w(\tau)\, d\tau$$

whose solution has the form

$$w(t) = e^{t\boldsymbol{\Lambda}} \boldsymbol{L} e^{-t\boldsymbol{\Lambda}} \exp\left(\int_0^t e^{\tau\boldsymbol{\Lambda}} \boldsymbol{L} e^{-\tau\boldsymbol{\Lambda}}\, d\tau \right) \phi(0). \tag{18}$$

Observe that $w_j(t) = \boldsymbol{e}_j^T \boldsymbol{w}(t)$ and $\phi(0) = (\phi_j(0)) \in l^2$ because $\phi_j(0)$ are Fourier coefficients of $u(0,\cdot)$ in the Hilbert space $\bar{\mathcal{X}}$. Then (17) can be written in the following form

$$\begin{aligned} u(t,s) = & \sum_{j=1}^{\infty} \phi_j(0) e^{-t(\lambda_j+\mu)} e_j(s) \\ & + \int_0^t \sum_{j=1}^{\infty} e^{-t(\lambda_j+\mu)} e_j(s) \boldsymbol{e}_j^T \frac{d}{d\tau} \exp\left(\int_0^\tau e^{\tau'\boldsymbol{\Lambda}} \boldsymbol{L} e^{-\tau'\boldsymbol{\Lambda}} d\tau' \right) \boldsymbol{\phi}(0)\, d\tau \\ = & \sum_{j=1}^{\infty} e^{-t(\lambda_j+\mu)} e_j(s) \boldsymbol{e}_j^T \exp\left(\int_0^t e^{\tau\boldsymbol{\Lambda}} \boldsymbol{L} e^{-\tau\boldsymbol{\Lambda}} d\tau \right) \boldsymbol{\phi}(0). \end{aligned}$$

By Lemma 4.2 we easily get (14). □

We conclude our discussion with the following result.

Corollary 3. *Let $\beta_j = 0$ for $j > k$. If the infinite matrix $\boldsymbol{L} - \boldsymbol{\Lambda}$ has the block structure*

$$\begin{bmatrix} \tilde{L} - \tilde{\Lambda} & B \\ 0 & -\hat{\Lambda} \end{bmatrix}, \quad B = \begin{bmatrix} B_1 & B_2 & \dots \end{bmatrix}$$

with negative real parts of eigenvalues of the $k \times k$-block $\tilde{\Lambda} - \tilde{L} - \lambda_{k+1}\tilde{I}$ then the asymptotic behaviour $u(t,s)$ is determined by the block $\tilde{L} - \tilde{\Lambda}$ in the form

$$e^{-t\mu} \tilde{\boldsymbol{e}}^T(s) e^{t(\tilde{L}-\tilde{\Lambda})} \left[\hat{\phi}(0) + \sum_{l=k+1}^{\infty} \phi_l(0)(\lambda_l \tilde{I} - \tilde{\Lambda} + \tilde{L})^{-1} B_{l-k} \right], \tag{19}$$

where $\tilde{I}$ is the $k \times k$ identity matrix and

$$\tilde{\boldsymbol{e}}(s) = [e_1(s) \dots e_k(s)]^T, \quad \phi = \begin{bmatrix} \tilde{\phi} \\ \hat{\phi} \end{bmatrix}, \quad \tilde{\phi} = \begin{bmatrix} \tilde{\phi}_1 & \dots & \tilde{\phi}_k \end{bmatrix}^T.$$

Proof. By the assumption the infinite matrix $\boldsymbol{L} - \boldsymbol{\Lambda}$ has the block structure, hence

$$e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})} = \begin{bmatrix} e^{t(\tilde{L}-\tilde{\Lambda})} & Q(t) \\ 0 & e^{-t\hat{\Lambda}} \end{bmatrix}.$$

It has to satisfy the initial condition $Q(0) = 0$ and the differential equation

$$\frac{d}{dt}\begin{bmatrix} e^{t(\tilde{L}-\tilde{\Lambda})} & Q(t) \\ 0 & e^{-t\hat{\Lambda}} \end{bmatrix} = \begin{bmatrix} \tilde{L}-\tilde{\Lambda} & B \\ 0 & -\hat{\Lambda} \end{bmatrix}\begin{bmatrix} e^{t(\tilde{L}-\tilde{\Lambda})} & Q(t) \\ 0 & e^{-t\hat{\Lambda}} \end{bmatrix}$$

thus Q(t) satisfies the Cauchy problem

$$\frac{d}{dt}Q(t) = (\tilde{L}-\tilde{\Lambda})Q(t) + Be^{-t\hat{\Lambda}}, \quad Q(0) = 0.$$

The solution of this problem is of the form

$$Q(t) = e^{t(\tilde{L}-\tilde{\Lambda})}\int_0^t e^{-\tau(\tilde{L}-\tilde{\Lambda})}Be^{-\tau\hat{\Lambda}}\,d\tau.$$

Thus the term $e^{t(\boldsymbol{L}-\boldsymbol{\Lambda})}\boldsymbol{\phi}(0)$ in (14) can be written as

$$\begin{bmatrix} e^{t(\tilde{L}-\tilde{\Lambda})}\widetilde{\phi}(0) + Q(t)\hat{\phi}(0) \\ e^{-t\hat{\Lambda}}\hat{\phi}(0) \end{bmatrix}.$$

Note that

$$Q(t)\hat{\phi}(0) = \int_0^t e^{-\tau(\tilde{L}-\tilde{\Lambda})}\sum_{i=1}^{\infty}\phi_{k+i}(0)e^{-\tau\lambda_{k+i}}B_i.$$

Thus the asymptotic behaviour of $Q(t)\hat{\phi}(0)$ is like

$$e^{t(\tilde{L}-\tilde{\Lambda})}\sum_{i=1}^{\infty}\phi_{k+i}(0)(\lambda_{k+i}\tilde{I}-\tilde{\Lambda}+\tilde{L})^{-1}B_i.$$

Therefore the asymptotic behaviour of the solution of (9) is like (19). □

Remark 3. In the case $k = 1$, we have

$$\begin{bmatrix} e^{t(L_{11}-\lambda_1)}\phi_1(0) + \phi_2(0)Q_{11}(t) + \phi_3(0)Q_{12}(t) + \dots \\ e^{-t\lambda_2\phi_2(0)} \\ \vdots \end{bmatrix}$$

and from (14) the solution u of (9) has the form

$$e^{-\mu t}\Bigg\{e_1(s)\left[e^{t(L_{11}-\lambda_1)}\phi_1(0) + \phi_2(0)Q_{11}(t) + \phi_3(0)Q_{12}(t) + \dots\right] + \sum_{j=2}^{\infty}e_j(s)e^{-t\lambda_j}\phi_j(0)\Bigg\}.$$

Thus the size profile is proportional to the term

$$e_1(s)\left[\phi_1(0) + \phi_2(0)\frac{b_2}{L_{11}-\lambda_1+\lambda_2} + \phi_3(0)\frac{b_3}{L_{11}-\lambda_1+\lambda_3} + \dots\right].$$

Remark 4. Under the assumptions of Corollary 3 the size profile $v(s)$ is a linear combination of $e_1(s), \dots, e_k(s)$ with coefficients dependent on the $k\times k$–matrix $\tilde{L}-\tilde{\Lambda}$ and the vector

$$\hat{\phi}(0) + \sum_{l=k+1}^{\infty}\phi_l(0)(\lambda_l\tilde{I}-\tilde{\Lambda}+\tilde{L})^{-1}B_{l-k}.$$

Remark 5. The assertion of Corollary 3 is valid for some infinite matrices L, *e.g.* it suffices to assume that

$$\max_{i=1,\dots,k}\left\{\lambda_i - l_{ii} + \sum_{j,\, j\neq i}^{\infty} |l_{ij}|\right\} < \inf_{i>k}\left\{\lambda_i - l_{ii} - \sum_{j,\, j\neq i}^{\infty} |l_{ij}|\right\}.$$

The localization of eigenvalues is here achieved like in Gershgorin's theorem.

5. **Examples.** In this section we consider biological models with constant coefficients. We admit that models with constant diffusion coefficient allow for efficient computations of eigenvalues. Furthermore, models with constant growth and mortality coefficients can be easily solved by numerical procedures. We discuss two boundary value problems for the differential equation

$$u_t(t,s) = u_{ss}(t,s) + \int_0^1 u(t,y)\,dy \tag{20}$$

with a nonnegative initial function: 1. $c_0 = c_1 = 0$, 2. $c_0 + c_1 > 0$. The equation for the size profile function is as follows

$$v''(s) + \int_0^1 v(y)\,dy = \lambda v(s), \tag{21}$$

where $\lambda > 0$ is chosen so that v is normalized. The constant birth kernel $\beta = 1$ is interpreted as size-uniform loads of new individuals.

Example 1. Consider the easier case $c_0 = c_1 = 0$, *i.e.* equation (20) with the boundary conditions

$$u_{ss}(t,0) - b_0\, u_s(t,0) = 0, \quad u_{ss}(t,1) + b_1\, u_s(t,1) = 0. \tag{22}$$

As in Section 2 it is assumed that $b_0, b_1 > 0$. We introduce the variable $w = v'$ and obtain the system

$$\begin{cases} w''(s) - \lambda w(s) = 0 \\ w'(0) - b_0 w(0) = 0 \\ w'(1) + b_1 w(1) = 0. \end{cases}$$

This problem has a unique zero solution. Thus $v \equiv const.$, hence $\lambda = 1$, which is consistent with our previous considerations. The same transform $w = u'$ leads to an efficient derivation of the eigenfunctions $e_1, e_2, \dots$ Suppose that $f_1, f_2, \dots$ are the eigenfunctions of the operator $-w''$ with the Robin boundary conditions

$$w'(0) - b_0 w(0) = 0, \quad w'(1) + b_1 w(1) = 0.$$

Since $-w''$ is self-adjoint, the eigenfunctions $f_1, f_2, \dots$ are orthogonal with respect to the inner scalar product in L^2. Define $e_1 = const.$ and $e_k = -f_k'/\sqrt{\lambda_k}$ for $k = 2, 3, \dots$ This system is orthogonal with respect to $\langle\cdot,\cdot\rangle$ in $\mathcal{X}$. Since e_1 and β are proportional to 1, this example illustrates Corollary 3, *i.e.* the size profile is constant.

Example 2. Consider the case $c_0 + c_1 > 0$. The assumptions of Corollary 3 are not fulfilled, and the size profile has an infinite Fourier expansion. We examine equation (20) with the boundary conditions

$$u_{ss}(t,0) - u_s(t,0) + u(t,0) = 0, \quad u_{ss}(t,1) + u_s(t,1) = 0. \tag{23}$$

Then the equation of the size profile takes the form (21) with the boundary conditions

$$v''(0) - v'(0) + v(0) = 0, \quad v''(1) + v'(1) = 0. \tag{24}$$

The solution of this problem has the form

$$v(s) = c_1 e^{\sqrt{\lambda} s} + c_2 e^{-\sqrt{\lambda} s} + \frac{1}{\lambda},$$

where the constants c_1, c_2 are derived from (24) and λ is calculated from the equation

$$\sqrt{\lambda} c_1 e^{\sqrt{\lambda}} + \sqrt{\lambda} c_2 (1 - e^{-\sqrt{\lambda}}) = \lambda - 1.$$

The solution of the size-profile equation (21) with the boundary conditions (24) is shown in Fig. 1.

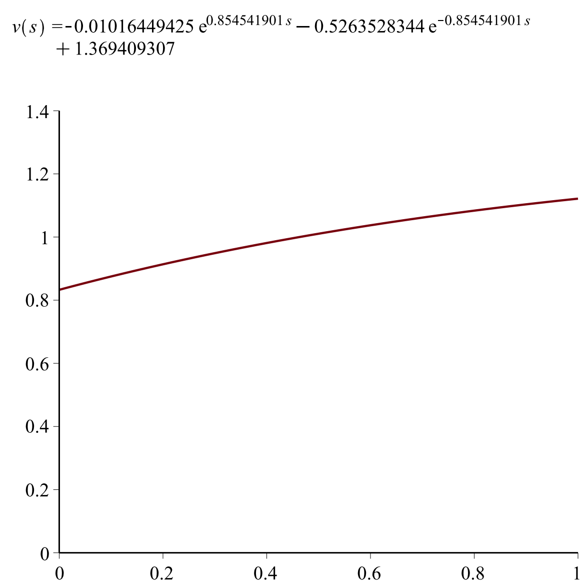

FIGURE 1. Size profile.

We solve the problem (20), (23) by making use of the eigenfunctions $e_1, e_2, \ldots$ The eigenfunctions (see Fig. 2) are of the form $const. \sin(ps + q)$ where

$$q = \frac{k\pi - p}{2} \quad \text{and} \quad \tan\left(\frac{\mathrm{k}\pi - \mathrm{p}}{2}\right) = \frac{\mathrm{p}}{1 - \mathrm{p}^2}.$$

Fig. 3 shows the eigenfunctions of the operator $-u''$ corresponding to the problem (20), (23). It is seen that e_k has $k-1$ zeros. The Fourier series expansion of the function identically equal to 1 is shown in Fig. 4. Our computation is done for e_1, e_2, e_3, e_4, e_5.

Example 3. Consider the problem (20), (22). Let $U = \int_0^1 u(t,y)\,dy$ and $w(t,s) = u_s(t,s)$. With this notation we write the Robin problem

$$\begin{cases} w_t = w_{ss} \\ w_s(t,0) - b_0 w(t,0) = 0 \\ w_s(t,1) + b_1 w(t,1) = 0 \end{cases} \tag{25}$$

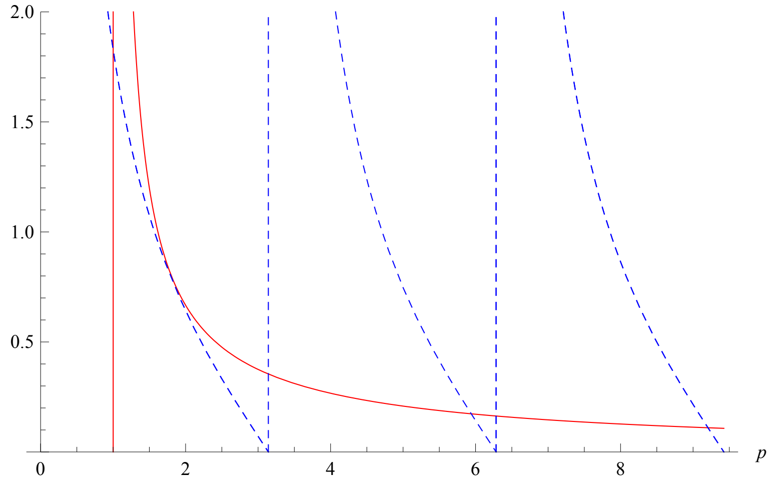

FIGURE 2. Values of p.

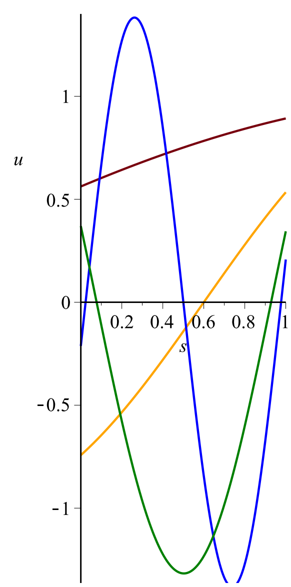

FIGURE 3. Four eigenfunctions of the operator $-u''$.

whose solution can be expressed as the series

$$w(t,s) = \sum_{k=1}^{\infty} c_k e^{-\lambda_k t} \sin(\sqrt{\lambda}_k s + r_k)$$

because the method of separation of variables leads to the components

$$w_k(t,s) = e^{-\lambda_k t} \sin(\sqrt{\lambda}_k s + r_k).$$

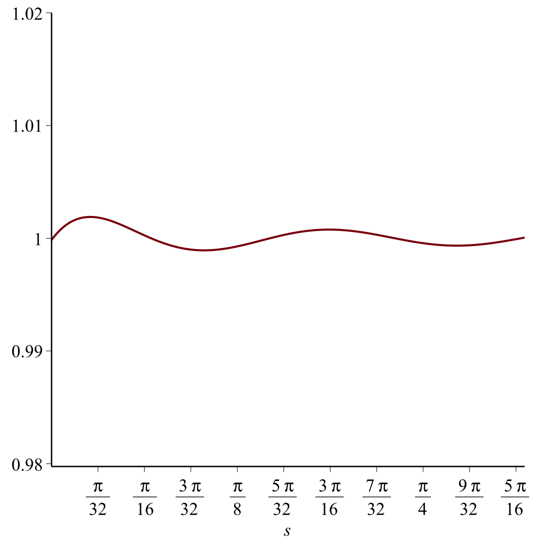

FIGURE 4. Fourier series expansions of the function 1.

Eigenvalues λ_k are positive and depend on the data b_0 and b_1. The solution can be derived by means of elementary ODE's. Denote $U = \int_0^1 u\,dy$ and $u^0 = u(\cdot, 0)$, $u^1 = u(\cdot, 1)$. Furthermore, $w^0 = w(\cdot, 0)$, $w^1 = w(\cdot, 1)$ where $w = u'$ is a solution of (25). Then we get

$$U_t = w_s(t, s)|_0^1 + U = -b_0 w^0 - b_1 w^1 + U.$$

From the dynamical conditions we have

$$u_t^0 = b_0 w^0 + U, \qquad u_t^1 = -b_1 w^1 + U.$$

Since the functions $w(t, s)$ and $U(t)$, $u^0(t)$, $u^1(t)$ can be easily calculated, we get the function $u(t, s)$ as a solution of the Dirichlet boundary-value problem

$$u_t = u_{ss} + U(t), \qquad u(t, 0) = u^0(t), \; u(t, 1) = u^1(t).$$

6. **Conclusions.**

1. Our analysis of the size profile is done for the death rate $\mu = const$. This assumption can be omitted and the whole construction is valid, provided that we represent $-\mu(s) = -\bar{\mu} + (\bar{\mu} - \mu(s))$, $\bar{\mu} = \max \mu$ and replace the coefficients L_{ij} by the following

$$\int_0^m [(\bar{\mu} - \mu(y))M_i(y) + \beta_i(y)]\; e_j(y)\,dy,$$

where $M_i(y)$ are the Fourier coefficients of the Dirac delta function δ_y. More precisely, the idea is as follows: $\bar{\mu} - \mu(s) \geq 0$ is regarded as an additional birth term

$$(\bar{\mu} - \mu(s))u(t, s) = \int_0^m (\bar{\mu} - \mu(y))\delta_y(s)u(t, y)\,dy,$$

where $\delta_y(s) = \sum_k M_k(y)e_k(s)$ is the Fourier expansion of the Dirac delta function δ_y, see Fig. 5.

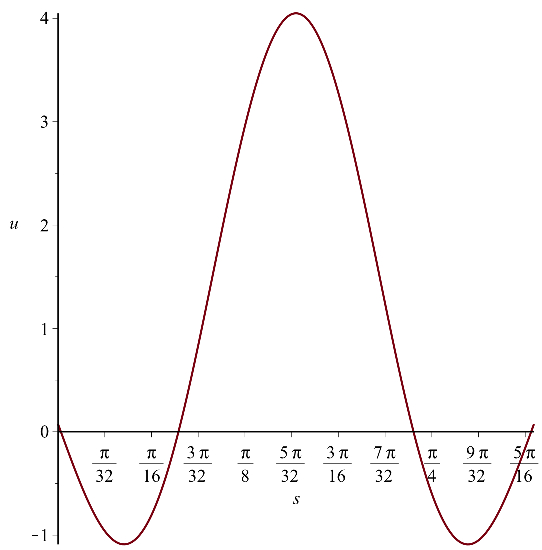

FIGURE 5. Representation of the Dirac delta function by the eigenfunctions $e_1, \dots e_5$.

2. It turns out that if we introduce a new function

$$\bar{u}(t,s) = u(t,s) \cdot \exp\left(-\int_0^s \frac{\gamma(y)}{2d(y)}\,dy\right),$$

then problem (1)–(2) reduces to the form

$$\begin{aligned}
&\bar{u}_t(t,s) = (d(s)\cdot \bar{u}_s(t,s))_s - \bar{\mu}(s)\bar{u}(t,s) + \int_0^s \bar{\beta}(s,y)\bar{u}(t,s)\,dy + \bar{g}(t,s),\\
&(d(s)\cdot \bar{u}_s(t,s))_s\,|_{s=0} - \bar{b}_0\bar{u}_s(t,0) + \bar{c}_0\bar{u}(t,0) = 0,\\
&(d(s)\cdot \bar{u}_s(t,s))_s\,|_{s=m} + \bar{b}_m\bar{u}_s(t,m) + \bar{c}_m\bar{u}(t,m) = 0,
\end{aligned}$$

where the mortality, reproduction and immigration are defined as

$$\begin{aligned}
\bar{\mu}(s) &= \frac{\gamma^2(s)}{4d(s)} + \frac{\gamma'(s)}{2} + \mu(s),\\
\bar{\beta}(s,y) &= \beta(s,y)\cdot \exp\left(-\int_0^y \frac{\gamma(\tilde{y})}{2d(\tilde{y})}\,d\tilde{y}\right),\\
\bar{g}(t,s) &= g(t,s)\cdot \exp\left(-\int_0^s \frac{\gamma(y)}{2d(y)}\,dy\right)
\end{aligned}$$

and

$$\bar{b}_0 = b_0 - \gamma(0), \qquad \bar{c}_0 = c_0 + \frac{\gamma^2(0)}{4d(0)} + \frac{\gamma'(0)}{2} - b_0 \frac{\gamma(0)}{2d(0)},$$
$$\bar{b}_m = b_m + \gamma(m), \qquad \bar{c}_m = c_m + \frac{\gamma^2(m)}{4d(m)} + \frac{\gamma'(m)}{2} + b_m \frac{\gamma(m)}{2d(m)}.$$

The fundamental assumptions of the model ($\bar{b}_0, \bar{b}_m > 0$, $\bar{c}_0, \bar{c}_m \geq 0$) are preserved provided that $b_0 - \gamma(0) > 0$, $b_m + \gamma(m) > 0$ and γ, γ' are sufficiently small at $s = 0, m$. The idea is that the sign of the coefficient of the derivative u_s is positive for $s = 0$ and negative for $s = m$. Thus the flux of this population goes inwards.

3. If any of the vital quantities like growth, diffusion, reproduction and mortality, depend on the density u, then the model (1) becomes nonlinear, see [15, 21]. The dynamics of a size-structured population with coefficients dependent on the unknown function, living in a closed territory is considered in [9]. Our methods, especially Fourier analysis, can be extended to open models ($g \neq 0$). We admit that the PDE model can be solved by modern numerical methods, see [3].

Acknowledgments. We are greatly indebted to Professor A. Bobrowski for his kind remarks and indications at the beginning of our research.

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Received February 04, 2015; Accepted September 21, 2015.

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