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Comparison between two models for multistage age dependent population dynamics (**)

1 - Introduction

Only in recent years the first models describing the time evolution of age dependent populations structured in several stages appear in the literature [5]. In this work we just consider the case in which only two stages are important; we denote with the index a the adult stage, the reproducing one, with the index e the egg stage, which may be thought to be constituted by embryos or eggs or juveniles, in other words by individuals not able to reproduce. We do not consider a possible bisexual distinction.

The individual distribution depends on the own age z for the adults, on the own age x and, possibly, on y for the eggs, as well as on the time t. y is the real age of the mother, or the age she would have if she would be still alive; so y may be greater than z_a, the limit age for adults, and, obviously, if $y < z_a$ then $y = z$. Age and time increase at the same rate, so that the evolution of the numerical density of adults $n_a(z, t)$ obeys the relation

$$\frac{\partial n_a}{\partial t} + \frac{\partial n_a}{\partial z} = -\mu_a(z)\, n_a(z, t) \qquad 0 < z < z_a,\, t > 0$$

$$n_a(0, t) = l_a(n_e, n_a)(t)$$

where $l_a(n_e, n_a)$ is a functional of the distributions n_e, n_a, while the evolution of

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the numerical density of embryos or eggs obeys

$$\frac{\partial n_e}{\partial t} + \frac{\partial n_e}{\partial x} = -\mu(x) n_e(x, t) \qquad 0 < x < x_e, t > 0$$

$$n_e(0, t) = l_e(n_e, n_a)(t)$$

where l_e is a functional of the distributions n_a, n_e, and x_e is the limit age for eggs. So the numerical densities are coupled by the boundary conditions.

In the parameter μ we can distinguish a term due to the natural mortality: μ_e and a term due to the removal caused by the individual passing to the adult stage: γ, so $\mu = \mu_e + \gamma$.

When we want to distinguish the embryos on the basis of the parent age (mother age for semplicity), the equation for the numerical density n_e is

$$\frac{\partial n_e}{\partial t} + \frac{\partial n_e}{\partial x} + \frac{\partial n_e}{\partial y} = -\mu(x, y) n_e(x, y, t) \qquad 0 < x < x_e, x < y < x + z_a, t > 0$$

$$n_e(0, y, t) = L_e(n_e, n_a)(y, t)$$

where L_e is a function of the distributions n_e, n_a.

In this work we study existence, uniqueness, positivity of the solutions by means of the theory of semigroups of linear operators in Banach spaces (here in Lebesgue spaces as L_1). The generators are given by unbounded perturbations (as $\mu \notin L_\infty$ if $x_e < \infty$, $z_a < \infty$) of the streaming operators with respect to the age. The boundary conditions themselves, linking a population of age zero to the entire population in the other stage as in a circle, cause troubles in the simple and direct check of the density of the domain of the generators, this condition being necessary to apply the Hille-Yosida theorem ([1] Th. 4.4, p. 154, [**6**] Th. 3.1, p. 8).

The study of the spectrum allows us to check the existence of persistent distributions in both the models. If $x_e < \infty$, $z_a < \infty$, the spectrum consists only of point spectrum. We note that, assuming μ_a, β, μ_e, and γ to be equal in the two models, the maximum real eigenvalue λ_1 is greater in the first case than in the second. In both cases the asymptotic behaviour of the solutions shows a convergence to a suitable element of the eigenspace associated to λ_1, that is to a multiple of the eigenfunction of λ_1.

2 - The models

Let us simultaneously consider two models of evolution for a population structured in two stages of individuals, each stage being age dependent, and let us carefully examine the spectrum of the linear, closed operators related to the evolution of each system. It is assumed a life-history consisting of two stages: the individuals in the first stage are eggs (juveniles), not able to reproduce; juveniles maturing become adults and can begin to produce eggs. The permanence in each stage is variable and governed by a probability distribution; the maturation rate of eggs is allowed to vary with age, as are the mortality rates of the two stages; eggs production (or conception) is also dependent on mother's age.

The main difference between the two models is that in the second model we allow the possibility that an egg dies as its mother does, and this possibility depends on egg age.

Each model of the time evolution of the distributions of the individuals belonging to the two stages consists of two linear, first order, partial differential equations and corresponding initial and boundary conditions. The independent variables are: the time $t \geqslant 0$, the egg age $x \geqslant 0$, the adult age $z \geqslant 0$ or $y > 0$, according to the two quoted meanings. The dependent variables, whose evolution has to be determined, are the numerical densities of assigned age individuals at a certain time: n_e, n_a. In the second model, as we consider the strict tie existing between mother and offspring, the numerical density of eggs turns out to be also function of mother's age y, with $0 \leqslant x < y < z_a + x$.

The models lead to the following *balance equations* governing egg and adult numerical distributions

M₁

$$\frac{\partial n_e(x,t)}{\partial t} + \frac{\partial n_e(x,t)}{\partial x} + [\mu_e(x) + \gamma(x)]\, n_e(x,t) = 0$$

$$\frac{\partial n_a(z,t)}{\partial t} + \frac{\partial n_a(z,t)}{\partial z} + \mu_a(z)\, n_a(z,t) = 0$$

$$n_e(0,t) = \int_0^{z_a} \beta(z)\, n_a(z,t)\, dz \qquad n_a(0,t) = \int_0^{x_e} \gamma(x)\, n_e(x,t)\, dx$$

$$n_e(x,0) = \psi_e^{(1)}(x) \qquad n_a(z,0) = \psi_a(z).$$

M₂

$$\frac{\partial n_e(x,y,t)}{\partial t} + \frac{\partial n_e(x,y,t)}{\partial x} + \frac{\partial n_e(x,y,t)}{\partial y} + [\varphi(x)\mu_a(y) + \mu_e(x) + \gamma(x)]\, n_e(x,y,t) = 0$$

$$\frac{\partial n_a(z,t)}{\partial t} + \frac{\partial n_a(z,t)}{\partial z} + \mu_a(z)\, n_a(z,t) = 0$$

$$n_e(0,y,t) = \beta(y)\, n_a(y,t) \qquad n_a(0,t) = \int_0^{x_e} \int_0^{z_a + x} \gamma(x)\, n_e(x,z,t)\, dz\, dx$$

$$n_e(x,y,0) = \psi_e^{(2)}(x,y) \qquad n_a(z,0) = \psi_a(z).$$

Having in mind that we wish compare the total number of individuals, we assume $\psi_e^{(1)}(x) = \int_x^{z_a+x} \psi_e^{(2)}(x, y)\,dy$.

The assigned parameters in the problems are the mortality rates of eggs and adults at the specific age: $\mu_e(x)$, $\mu_a(z)$; the maturation rate of eggs at age $x: \gamma(x)$; the egg production rate $\beta(z)$ at adult age z; the probability that an egg of age x dies if its mother does: $\varphi(x)$. This functions are non negative by biological reasons.

We assume that in each stage there exists a limit age: x_e for eggs, z_a for adults. Over these ages no individual can be found. All the vital rates are independent of density and time; they satisfy the following hypotheses:

a. $\varphi, \gamma \in L_\infty(0, x_e)$, $\beta \in L_\infty(0, z_a)$; they are nonnegative almost everywhere. $\overline{\varphi}, \overline{\gamma}, \overline{\beta}$ are their essential suprema.

b. $\mu_e \in L_1(0, x) \quad 0 < x < x_e \qquad \mu_e \geqslant 0$ a.e. in $(0, x_e)$

$\mu_a \in L_1(0, z) \quad 0 < z < z_a \qquad \mu_a \in L_\infty(z_a, z_a + x_e)$

$\mu \geqslant 0$ a.e. in $(0, z_a + x_e)$

$$\lim_{x \to x_e} \int_0^x \mu_e(u)\,du = +\infty \quad x > 0; \qquad \lim_{z \to z_a} \int_0^z \mu_a(u)\,du = +\infty \quad z > 0.$$

The hypothesis **b** assures (see next section) that each solution of the problems M_1 and $M_2 : n^{(i)} = (n_e^{(i)}, n_a^{(i)})$, $i = 1, 2$, has components with compact support, with $0 \leqslant x < x_e$, $0 \leqslant z < z_a$ if $i = 1$, $0 \leqslant x \leqslant y < z_a + x$, $0 \leqslant x < x_e$, $0 \leqslant z < z_a$ if $i = 2$.

Remark. In the second model, we consider $N_e(x, t) = \int_x^{z_a+x} n_e(x, y, t)\,dy$. By formal integration of the first equation of M_2, as

$$\frac{\partial N_e(x, t)}{\partial x} = \int_x^{z_a+x} \frac{\partial n_e(x, z, t)}{\partial x}\,dz + n_e(x, z_a + x, t) - n_e(x, x, t)$$

we obtain

$$\frac{\partial N_e(x,t)}{\partial t} + \frac{\partial N_e(x,t)}{\partial x} + \varphi(x) \int_x^{z_a+x} \mu_a(z)\, n_e(x,z,t)\,dz + [\mu_e(x) + \gamma(x)]\, N_e(x,t) = 0$$

with boundary condition $N_e(0, t) = \int_0^{z_a} \beta(z)\, n_a(z, t)\,dz$. If $\varphi = 0$ a.e. the two models coincide.

3 - Existence and asymptotic behaviours

If we put $T = \{(x, y) | 0 < x < y < x + z_a, x < x_e\}$, the natural Banach spaces in which to study the evolution problems M_1 and M_2, respectively are

$$X = X_1 \times X_2 = L_1((0, x_e); dx) \times L_1((0, z_a); dz)$$

$$Y = Y_1 \times Y_2 = L_1(T; dy\, dx) \times L_1((0, z_a); dz)$$

with norm

$$\|f^{(1)}\|_X = \|f_1^{(1)}\|_{X_1} + \|f_2^{(1)}\|_{X_2} \qquad f^{(1)} \in X$$
$$\|f^{(2)}\|_Y = \|f_1^{(2)}\|_{Y_1} + \|f_2^{(2)}\|_{Y_2} \qquad f^{(2)} \in Y$$

where $\|\cdot\|_{X_k}$, $\|\cdot\|_{Y_k}$, $k = 1, 2$, are the usual L_1-norms in X_k, Y_k.

Let us transform M_1, M_2 in *abstract evolution problems.*

We consider first M_1 and we introduce the following *linear operators*:

$$A_1 : \mathcal{D}(A_1) \subset X \to \mathcal{R}(A_1) \subset X$$

$\mathcal{D}(A_1) = \{f^{(1)} \in X | f_1^{(1)}, f_2^{(1)}$ absolutely continuous with derivative belonging to X_1, X_2 respectively, $f_1^{(1)}(0) = \int_0^{z_a} \beta(z) f_2^{(1)}(z)\, dz$, $f_2^{(1)}(0) = \int_0^{x_e} \gamma(x) f_1^{(1)}(x)\, dx\}$.

A_1 acts on $f^{(1)} \in \mathcal{D}(A_1)$ in the following way

$$A_1 f^{(1)} = -\left(\frac{df_1^{(1)}}{dx}, \frac{df_2^{(1)}}{dz}\right).$$

$$B_1 : \mathcal{D}(B_1) \subset X \to \mathcal{R}(B_1) \subset X$$

$\mathcal{D}(B_1) = \{f^{(1)} \in X | \mu_e f_1^{(1)} \in X_1, \mu_a f_2^{(1)} \in X_2\}$.

B_1 acts on $f^{(1)} \in \mathcal{D}(B_1)$ in the following way

$$B_1 f^{(1)} = -([\mu_e + \gamma] f_1^{(1)}, \mu_a f_2^{(1)}).$$

With regard to problem M_2 we introduce the following *linear operators*:

$$A_2 : \mathcal{D}(A_2) \subset Y \to \mathcal{R}(A_2) \subset Y$$

$\mathcal{D}(A_2) = \{f^{(2)} \in Y | f_1^{(2)}$ absolutely continuous along the direction (1,1) for almost every $(x, y) \in T$ with distributional derivative along the vector (1,1) belonging to Y_1; $f_2^{(2)}$ absolutely continuous with derivative belonging to Y_2; $f_1^{(2)}(0, y) = \beta(y) f_2^{(2)}(y)$, $f_2^{(2)}(0) = \int_0^{x_e} \int_x^{z_a + x} \gamma(x) f_1^{(2)}(x, y)\, dy\, dx\}$.

A_2 acts on $f^{(2)} \in \mathcal{D}(A_2)$ in the following way

$$A_2 f^{(2)} = -\Big(\frac{\partial f_1^{(2)}}{\partial x} + \frac{\partial f_1^{(2)}}{\partial y}, \frac{\mathrm{d} f_2^{(2)}}{\mathrm{d}z}\Big).$$

$$B_2 : \mathcal{D}(B_2) \subset Y \to \mathcal{R}(B_2) \subset Y$$

$\mathcal{D}(B_2) = \{f^{(2)} \in Y \,|\, [\varphi\mu_a + \mu_e] f_1^{(2)} \in Y_1,\ \mu_a f_2^{(2)} \in Y_2\}$.

B_2 acts on $f^{(2)} \in \mathcal{D}(B_2)$ in the following way

$$B_2 f^{(2)} = -([\varphi\mu_a + \mu_e + \gamma] f_1^{(2)}, \mu_a f_2^{(2)}).$$

So we obtain the following *abstract problems* for $i = 1, 2$

$$\text{(1)} \qquad \frac{\mathrm{d} n^{(i)}(t)}{\mathrm{d}t} = (A_i + B_i)\, n^{(i)}(t) \quad t > 0 \qquad n^{(i)}(0) = n_0^{(i)} \in \mathcal{D}(A_i + B_i).$$

We first investigate existence, properties and structure of the resolvent operators $R(\lambda; A_i + B_i) = [\lambda I - (A_i + B_i)]^{-1}$, $i = 1, 2$, that is we consider the equations, with $\lambda \in \boldsymbol{C}$

$$\text{(2)} \qquad [\lambda - (A_i + B_i)]\, n^{(i)} = g^{(i)} \qquad g^{(1)} \in X,\ g^{(2)} \in Y$$

i.e. the systems

$$\text{(2')} \qquad \begin{aligned} &\frac{\mathrm{d} n_e^{(1)}(x)}{\mathrm{d}x} + [\lambda + \mu_e(x) + \gamma(x)]\, n_e^{(1)}(x) = g_e^{(1)}(x) \\ &\frac{\mathrm{d} n_a^{(1)}(z)}{\mathrm{d}z} + [\lambda + \mu_a(z)]\, n_a^{(1)}(z) = g_a^{(1)}(z) \end{aligned}$$

$$\text{(2'')} \qquad \begin{aligned} &\frac{\partial n_e^{(2)}(x,y)}{\partial x} + \frac{\partial n_e^{(2)}(x,y)}{\partial y} + [\lambda + \varphi(x)\mu_a(y) + \mu_e(x) + \gamma(x)]\, n_e^{(2)}(x,y) = g_e^{(2)}(x,y) \\ &\frac{\mathrm{d} n_a^{(2)}(z)}{\mathrm{d}z} + [\lambda + \mu_a(z)]\, n_a^{(2)}(z) = g_a^{(2)}(z) \end{aligned}$$

equipped with boundary conditions. Let us put:

$$\Phi_e^{(1)}(x) = \exp\{-\int_0^x [\mu_e(u) + \gamma(u)]\,\mathrm{d}u\} \qquad \Phi_a(z) = \exp\{-\int_0^z \mu_a(u)\,\mathrm{d}u\}$$

$$\Phi_e^{(2)}(x, y) = \exp\{-\int_0^x [\varphi(u)\mu_a(u + y) + \mu_e(u) + \gamma(u)]\,\mathrm{d}u\}.$$

If $n^{(i)} \in \mathcal{D}(A_i + B_i)$, $n^{(i)} = (n_e^{(i)}, n_a^{(i)})$, $i = 1, 2$, is a solution of (2), then necessarily $n^{(i)}$ satisfies the integral system

$$n^{(i)} = H_\lambda^{(i)} n^{(i)} + G^{(i)}(\lambda) \tag{3}$$

where $H_\lambda^{(i)}$ is the linear operator defined by

$$H_\lambda^{(i)} f^{(i)} = \begin{pmatrix} 0 & H_{ea}^{(i)}(\lambda) \\ H_{ae}^{(i)}(\lambda) & 0 \end{pmatrix} \cdot \begin{pmatrix} f_e^{(i)} \\ f_a^{(i)} \end{pmatrix} \tag{3.I}$$

and

$$\begin{aligned} (H_{ea}^{(1)}(\lambda)\, f_a^{(1)})(x) &= e^{-\lambda x} \Phi_e^{(1)}(x) \int_0^{z_a} \beta(z)\, f_a^{(1)}(z)\,\mathrm{d}z \\ (H_{ae}^{(1)}(\lambda)\, f_e^{(1)})(z) &= e^{-\lambda z} \Phi_a(z) \int_0^{x_e} \gamma(x)\, f_e^{(1)}(x)\,\mathrm{d}x \end{aligned} \tag{3.II}$$

$$\begin{aligned} (H_{ea}^{(2)}(\lambda)\, f_a^{(2)})(x, y) &= e^{-\lambda y} \Phi_e^{(2)}(x, y-x) \beta(y-x)\, f_a^{(2)}(y-x) \\ (H_{ae}^{(2)}(\lambda)\, f_e^{(2)})(z) &= e^{-\lambda z} \Phi_a(z) \int_0^{x_e} \int_x^{z_a + x} \gamma(x)\, f_e^{(2)}(x, y)\,\mathrm{d}y\,\mathrm{d}x \end{aligned} \tag{3.III}$$

and $G^{(i)}(\lambda) = (G_e^{(i)}(\lambda), G_a^{(i)}(\lambda))$, $i = 1, 2$, with

$$\begin{aligned} G_e^{(1)}(x; \lambda) &= \int_0^x e^{-\lambda(x - x')} \frac{\Phi_e^{(1)}(x)}{\Phi_e^{(1)}(x')}\, g_e^{(1)}(x')\,\mathrm{d}x' \\ G_a^{(1)}(z; \lambda) &= \int_0^z e^{-\lambda(z - z')} \frac{\Phi_a(z)}{\Phi_a(z')}\, g_a^{(1)}(z')\,\mathrm{d}z' \end{aligned} \tag{3.IV}$$

$$\begin{aligned} G_e^{(2)}(x, y; \lambda) &= \int_0^x e^{-\lambda(x - x')} \frac{\Phi_e^{(2)}(x, y - x + x')}{\Phi_e^{(2)}(x', y - x + x')}\, g_e^{(2)}(x', y - x + x')\,\mathrm{d}x' \\ G_a^{(2)}(z; \lambda) &= \int_0^z e^{-\lambda(z - z')} \frac{\Phi_a(z)}{\Phi_a(z')}\, g_a^{(2)}(z')\,\mathrm{d}z'\,. \end{aligned} \tag{3.V}$$

Lemma 1. *$H_\lambda^{(i)}$ is a bounded linear operator, with domain the whole space (X if $i = 1$, Y if $i = 2$) and range in $\mathcal{D}(A_i + B_i)$, for all $\lambda \in \mathbf{C}$, $i = 1, 2$*

$$H_\lambda^{(1)} : X \to \mathcal{D}(A_1 + B_1) \quad \forall \lambda \in \mathbf{C}, \qquad H_\lambda^{(2)} : Y \to \mathcal{D}(A_2 + B_2) \quad \forall \lambda \in \mathbf{C}\,.$$

Furthermore, $H_\lambda^{(i)}$ is positive if $\lambda \in \mathbf{R}$.

Proof. $\forall \lambda \in \boldsymbol{C}$ we have

$$H_{ea}^{(1)}(\lambda): X_2 \to X_1 \qquad H_{ea}^{(2)}(\lambda): Y_2 \to Y_1$$
$$H_{ae}^{(2)}(\lambda): X_1 \to X_2 \qquad H_{ae}^{(2)}(\lambda): Y_1 \to Y_2 .$$

It is easily seen that for $\lambda \in \boldsymbol{R}$, $H_{ea}^{(i)}(\lambda)$ and $H_{ae}^{(i)}(\lambda)$ are positive bounded operators and therefore $H_\lambda^{(i)}$ too is positive and bounded with domain the whole space X if $i=1$, Y if $i=2$, for all $\lambda \in \boldsymbol{R}$.

Obviously, $H_{ea}^{(1)}(\lambda) f_a^{(1)}$, $H_{ae}^{(i)}(\lambda) f_e^{(i)}$, $i=1,2$, have ordinary derivatives with respect to their arguments almost everywhere; the function $H_{ea}^{(2)}(\lambda) f_a^{(2)}$, is differentiable too, in ordinary sense, along the direction $(1,1)$ a.e., and

$$\left(\frac{\partial}{\partial x}+\frac{\partial}{\partial y}\right)(H_{ea}^{(2)}(\lambda) f_a^{(2)})(x,y) = -[\lambda+\varphi(x)\mu_a(y)+\mu_e(x)+\gamma(x)](H_{ea}^{(2)}(\lambda) f_a^{(2)})(x,y) .$$

To see this it is sufficient to consider the variable change

$$\xi = \frac{\sqrt{2}}{2}(y+x), \qquad \eta = \frac{\sqrt{2}}{2}(y-x)$$

corresponding to a $\frac{\pi}{2}$ radians anticlockwise rotation of the cartesian axes.

The boundary conditions defining the domains $\mathcal{D}(A_i)$ are satisfied, as it is immediate to verify, $\forall f^{(1)} \in X$, $\forall f^{(2)} \in Y$. It is now sufficient to prove that:

$$\mu_e (H_{ea}^{(1)}(\lambda) f_a^{(1)}) \in X_1 , \quad \mu_a (H_{ae}^{(i)}(\lambda) f_e^{(i)}) \in X_2 = Y_2, \quad (\mu_e + \varphi\mu_a)(H_{ea}^{(2)}(\lambda) f_a^{(2)}) \in Y_1$$

for any λ of $\boldsymbol{C}$, to be able to state that

$$H_\lambda^{(i)} f^{(i)} \in \mathcal{D}(A_i + B_i) = \mathcal{D}(A_i) \cap \mathcal{D}(B_i) \qquad i=1,2, \quad \forall f^{(1)} \in X, \quad \forall f^{(2)} \in Y .$$

If $\lambda \in \boldsymbol{R}$ it results

$$\int_0^{x_e} [\gamma(x) + \mu_e(x)] \, |(H_{ea}^{(1)}(\lambda) f_a^{(1)})(x)| \, dx \leq \bar{\beta} (\max_{x \in [0, x_e]} e^{-\lambda x}) \|f_a^{(1)}\|_2$$

as $\Phi_e^{(1)}(x_e) = 0$ because of hypothesis **b** on mortality rate μ_e. In the same way, as $\Phi_e^{(2)}(x_e, y) = 0$, $\Phi_a(z_a) = 0$, we have:

$$\int_0^{x_e} \int_x^{z_a + x} [\varphi(x)\mu_a(y) + \mu_e(x) + \gamma(x)]\, |H_{ea}^{(2)}(\lambda) f_a^{(2)}|(x, y)\, dy\, dx \leqslant \overline{\beta}(\max_{x \in [0, x_e]} e^{-\lambda x}) \|f_a^{(2)}\|_2$$

$$\int_0^{z_a} \mu_a(z)\, |H_{ae}^{(i)}(\lambda) f_e^{(i)}|(z)\, dz \leqslant \overline{\gamma}(\max_{z \in [0, z_a]} e^{-\lambda z}) \|f_e^{(i)}\|_1 \qquad i = 1, 2.$$

It results from that: $H_\lambda^{(i)} f^{(i)} \in \mathcal{D}(A_i + B_i)$, $\forall f^{(1)} \in X$, $\forall f^{(2)} \in Y$, $\forall \lambda \in \boldsymbol{R}$. Taking into account that each $X_i(Y_i)$ is the complexification of a real Lebesgue space and that $\forall f^{(1)} \in X (\forall f^{(2)} \in Y)$ we may split: $f_j^{(l)} = f_{j1}^{(l)} - f_{j2}^{(l)} + i f_{j3}^{(l)} - i f_{j4}^{(l)}$, where: $f_{jk}^{(l)} \geqslant 0$, $j = e, a$, $k = 1, 2, 3, 4$; $l = 1, 2$, we can also state

$$H_\lambda^{(l)} f^{(l)} \in \mathcal{D}(A_i + B_i) \qquad \forall f^{(1)} \in X, \ \forall f^{(2)} \in Y, \ \forall \lambda \in \boldsymbol{C}.$$

Lemma 2. *If $g^{(1)} \in X$, ($g^{(2)} \in Y$) then: $G^{(1)}(\lambda) \in X$, ($G^{(2)}(\lambda) \in Y$), with differentiable components, a.e. so that*

$$G^{(i)}(\lambda) + H_\lambda^{(i)} f^{(i)} \in \mathcal{D}(A_i + B_i) \qquad \forall \lambda \in \boldsymbol{C};\ i = 1, 2.$$

Thus problems (2) and (3) are equivalent.

The easy proof is omitted.

Now we solve the problem, equivalent to (3), obtained by obvious substitutions

$$(4) \qquad \begin{aligned} n_e^{(i)} &= H_{ea}^{(i)}(\lambda) H_{ae}^{(i)}(\lambda) n_e^{(i)} + H_{ea}^{(i)}(\lambda) G_a^{(i)}(\lambda) + G_e^{(i)}(\lambda) \\ n_a^{(i)} &= H_{ae}^{(i)}(\lambda) H_{ea}^{(i)}(\lambda) n_a^{(i)} + H_{ae}^{(i)}(\lambda) G_e^{(i)}(\lambda) + G_a^{(i)}(\lambda). \end{aligned}$$

We can note that it is sufficient that one of the two equations of system (4) be solvable, in order to be solvable the other too; for instance, the first equation of (4) has an unique solution if and only if $0 \notin P_\sigma(I - H_{ea}^{(i)}(\lambda) H_{ae}^{(i)}(\lambda))$ i.e. 1 is not an eigenvalue of the operator $H_{ea}^{(i)}(\lambda) H_{ae}^{(i)}(\lambda)$.

Lemma 3. *The linear operators $H_{ea}^{(i)}(\lambda) H_{ae}^{(i)}(\lambda)$, $H_{ae}^{(i)}(\lambda) H_{ea}^{(i)}(\lambda)$ are Fredholm integral operators with degenerate kernel (and so compact operators), well defined for all $\lambda \in \boldsymbol{C}$ with domain X_1, X_2, respectively if $i = 1$, Y_1, Y_2, if $i = 2$. They are positive if $\lambda \in \boldsymbol{R}$. If they are not null operators, as it happens if and only if the following assumptions are fulfilled:*

c. *$\gamma > 0$ in a set with positive measure in $(0, x_e)$*

d. *$\beta > 0$ in a set with positive measure in $(0, z_a)$,*

then they have only one not null eigenvalue $\sigma^{(i)}(\lambda)$, $i = 1, 2$, depending on λ, the same for all two the operators.

Proof. We omit the dependence of the operators on λ for sake of semplicity. These four operators are positive for $\lambda \in \mathbf{R}$. Let us consider, for example, the positive operator $H_{ea}^{(1)} H_{ae}^{(1)}$ and let us determine its spectrum; first, we note that the conditions **c**, **d**, are necessary and sufficient in order to have this operator not zero in X_1. They are necessary and sufficient in order the other three operators are not null. With these assumptions let us solve the following equation, with $p_e \in X_1$

$$[\sigma^{(1)} I - H_{ea}^{(1)} H_{ae}^{(1)}] p_e(x) = 0 \qquad \text{i.e.:}$$

$$\sigma^{(1)} p_e(x) = e^{-\lambda x} \Phi_e^{(1)}(x) \int_0^{z_a} \beta(z) \Phi_a(z) e^{-\lambda z} \, dz \int_0^{x_e} \gamma(x) p_e(x) \, dx = e^{-\lambda x} \Phi_e^{(1)}(x) c_1 c_2 .$$

The meaning of the factors c_1, c_2 is clear; $c_1 \neq 0$ because of the assumptions done. Let us suppose $c_2 \neq 0$, i.e. we suppose that exists $p_e \in X_1$ such that $\int_0^{x_e} \gamma(x) p_e(x) \, dx \neq 0$. If $c_2 \neq 0$ the term on the right hand is not zero, so that it must be $\sigma^{(1)} \neq 0$. By substitution we obtain

$$c_1 c_2 e^{-\lambda x} \Phi_e^{(1)}(x) = c_1 e^{-\lambda x} \Phi_e^{(1)}(x) \int_0^{x_e} \gamma(x) \frac{c_1 c_2}{\sigma^{(1)}} e^{-\lambda x} \Phi_e^{(1)}(x) \, dx .$$

So it necessarily results

$$\sigma^{(1)} = \int_0^{z_a} \beta(z) \Phi_a(z) e^{-\lambda z} \, dz \cdot \int_0^{x_e} \gamma(x) \Phi_e^{(1)}(x) e^{-\lambda x} \, dx > 0 .$$

This is the only eigenvalue not zero; the corresponding eigenfunction is, but for a factor, $p_e(x) = e^{-\lambda x} \Phi_e^{(1)}(x)$. It results: $c_2 = c_2(p_e) = \int_0^{x_e} \gamma(x) e^{-\lambda x} \Phi_e^{(1)}(x) \, dx > 0$ because of the assumption **c**, showing that really this unique not zero eigenvalue exists. By means of similar arguments, we can prove that the operator $H_{ae}^{(1)} H_{ea}^{(1)}$ too has $\sigma^{(1)}$ as unique not null eigenvalue, with eigenfunction $p_a(z) = e^{-\lambda z} \Phi_a(z)$, but for a factor.

The operators $H_{ae}^{(2)} H_{ea}^{(2)}$, $H_{ea}^{(2)} H_{ae}^{(2)}$ too have the same not null, positive eigenvalue, that is unique

$$\sigma^{(2)} = \int_0^{x_e} \int_x^{z_a + x} \gamma(x) e^{-\lambda y} \Phi_e^{(2)}(x, y - x) \beta(y - x) \Phi_a(y - x) \, dy \, dx$$

with eigenfunctions, respectively:

$$q_e(x, y) = e^{-\lambda y} \Phi_e^{(2)}(x, y - x) \beta(y - x) \Phi_a(y) \qquad q_a(z) = e^{-\lambda z} \Phi_a(z)$$

but for a factor.

Remark. We have the following relation between the eigenvalues $\sigma^{(i)}(\lambda)$ of $H_{ea}^{(i)}(\lambda) H_{ae}^{(i)}(\lambda)$, $i = 1, 2$

$$\sigma^{(2)}(\lambda) \leqslant \sigma^{(1)}(\lambda) \qquad \forall \lambda \in \boldsymbol{R}.$$

In fact, if we consider $\sigma^{(2)}(\lambda)$, putting $\eta = y - x$, we have

$$\sigma^{(2)}(\lambda) \leqslant \int_0^{x_e} \gamma(x) \Phi_e^{(1)}(x) e^{-\lambda x} \, dx \int_0^{z_a} \beta(\eta) \Phi_a(\eta) e^{-\lambda \eta} \, d\eta = \sigma^{(1)}(\lambda).$$

If the integral operators in Lemma 3 are not null, then the eigenfunctions defined in the proof are the components of the eigenfuncions $p \in X$, $q \in Y$ corresponding to the eigenvalue 1 of $H_\lambda^{(i)}$, $i = 1, 2$ respectively, if the numerical factors are suitably chosen. Indeed $H_\lambda^{(1)}$ has eigenvalue

$$\varrho^{(1)}(\lambda) = \sqrt{\int_0^{z_a} \beta(z) \Phi_a(z) e^{-\lambda z} \, dz} \cdot \sqrt{\int_0^{x_e} \gamma(x) \Phi_e^{(1)}(x) e^{-\lambda x} \, dx}$$

with eigenvector: $p = p(\varrho^{(1)}) = (p_e, p_a)$, where:

$$p_e(x) = b \, \Phi_e^{(1)}(x) e^{-\lambda x}$$

$$p_a(z) = b \, \Phi_a(z) e^{-\lambda z} \Big(\int_0^{x_e} \gamma(x) \Phi_e^{(1)}(x) e^{-\lambda x} \, dx \Big)^{\frac{1}{2}} \cdot \Big(\int_0^{z_a} \beta(z) \Phi_a(z) e^{-\lambda z} \, dz \Big)^{-\frac{1}{2}}$$

and $H_\lambda^{(2)}$ has eigenvalue

$$\varrho^{(2)}(\lambda) = \sqrt{\int_0^{x_e} \int_x^{z_a + x} \gamma(x)\, e^{-\lambda y}\, \Phi_e^{(2)}(x, y - x)\, \beta(y - x)\, \Phi_a(y - x)\, \mathrm{d}y\, \mathrm{d}x}$$

with eigenvector: $q = q(\varrho^{(2)}) = (q_e, q_a)$, where

$$q_e(x, y) = b\, \Phi_e^{(2)}(x, y - x)\, e^{-\lambda y} \beta(y - x)\, \Phi_a(y - x),$$

$$q_a(z) = b e^{-\lambda z}\, \Phi_a(z) \Big(\int_0^{x_e} \int_x^{z_a + x} \gamma(x) e^{-\lambda y}\, \Phi_e^{(2)}(x, y - x) \beta(y - x)\, \Phi_a(y - x)\, \mathrm{d}y\, \mathrm{d}x \Big)^{\frac{1}{2}}$$

with the constant $b \neq 0$, arbitrary. If the eigenvalue $\varrho^{(i)} = 1$ then we have the following couples:

$$(5') \qquad p_e(x) = b e^{-\lambda x}\, \Phi_e^{(1)}(x) \qquad\qquad p_a(z) = b e^{-\lambda z}\, \Phi_a(z) \int_0^{x_e} \gamma(x) \Phi_e^{(1)}(x)\, e^{-\lambda x}.$$

$$(5'') \qquad \begin{aligned} q_e(x, y) &= b e^{-\lambda y}\, \Phi_e^{(2)}(x, y - x)\, \beta(y - x)\, \Phi_a(y - x) \\ q_a(z) &= b e^{-\lambda z}\, \Phi_a(z) \int_0^{x_e} \int_x^{z_a + x} \gamma(x) e^{-\lambda y}\, \Phi_e^{(2)}(x, y - x) \beta(y - x)\, \Phi_a(y - x)\, \mathrm{d}y\, \mathrm{d}x \\ &= b e^{-\lambda z}\, \Phi_a(z). \end{aligned}$$

In other words: $p \in \mathcal{D}(A_1 + B_1) \subset X$, $(q \in \mathcal{D}(A_2 + B_2) \subset Y)$ is an eigenfunction associated to the eigenvalue $\lambda \in \boldsymbol{C}$ of the operator $(A_1 + B_1)$ $((A_2 + B_2))$ if and only if $p(q)$ has the form (5′), ((5″)), i.e. $\lambda \in \boldsymbol{C}$ is eigenvalue of $(A_i + B_i)$ if and only if one of the integral operators above defined as functions of λ, has 1 as eigenvalue.

From the preceding results we easily deduce

Theorem 4. *If the functions γ, β satisfy the hypotheses* **c**, **d**, *of Lemma* 3, *then $\lambda \in \boldsymbol{C}$ is an eigenvalue of the operator $(A_i + B_i)$ if and only if: $\sigma^{(i)}(\lambda) = 1$, $i = 1, 2$. On the contrary, even if only one of the two hypotheses is not satisfied, the operator $(A_i + B_i)$ has no eigenvalues.*

Now, we put $\Delta^{(i)}(\lambda) = 1 - \sigma^{(i)}(\lambda)$, $i = 1, 2$. The equation

$$(6) \qquad \Delta^{(i)}(\lambda) = 0,$$

is said characteristic equation. We can define:

$$k_e^{(1)}(x) = \gamma(x)\,\Phi_e^{(1)}(x) \qquad\qquad k_a(z) = \beta(z)\,\Phi_a(z)$$

$$k_e^{(2)}(y) = \int_0^y \gamma(y)\,\Phi_e^{(2)}(x, y-x)\,\beta(y-x)\,\Phi_a(y-x)\,\mathrm{d}x$$

with $k_e^{(2)}(y) = 0$ if $y \geqslant x_e$ being $\Phi_e^{(2)}(x_e, y) = 0$.

Because of the hypotheses on the mortality rates μ_e, μ_a, it results that k_a has compact support in $[0, z_a]$, $k_e^{(i)}$ $i = 1, 2$ have compact support in $[0, x_e]$ and so are well-defined their Laplace transforms. It results

$$\sigma^{(1)}(\lambda) = \bar{k}_a(\lambda)\,\bar{k}_e^{(1)}(\lambda) \qquad\qquad \sigma^{(2)}(\lambda) = \bar{k}_e^{(2)}(\lambda)$$

where the over-bar denotes Laplace transforms. As $k_e^{(i)}$, k_a have compact supports, they are of exponential order $-\infty$, and $\bar{k}_e^{(i)}(\lambda)$, $\bar{k}_a(\lambda)$ are entire functions $\forall\lambda \in \boldsymbol{C}$. For λ on the real axis, all three transforms are strictly decreasing functions of λ, which approach 0 as $\lambda \to +\infty$ and approach $+\infty$ as $\lambda \to -\infty$; it follows that equation (6) has an unique real root $\lambda = \lambda_1^{(i)}$, $i = 1, 2$; $\lambda_1^{(i)}$ is called the intrinsic growth constant. On the other hand, if $\lambda_2^{(i)} \in \boldsymbol{C}$ is another root of (6), we have

$$1 = \bar{k}_e^{(1)}(\lambda_2^{(1)})\,\bar{k}_a(\lambda_2^{(1)}) < \bar{k}_e^{(1)}(\mathrm{Re}\ \lambda_2^{(1)})\,\bar{k}_a(\mathrm{Re}\ \lambda_2^{(1)})$$
$$1 = \bar{k}_e^{(2)}(\lambda_2^{(2)}) < \bar{k}_e^{(2)}(\mathrm{Re}\ \lambda_2^{(2)}).$$

Because of the strictly decreasing behaviour of $\bar{k}_e^{(i)}(\lambda)$, $\bar{k}_a(\lambda)$, as functions of $\lambda \in \boldsymbol{R}$, it follows that Re $\lambda_2^{(i)} < \lambda_1^{(i)}$, $i = 1, 2$, $\forall\lambda_2^{(i)} \in \boldsymbol{C}$, $\lambda_2^{(i)}$ root of (6). So the real root $\lambda_1^{(i)}$ not only is unique real, but is grater than the real part of any other root. Further, since $\Delta^{(i)}(\lambda)$ is holomorphic, its zeros cannot accumulate in any bounded region, i.e. $P_\sigma(A_i + B_i)$ consists of isolated points, $i = 1, 2$.

Since, as a function of $\lambda \in \boldsymbol{R}$, $\Delta^{(i)}(\lambda)$ is increasing from $-\infty$ to 1, it follows that the sign of the unique real root $\lambda_1^{(i)}$ is that of $-\Delta^{(i)}(0)$, $i = 1, 2$.

Remark. As $\sigma^{(2)}(\lambda) \leqslant \sigma^{(1)}(\lambda)$, $\lambda \in \boldsymbol{R}$, it results $\lambda_1^{(1)} \geqslant \lambda_1^{(2)}$, i.e. the intrinsic growth constant in a population whose dynamics is described by model M_1 is always greater or equal than that in a population described by M_2.

Let us go back to problems (2) and (3). Since

$$P_\sigma(A_i + B_i) \subset \{\lambda \in \boldsymbol{C}: \mathrm{Re}\ \lambda \leqslant \lambda_1^{(i)}\} \qquad i = 1, 2$$

and

$$G^{(i)}(\lambda) + H_\lambda^{(i)} f^{(i)} \in \mathcal{D}(A_i + B_i), \qquad \forall \lambda \in C;\ \ \forall f^{(1)}, g^{(1)} \in X,\ \ \forall f^{(2)}, g^{(2)} \in Y$$

we can assert that problem (3) has an unique solution in $X(Y)$ $\forall g^{(1)} \in X$, $(\forall g^{(2)} \in Y)$, $\forall \lambda \in C$ such that $\Delta^{(i)}(\lambda) \neq 0$, $i = 1, 2$. We can summarize this fact in

Theorem 5. *For* $i = 1, 2$, $\varrho(A_i + B_i) = \{\lambda \in C : \Delta^{(i)}(\lambda) \neq 0\}$ *and the spectrum of the operator* $(A_i + B_i)$ *contains only eigenvalues.*

Under the hypothesis: $\operatorname{Re} \lambda > \lambda_1$, we can explicitly determine the solution of the system of integral equations (4) and so of (2). For example, if $i = 1$, let us consider the operator $H_{ea}^{(1)}(\lambda) H_{ae}^{(1)}(\lambda)$. As $\lambda \notin P_\sigma(A_1 + B_1)$, and so $\Delta^{(1)}(\lambda) \neq 0$, the operator $I - H_{ea}^{(1)}(\lambda) H_{ae}^{(1)}(\lambda)$ has an inverse that is

$$(I - H_{ea}^{(1)}(\lambda) H_{ae}^{(1)}(\lambda))^{-1} = \sum_{k=0}^{\infty} (H_{ea}^{(1)}(\lambda) H_{ae}^{(1)}(\lambda))^k .$$

By computation of the subsequent iterates we obtain the solution of the first equation of (4) with $i = 1$, which is given by

$$n_e^{(1)}(x) = G_e^{(1)}(x; \lambda) + \frac{\bar{k}_a(\lambda)}{\Delta^{(1)}(\lambda)}\, e^{-\lambda x}\, \Phi_e^{(1)}(x) \int_0^{x_e} \gamma(x)\, G_e^{(1)}(x; \lambda)\, dx$$
$$+ \frac{1}{\Delta^{(1)}(\lambda)}\, e^{-\lambda x}\, \Phi_e^{(1)}(x) \int_0^{z_a} \beta(z)\, G_a^{(1)}(z; \lambda)\, dz .$$

Because of the equivalence of problems (2) and (4), $n_e^{(1)}$ is solution of the first equation of system (2′) $\forall g^{(1)} \in X$ and, in particular, $\|n_e^{(1)}\|_1 < \infty$. We can go on in the same way to determine the solution of the second equation of (2′), or we can determine $n_a^{(1)}$ by substitution in (4). We choose this last method. We have

$$n_a^{(1)}(z) = G_a^{(1)}(z; \lambda) + \frac{\bar{k}_e^{(1)}(\lambda)}{\Delta^{(1)}(\lambda)}\, e^{-\lambda z}\, \Phi_a(z) \int_0^{z_a} \beta(z)\, G_a^{(1)}(z; \lambda)\, dz$$
$$+ \frac{1}{\Delta^{(1)}(\lambda)}\, e^{-\lambda z}\, \Phi_a(z) \int_0^{x_e} \gamma(x)\, G_e^{(1)}(x; \lambda)\, dx .$$

Proceeding in the same way, we can calculate the solution of problem (2) if $i=2$. We obtain the function $n^{(2)}=(n_e^{(2)}, n_a^{(2)})$, with components:

$$n_e^{(2)}(x, y) = G_e^{(2)}(x, y; \lambda) + \frac{1}{\Delta^{(2)}(\lambda)} e^{-\lambda y} \Phi_e^{(2)}(x, y-x)\beta(y-x)\Phi_a(y-x) \cdot$$

$$\cdot \int_0^{x_e}\int_x^{z_a+x} \gamma(x) G_e^{(2)}(x, y; \lambda)\, dy\, dx + e^{-\lambda x}\Phi_e^{(2)}(x, y-x)\beta(y-x) G_a^{(2)}(y; \lambda)$$

$$+ \frac{1}{\Delta^{(2)}(\lambda)} e^{-\lambda y}\Phi_e^{(2)}(x, y-x)\beta(y-x)\Phi_a(y-x) \cdot$$

$$\cdot \int_0^{x_e}\int_x^{z_a+x} \gamma(x) e^{-\lambda x}\Phi_e^{(2)}(x, y-x)\beta(y-x) G_a^{(2)}(y-x; \lambda)\, dy\, dx .$$

$$n_a^{(2)}(z) = G_a^{(2)}(z; \lambda) + \frac{1}{\Delta^{(2)}(\lambda)} e^{-\lambda z}\Phi_a(z) \int_0^{x_e}\int_x^{z_a+x} \gamma(x) G_e^{(2)}(x, y; \lambda)\, dy\, dx$$

$$+ \frac{1}{\Delta^{(2)}(\lambda)} e^{-\lambda z}\Phi_a(z) \int_0^{x_e}\int_x^{z_a+x} \gamma(x) e^{-\lambda x}\Phi_e^{(2)}(x, y-x)\beta(y-x) G_a^{(2)}(y-x; \lambda) dy\, dx .$$

We remark that, if $\lambda \in \mathbf{R}$, $\lambda > \lambda_1^{(i)}$, then the resolvent operator $[\lambda I - (A_i + B_i)]^{-1}$, is a positive operator. We can estimate $\|R(\lambda; A_i + B_i)\|$ by using this property; we consider $g^{(1)} \in X^+$, the positive cone of X, $g^{(2)} \in Y^+$, and $n^{(i)}$ solution of (2), i.e.: $n^{(i)} = R(\lambda; A_i + B_i) g^{(i)}$, under the hypothesis $\lambda > \lambda^{(i)}$. By integration of systems (2′) and (2″) with respect to the age variables, taking into account the boundary conditions, we obtain

$$\lambda \|n^{(1)}\|_X + \mathrm{m}^{(1)}\|n^{(1)}\|_X \leqslant \|g^{(1)}\|_X \qquad \lambda\|n^{(2)}\|_Y + \mathrm{m}^{(2)}\|n^{(2)}\|_Y \leqslant \|g^{(2)}\|_Y$$

where $$\mathrm{m}^{(1)} = \min\{\operatorname*{ess\,inf}_{x \in (0, x_e)} \mu_e(x), \operatorname*{ess\,inf}_{z \in (0, z_a)} [\mu_a(z) - \beta(z)]\},$$

and $$\mathrm{m}^{(2)} = \min\{\operatorname*{ess\,inf}_{(x, y) \in T} [\varphi(x)\mu_a(y) + \mu_e(x)], \operatorname*{ess\,inf}_{z \in (0, z_a)} [\mu_a(z) - \beta(z)]\}.$$

Note that, because of the non negativity of the known parameters of the problem, it results $\mathrm{m}^{(1)} \leqslant \mathrm{m}^{(2)}$. Furthermore: $-\mathrm{m}^{(i)} > \lambda^{(i)}$, $i = 1, 2$, as $\Delta^{(i)}(-\mathrm{m}^{(i)}) > 0$. In fact, for example

$$\bar{k}_e^{(1)}(-\mathrm{m}^{(1)}) = \int_0^{x_e} \gamma(x)\, \Phi_e^{(1)}(x)\, e^{\mathrm{m}^{(1)}x}\, \mathrm{d}x = \int_0^{x_e} \gamma(x)\, e^{-\int_0^x [\gamma(u) + \mu_e(u) - \mathrm{m}^{(1)}]\mathrm{d}u}\, \mathrm{d}x$$

$$\leqslant \int_0^{x_e} \gamma(x)\, e^{-\int_0^x \varphi(u)\mathrm{d}u}\, \mathrm{d}x = 1 - e^{-\int_0^{x_e} \gamma(u)\mathrm{d}u} < 1$$

if the hypothesis **c** of Lemma 3 is fullfilled.

In this way we have obtained an extimate of $\|R(\lambda; A_i + B_i)\|$ useful to the application of the Hille-Yosida theorem [1], [6]: if $\lambda > -\mathrm{m}^{(i)}$, $\lambda \in \boldsymbol{R}$ then $\lambda \in \varrho(A_i + B_i)$ and $\|R(\lambda; A_i + B_i)\| \leqslant \dfrac{1}{\lambda + \mathrm{m}^{(i)}}$, $i = 1, 2$.

Note that $-\mathrm{m}^{(i)}$ may be positive; in particular this happens if we have

$$\operatorname*{ess\,inf}_{z \in (0, z_a)} [\mu_a(z) - \beta(z)] < 0$$

corresponding to a population in which the birth rate per capita is greater then the mortality rate in adult stage, at least in a neighbourhood of a suitable age.

To apply the Hille-Yosida theorem, we have to prove that $\mathcal{D}(A_i + B_i)$ is dense in X if $i = 1$, in Y if $i = 2$.

Lemma 6. *$\mathcal{D}(A_i + B_i)$ is dense,* $i = 1, 2$.

Proof. Let $(A_i + B_i)_0$ the operator with *non reentry* boundary conditions, defined starting from $(A_i + B_i)$, $i = 1, 2$, i.e. with γ, $\beta = 0$ a.e. in their domain. It is known that $(A_i + B_i)_0$ is the generator of a strongly continuous semigroup and that, in particular, its domain is dense in X if $i = 1$, in Y if $i = 2$.

Let $R(\lambda; (A_i + B_i)_0)$ be the resolvent operator of $(A_i + B_i)_0$, with $\lambda \in \boldsymbol{C}$ as $\sigma(A_i + B_i)_0 = \emptyset$ because of Lemma 4; if $\lambda > \lambda_1^{(i)}$ we can consider $R(\lambda; (A_i + B_i))$ and we note that it is possible to write it as

$$R(\lambda; (A_i + B_i))\, g^{(i)} = R(\lambda; (A_i + B_i)_0)\, g^{(i)} + M^{(i)}(\lambda)\, g^{(i)}$$

$\forall \lambda > \lambda_1^{(i)}$, $\forall g^{(1)} \in X$, $\forall g^{(2)} \in Y$, $i = 1, 2$, where $M^{(i)}$ is a suitable linear operator, whose components act as (for $i = 1$)

$$(M^{(1)}(\lambda) g^{(1)})_e(x) = \frac{\bar{k}_a(\lambda)}{\Delta^{(1)}(\lambda)} e^{-\lambda x} \Phi_e^{(1)}(x) \int_0^{x_e} \gamma(x) G_e^{(1)}(x; \lambda) \, dx$$

$$+ \frac{1}{\Delta^{(1)}(\lambda)} e^{-\lambda x} \Phi_e^{(1)}(x) \int_0^{z_a} \beta(z) G_a^{(1)}(z; \lambda) \, dz$$

$$(M^{(1)}(\lambda) g^{(1)})_a(z) = \frac{\bar{k}_e^{(1)}(\lambda)}{\Delta^{(1)}(\lambda)} e^{-\lambda z} \Phi_a(z) \int_0^{z_a} \beta(z) G_a^{(1)}(z; \lambda) \, dz$$

$$+ \frac{1}{\Delta^{(1)}(\lambda)} e^{-\lambda z} \Phi_a(z) \int_0^{x_e} \gamma(x) G_e^{(1)}(x; \lambda) \, dx$$

with $G_e^{(1)}(\lambda)$, $G_a^{(1)}(\lambda)$ defined by (3.IV). The definition of $M^{(2)}(\lambda)$ is quite the same, see the expression of the resolvent operator found in the previous section.

If $\|\lambda M^{(1)}(\lambda) g^{(1)}\|_X \to 0$ as $\lambda \to \infty$, $\forall g^{(1)} \in X$, then we can assert that $\mathcal{D}(A_1 + B_1)$ is dense in X; the proof of this statement can be found in a work of A. Belleni-Morante and G. Busoni [2].

Because of the definition of $G_e^{(1)}(\lambda)$, $G_a^{(1)}(\lambda)$, $M^{(1)}(\lambda)$, if $\lambda > 0$ we have:

$$\|\lambda (M^{(1)}(\lambda) g^{(1)})_e\|_1 \leqslant \frac{\bar{\beta}\bar{\gamma} \|g_e^{(1)}\|_1 + \lambda \bar{\beta} \|g_a^{(1)}\|_2}{\lambda^2 - \bar{\beta}\bar{\gamma}}$$

$$\|\lambda (M^{(1)}(\lambda) g^{(1)})_a\|_2 \leqslant \frac{\bar{\beta}\bar{\gamma} \|g_a^{(1)}\|_2 + \lambda \bar{\beta} \|g_e^{(1)}\|_1}{\lambda^2 - \bar{\beta}\bar{\gamma}}$$

and these expressions approach zero as $\lambda \to \infty$, $\forall g^{(1)} \in X$. In the same way it can be shown that $\|\lambda M^{(2)}(\lambda) g^{(2)}\|_Y \to 0$ as $\lambda \to \infty$, $\forall g^{(2)} \in Y$.

In consenquence of Theorem 5, the subsequent discussion, and Lemma 6, the Hille-Yosida theorem may be applied and the following theorem may be stated.

Theorem 7. *System* (1) *has an unique strict solution* $n^{(i)} = n^{(i)}(t)$, $n^{(1)}: \boldsymbol{R}^+ \to X$, $n^{(2)}: \boldsymbol{R}^+ \to Y$, *which belongs to* $\mathcal{D}(A_i + B_i)$, $\forall t \geqslant 0$, *provided that* $n_0^{(i)} \in \mathcal{D}(A_i + B_i)$, $i = 1, 2$. *This solution is non negative if* $n_0^{(i)} \geqslant 0$ *and can be represented as*

$$n^{(i)}(t) = T^{(i)}(t) \, n_0^{(i)} \qquad t \geqslant 0, \quad i = 1, 2$$

where $\{T^{(i)}(t),\, t \geq 0\}$ *is the positive, strongly continuous semigroup in* $X(Y)$, *generated by* $(A_i + B_i)$, $i = 1, 2$. *Such a solution satisfies*

$$\|n^{(i)}(t)\|_X \leq e^{-\mathrm{m}^{(i)} t}\, \|n_0^{(i)}\|\,.$$

It is possible to determine explicitly the structure of the semigroup $\{T^{(i)}(t),\, t \geq 0\}$, $i = 1, 2$. First we can integrate along the characteristic lines systems M_1, M_2, equipped with the boundary conditions and the assigned initial conditions:

$$n_e^{(1)}(x, t) = \begin{cases} \Psi_e^{(1)}(x-t)\, \dfrac{\Phi_e^{(1)}(x)}{\Phi_e^{(1)}(x-t)} & 0 \leq t < x \\ n_e^{(1)}(0, t-x)\, \Phi_e^{(1)}(x) & 0 \leq x < t \end{cases}$$

$$n_e^{(2)}(x, y, t) = \begin{cases} \Psi_e^{(2)}(x-t, y-t)\, \dfrac{\Phi_e^{(2)}(x, y-x)}{\Phi_e^{(2)}(x-t, y-x)} & 0 \leq t < x < y \\ n_e^{(2)}(0, y-x, t-x)\, \Phi_e^{(2)}(x, y-x) & 0 \leq x < t,\ y > x \end{cases}$$

$$n_a^{(i)}(z, t) = \begin{cases} \Psi_a(z-t)\, \dfrac{\Phi_a(z)}{\Phi_a(z-t)} & 0 \leq t < z \\ n_a^{(i)}(0, t-z)\, \Phi_a(z) & 0 \leq z < t\,. \end{cases}$$

This is not the explicit expression of the solution $T^{(i)}(t)\, \Psi^{(i)}$, as the boundary conditions involve the solution itself. However it is possible to express $n_e^{(1)}(0, t)$, $n_e^{(2)}(0, z, t)$, $n_a^{(i)}(0, t)$, $i = 1, 2$, only by means of the initial distributions $\Psi^{(i)}$, solving an integral Volterra equation [4], so we have the solution expressed only by means of known parameters, and the result of this heuristic procedure is a one parameter family of bounded, linear operators $\{S^{(i)}(t),\, t \geq 0\}$, $i = 1, 2$, operating on the initial distribution $\Psi^{(i)}$.

It can be shown that $\{S^{(i)}(t),\, t \geq 0\}$, $i = 1, 2$, is, at most, an extension of $\{T^{(i)}(t),\, t \geq 0\}$, $i = 1, 2$, so that

$$S^{(i)}(t)\, \Psi^{(i)} = T(t)^{(i)}\, \Psi^{(i)} \qquad \forall \Psi^{(i)} \in \mathcal{D}(A_i + B_i)$$

and $S^{(i)}(t)\, \Psi^{(i)}$ gives the explicit expression of the strongly continuously differentiable solution, $i = 1, 2$.

Because of the study done on the spectrum of $(A_i + B_i)$, $i = 1, 2$, we can assert that the essential spectral bound of the generator $(A_i + B_i)$ is $-\infty$ (see

H. H. Schaefer [7] for definitions), and the *type* (or growth bound) of the semigroup $\{T^{(i)}(t), t \geq 0\}$ coincides with $\lambda_1^{(i)} : \omega_{\text{ess}}(A_i + B_i) = -\infty$, $\omega(A_i + B_i) = \lambda_1^{(i)}$, $i = 1, 2$.

So, we can state the following theorem, that is a generalization of Sharpe-Lotka's theorem [8], [9] to the present problem

Theorem 8. *Under the assumptions* **c**, **d**, *done on the parameters* φ, β, *the following holds: there exist* $M^{(i)} > 0$, $\omega^{(i)} < 0$ *such that for any* $n_0^{(1)} \in X$, *for any* $n_0^{(2)} \in Y$ *it results*

$$\| e^{-\lambda_1^{(1)} t} n^{(1)}(t) - P_0^{(1)} n_0^{(1)} \|_X \leq M^{(1)} e^{\omega^{(1)} t} \| n_0^{(1)} \|_X$$

$$\| e^{-\lambda_1^{(2)} t} n^{(2)}(t) - P_0^{(2)} n_0^{(2)} \|_Y \leq M^{(2)} e^{\omega^{(2)} t} \| n_0^{(2)} \|_Y$$

where $P_0^{(i)}$ *is the projection onto the eigenspace associated to* $\lambda_1^{(i)}$, $i = 1, 2$.

Proof. As $\lambda_1^{(i)}$ is an isolated point of the spectrum $\sigma(A_i + B_i)$, $i = 1, 2$, there exists a closed, regular curve $\Gamma^{(i)}$ in the plane, surrounding $\lambda_1^{(i)}$ such that $\lambda_1^{(i)}$ is the unique point of the spectrum in the closed region surrounded by $\Gamma^{(i)}$. So we can consider the projection $P_0^{(i)}$, $P_0^{(1)} : X \to X$, $P_0^{(2)} : Y \to Y$, onto the eigenspace associated to the eigenvalue $\lambda_1^{(i)}$, $i = 1, 2$, such that

$$P_0^{(i)} g^{(i)} = \frac{1}{2\pi i} \int_{\Gamma^{(i)}} R(\lambda; A_i + B_i) g^{(i)} \, d\lambda \qquad \forall g^{(1)} \in X, \ \forall g^{(2)} \in Y.$$

Such a projection coincides with the residue of the resolvent operator in $\lambda_1^{(i)} : P_0^{(i)} = \text{Res}((\lambda; A_i + B_i); \lambda_1^{(i)})$. Because of the structure of $\Delta^{(i)}(\lambda)$, $i = 1, 2$ we see that $\lambda_1^{(i)}$ is a simple pole of $[\Delta^{(i)}(\lambda)]^{-1}$ and also of $R(\lambda; A_i + B_i)$, $i = 1, 2$.

The Laurent expansion of $[\Delta^{(i)}(\lambda)]^{-1}$ gives

$$\text{Res}\,[(\Delta^{(i)}(\lambda))^{-1}; \lambda_1^{(i)}] = \lim_{\lambda \to \lambda_1^{(i)}} (\lambda - \lambda_1^{(i)}) \frac{1}{\Delta^{(i)}(\lambda)} = \left(\frac{d}{d\lambda} \Delta^{(i)}(\lambda_1^{(i)})\right)^{-1}.$$

If we examine the structure of the resolvent operator, we have

$$R(\lambda; A_i + B_i) = \frac{1}{\Delta^{(i)}(\lambda)} F^{(i)}(\lambda) + L^{(i)}(\lambda) \qquad i = 1, 2$$

where $F^{(i)}(\lambda)g^{(i)}$, $L^{(i)}(\lambda)g^{(i)}$, are analitic functions $\forall g^{(1)} \in X$, $\forall g^{(2)} \in Y$. Therefore

$$\operatorname{Res}(R(\lambda; A_i + B_i)g^{(i)}; \lambda_1^{(i)}) = (\frac{d}{d\lambda} \Delta^{(i)}(\lambda_1^{(i)}))^{-1} F^{(i)}(\lambda_1^{(i)})g^{(i)} \qquad i = 1, 2.$$

The projections $P_0^{(i)}$ are given by

$$P_0^{(1)} g^{(1)} = \frac{1}{(\Delta^{(1)}(\lambda_1^{(1)}))'} \begin{pmatrix} e^{-\lambda_1^{(1)} x} \Phi_e^{(1)}(x) \\ \bar{k}_e^{(1)}(\lambda_1^{(1)}) e^{-\lambda_1^{(1)} z} \Phi_a(z) \end{pmatrix} \cdot$$

$$\cdot [\bar{k}_a(\lambda_1^{(1)}) \int_0^{x_e} \gamma(x) G_e^{(1)}(x; \lambda_1^{(1)})\, dx + \int_0^{z_a} \beta(z) G_a^{(1)}(z; \lambda_1^{(1)})\, dz]$$

$$P_0^{(2)} g^{(2)} = \frac{1}{(\Delta^{(2)}(\lambda_1^{(2)}))'} \begin{pmatrix} e^{-\lambda_1^{(2)} y} \beta(y-x) \Phi_e^{(2)}(x, y-x) \Phi_a(y-x) \\ e^{-\lambda_1^{(2)} z} \Phi_a(z) \end{pmatrix} \cdot$$

$$\cdot [\int_0^{x_e} \int_x^{z_a + x} \gamma(x) e^{-\lambda_1^{(2)} x} \beta(y-x) \Phi_e^{(2)}(x, y-x) G_a^{(2)}(y-x; \lambda_1^{(2)})\, dy\, dx$$

$$+ \int_0^{x_e} \int_x^{z_a + x} \gamma(x) G_e^{(2)}(x, y; \lambda_1^{(2)})\, dy\, dx].$$

We may write, with obvious meaning

$$P_0^{(i)} g^{(i)} = \frac{C^{(i)}(\lambda_1^{(i)}; g^{(i)})}{(\Delta^{(i)}(\lambda_1^{(i)}))'} \Psi^{(i)} \qquad \forall g^{(1)} \in X, \quad \forall g^{(2)} \in Y$$

where $\Psi^{(i)}$ is the eigenfunction associated to the eigenvalue $\lambda_1^{(i)}$ of the operator $(A_i + B_i)$, not depending on $g^{(i)}$.

Let us consider the projection $P_1^{(i)} = I - P_0^{(i)}$; it is possible to prove that: if $\tilde{\omega}^{(i)} \in \boldsymbol{R}$, $\tilde{\omega}^{(i)} < \lambda_1^{(i)}$, then a constant $M^{(i)} \geq 1$ exists, such that:

$$\|T(t)^{(i)} P_1^{(i)}\| \leq M^{(i)} e^{\tilde{\omega}^{(i)} t} \|P_1^{(i)}\| \qquad t \geq 0,\ i = 1, 2 \text{ ([9] Prop. 4.15, p. 180).}$$

Then we have:

$$\|e^{-\lambda_1^{(1)} t} T(t)^{(1)} g^{(1)} - P_0^{(1)} g^{(1)}\|_X$$

$$= \|e^{-\lambda_1^{(1)} t} T^{(1)}(t) g^{(1)} - e^{-\lambda_1^{(1)} t} T^{(1)}(t) P_0^{(1)} g^{(1)} + e^{-\lambda_1^{(1)} t} T^{(1)}(t) P_0^{(1)} g^{(1)} - P_0^{(1)} g^{(1)}\|_X$$

$$\leq \|e^{-\lambda_1^{(1)} t} T^{(1)}(t) P_1^{(1)} g^{(1)}\|_X + \|e^{-\lambda_1^{(1)} t} T^{(1)}(t) P_0^{(1)} g^{(1)} - P_0^{(1)} g^{(1)}\|_X .$$

$$\|e^{-\lambda_1^{(2)}t}\,T(t)^{(2)}g^{(2)} - P_0^{(2)}g^{(2)}\|_Y$$

$$\leqslant \|e^{-\lambda_1^{(2)}t}\,T^{(2)}(t)\,P_1^{(2)}g^{(2)}\|_Y + \|e^{-\lambda_1^{(2)}t}\,T^{(2)}(t)\,P_0^{(2)}g^{(2)} - P_0^{(2)}g^{(2)}\|_Y\,.$$

As $P_0^{(i)}g^{(i)}$ is an eigenfunction associated to the eigenvalue $\lambda_1^{(i)}$, it results $T(t)^{(i)}P_0^{(i)}g^{(i)} = e^{\lambda_1^{(i)}t}P_0^{(i)}g^{(i)}$, $i = 1, 2$, and so $e^{-\lambda_1^{(i)}t}T^{(i)}(t)\,P_0^{(i)}g^{(i)} = P_0^{(i)}g^{(i)}$ and the second norm is zero in both cases.

From the above remark about $P_1^{(i)}$, $i = 1, 2$, as $\tilde{\omega}^{(i)} < \lambda_1^{(i)}$, we have:

$$\|e^{-\lambda_1^{(1)}t}\,T^{(1)}(t)\,P_1^{(1)}g^{(1)}\|_X \leqslant M^{(1)}e^{-(\lambda_1^{(1)}-\tilde{\omega}^{(1)})t}\,\|P_1^{(1)}g^{(1)}\|_X$$

$$\|e^{-\lambda_1^{(2)}t}\,T^{(2)}(t)\,P_1^{(2)}g^{(2)}\|_Y \leqslant M^{(2)}e^{-(\lambda_1^{(2)}-\tilde{\omega}^{(2)})t}\,\|P_1^{(2)}g^{(2)}\|_Y$$

and these norms approach zero as $t \to +\infty$.

Thus, we can make the following prediction: the population is asymptotic to a persistent age distribution, given by $e^{\lambda_1^{(i)}t}P_0^{(i)}g^{(i)}$, $i = 1, 2$, where $P_0^{(i)}g^{(i)}$ is defined in the preceding proof. In particular, if $\lambda_1^{(i)} = 0$, the population, whose evolution is described by model M_i, is asympotic to a stationary solution, given by the same expression with $\lambda_1^{(i)} = 0$.

4 - Further remarks

Let us examine shortly a possible change in problems seen till now, pointing out expecially the related variations of the spectrum of the evolution operator.

Models M_1, M_2 can be respectively considered in the spaces

$$\tilde{X} = L_1((0,\ \infty);\ dx) \times L_1((0,\ \infty);\ dz) = \tilde{X}_1 \times \tilde{X}_2$$

$$\tilde{Y} = L_1(\tilde{T};\ dy\,dx) \quad \times L_1((0,\ \infty);\ dz) = \tilde{Y}_1 \times \tilde{Y}_2$$

being $\tilde{T} = \{(x, y): 0 < x < y\}$, assuming that the parameters γ, φ, β belong to $L_\infty(0, \infty)$ and the mortality rates μ_a, μ_e satisfy the hypothesis **b** of divergent integral on a suitable bounded interval, with, in addition, the following behaviour after the limit ages: $\mu_e \in L_\infty(x_e, \infty)$, $\mu_a \in L_\infty(z_a, \infty)$. We point out that in this case the distinction between y and z is not very important.

If we tackle the study of the spectrum of the operator (A_i, B_i), $i = 1, 2$ under these assumptions, running over the done steps again, we note that, while the same results for the operator $H_\lambda^{(i)}$, $i = 1, 2$ are valid, (Lemma 1), as regard the function $G_j^{(i)}(\lambda)$, $j = e, a$, $i = 1, 2$, some restrictions to the domain of $\lambda \in \boldsymbol{C}$ are needed in order to state an analogous of Lemma 2. More precisely, in order to have $G^{(1)}(\lambda)$ belonging to $\widetilde{X}$, $\forall g^{(1)} \in \widetilde{X}$, $G^{(2)}(\lambda)$ belonging to $\widetilde{Y}$, $\forall g^{(2)} \in \widetilde{Y}$, it is sufficient that $\operatorname{Re} \lambda > -\nu^{(i)}$, $i = 1, 2$ respectively, being

$$\nu^{(1)} = \min(\operatorname*{ess\,inf}_{x > x_e} [\mu_e + \gamma], \operatorname*{ess\,inf}_{z > z_a} \mu_a)$$

$$\nu^{(2)} = \min(\operatorname*{ess\,inf}_{x > x_e,\, y > x} [\varphi\mu_a + \mu_e + \gamma], \operatorname*{ess\,inf}_{z > z_a} \mu_a).$$

We can note that $\nu^{(1)} \leqslant \nu^{(2)}$. This hypothesis is sufficient to assure the validity of the analogous of Lemma 2.

The Hille-Yosida theorem can be applied to the operator $(A_i + B_i)$ in this situation too, to assert that it generates a strongly continuous semigroup, which gives the solution of the evolution Cauchy problem.

If the hypotheses **c**, **d**, of Lemma 3 are satisfied, as the condition $\operatorname{Re} \lambda > -\nu^{(i)}$ is only sufficient to have

$$G^{(i)}(\lambda) + H_\lambda^{(i)} f^{(i)} \in \mathcal{D}(A_i + B_i) \qquad \forall f^{(1)}, g^{(1)} \in \widetilde{X}; \quad \forall f^{(2)}, g^{(2)} \in \widetilde{Y}; \qquad i = 1, 2$$

the essential spectral bound $\omega_{\text{ess}}(A_i + B_i)$ of the generator $(A_i + B_i)$ is not greater than $-\nu^{(i)}$, $i = 1, 2$. The following cases may occur:

i. $\lambda_1^{(i)} > -\nu^{(i)}$: the type (or growth bound) of the generated semigroup coincides with $\lambda_1^{(i)}$: $\omega(A_i + B_i) = \lambda_1^{(i)}$, $\omega_{\text{ess}}(A_i + B_i) \leqslant -\nu^{(i)}$

ii. $\lambda_1^{(i)} \leqslant -\nu^{(i)}$: we can only assert that the essential spectral bound is not greater than the type of the semigroup, which is not greater that $-\nu^{(i)}$: $\omega_{\text{ess}}(A_i + B_i) \leqslant \omega(A_i + B_i) \leqslant -\nu^{(i)}$. If $\lambda_1^{(i)} = -\nu^{(i)}$ we have: $\omega(A_i + B_i) = -\nu^{(i)} = \lambda_1^{(i)}$.

The analogous of Theorem 8 can be stated only if $\lambda_1^{(i)} > -\nu^{(i)}$, $i = 1, 2$; on the contrary, as the intrinsic growth constant can not be an isolated point of the spectrum of $(A_i + B_i)$, we can only assert that the type of the semigroup generated by $(A_i + B_i)$ is negative, and the population decays exponentially.

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Sommario

Si considerano esistenza, unicità, comportamento asintotico e altre proprietà per due modelli di dinamica delle popolazioni a molti stadi. Si confrontano poi i risultati più importanti.

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