

WELL-POSEDNESS OF AN INFINITE SYSTEM OF PARTIAL DIFFERENTIAL EQUATIONS MODELLING PARASITIC INFECTION IN AN AGE-STRUCTURED HOST

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ABSTRACT. We study a deterministic model for the dynamics of a population infected by macroparasites. The model consists of an infinite system of partial differential equations, with initial and boundary conditions; the system is transformed in an abstract Cauchy problem on a suitable Banach space, and existence and uniqueness of the solution are obtained through multiplicative perturbation of a linear C_0 -semigroup. Positivity and boundedness are proved using the specific form of the equations.

1. INTRODUCTION

The system of equations we analyse in this paper arises in the context of population biology: it describes the dynamics of a population of individuals (“hosts”), infected by one species of macroparasites. The host population is age-structured and is subdivided into a countable number of classes according to the number of parasites a host carries: for each $i \in \mathbb{N}$, $p_i(a, t)$ denotes the density of hosts of age a harbouring i parasites at time t . More precisely, if $0 \leq a_1 < a_2$ the integral

$$\int_{a_1}^{a_2} p_i(a, t) da$$

is the number of hosts that, at the time t , have age between a_1 and a_2 and carry i parasites; the variable a is supposed to vary in $[0, +\infty)$.

The dynamics of the host population is specified through the fertility and mortality rates: for the sake of simplicity, we assume here that only fertility depends on population size, while mortality is density-independent (see [7] or [13] for a general background on the equations for age-structured populations). Moreover, we assume that parasites affect host fertility and mortality according to the rules proposed in [11].

Namely, we assume that the fertility rate of hosts carrying i parasites is $\beta_i(a, \mathbf{p}) = \psi(N)\beta(a)\xi^i$, where $\mathbf{p} = (p_0(a), p_1(a), p_2(a), \dots)$ and

$$(1.1) \quad N = \int_0^{+\infty} \sum_{i=0}^{+\infty} p_i(a) da$$

represents the total number of hosts. The parameter ξ ($0 < \xi \leq 1$) describes the reduction in host fertility per parasite harboured, the function $\beta(a)$ specifies

the age-dependence of fertility, and ψ is the function of the total population that represents the density-dependence.

Hosts die at a natural death rate $\mu(a)$, to which a death rate $\alpha > 0$ is added for each parasite carried. The parasites also die, at a constant death rate $\sigma > 0$.

Finally, it is assumed that a host can acquire or lose one parasite at a time; the epidemic spreads among hosts according to an infection rate $\varphi(t)$ which, following Anderson and May [1], has the following shape

$$(1.2) \quad \varphi(t) = \frac{hP}{c + N},$$

where

$$P = \int_0^{+\infty} \sum_{i=1}^{+\infty} ip_i(a) da$$

represents the total number of parasites in the population.

All these assumptions lead to the following infinite system of differential equations:

$$(1.3) \quad \left\{ \begin{array}{l} \frac{\partial}{\partial t} p_i(a, t) = -\frac{\partial}{\partial a} p_i(a, t) - (\mu(a) + \varphi(t) + i(\alpha + \sigma)) p_i(a, t) \\ \quad + \sigma(i + 1) p_{i+1}(a, t) + \varphi(t) p_{i-1}(a, t) \quad i \geq 0 \\ p_0(0, t) = \psi(N(t)) \int_0^{+\infty} \beta(a) \sum_{i=0}^{+\infty} p_i(a, t) \xi^i da \\ p_i(0, t) = 0 \quad i > 0 \\ p_i(a, 0) = h_i(a) \quad i \geq 0 \end{array} \right.$$

where $N(t)$, $P(t)$ and $\varphi(t)$ are given in (1.1) and (1.2) and $p_{-1}(a, t) \equiv 0$.

To sum up, the equations in (1.3) are a model for an immigration-death process with two nonlinearities: the first one due to the infection rate $\varphi(t)$ and the second one because of the boundary condition that describes density-dependent fertility.

Infinite systems to model parasitism were first introduced in 1934 by Kostizin [9] that wrote down a system of ordinary differential equations, involving birth and death rates, coefficients of contamination, competition coefficient, all depending on the number of parasites in a host; however, in his paper only an analysis of the equilibrium points and their stability for some very special cases is accomplished.

More recently, a system very similar to (1.3) has been investigated by Haderler and Dietz [6], and by Kretzschmar [10, 11]. The difference between their models and ours is in the form of $\varphi(t)$, and in the boundary condition that is linear in their models: therefore, host population would grow exponentially in absence of parasites, and, due to their choice of $\varphi(t)$, exponential solutions may exist also in presence of parasites. Their approach is based on transforming the infinite system in a single partial differential equation satisfied by the generating function $G(a, t, z) = \sum_i p_i(a, t) z^i$. This method, however, works only under specific choices

for the transition rules; it seems, for instance, difficult to handle a general nonlinear boundary condition in this approach.

Instead, we prefer to set system (1.3) within the framework of semigroup theory. In this approach, it would be possible to allow the coefficients σ , α and ξ to depend rather arbitrarily on the number i of parasites, and to use more general forms for the host fertility and mortality functions, but, for the sake of simplicity, we stick to system (1.3) as written.

System (1.3) will be transformed into an abstract Cauchy problem of the form

$$(1.4) \quad \begin{cases} p'(t) = A(I + H)(p(t)) + F(p(t)) \\ p(0) = p^0 \end{cases}$$

where A is the generator of a C_0 -semigroup and H and F are non linear operators on a suitable Banach space. The multiplicative perturbation of a linear operator A by means of a nonlinear operator H , that is $A(I + H)$, was introduced by Desch, Schappacher and Zhang [5] to study some differential equations with nonlinear boundary conditions, following previous work on linear boundary conditions [4]. They studied the Cauchy problem

$$(1.5) \quad \begin{cases} p'(t) = A(I + H(t))p(t) \\ p(0) = p^0. \end{cases}$$

in a Banach space X , where the linear operator A is the generator of a C_0 -semigroup on X . They found suitable, but general enough, hypotheses on the family of operators $H(t)$, that guarantee well-posedness for (1.5) even if $\mathcal{R}(H(t)) \not\subset D(A)$. We follow and extend their results about existence and uniqueness of solutions to the case (1.4). In Section 2 we give conditions for existence, uniqueness and continuous dependence of solutions of the Cauchy problem (1.4) In Section 3 we prove the positivity of these solutions under suitable assumptions. Finally, in Section 4 we show how these results can be applied to the system (1.3), proving global existence and uniqueness of positive solutions. In a sequel to this paper, this framework is used to study the equilibria of (1.3) and their stability.

2. WELL-POSEDNESS OF AN ABSTRACT CAUCHY PROBLEM

2.1. Existence and uniqueness. Throughout this section $(X, \|\cdot\|)$ will denote a Banach space and $A : D(A) \rightarrow X$ will be a linear operator with domain $D(A) \subset X$ generating a C_0 -semigroup e^{tA} on X such that

$$(2.1) \quad \|e^{tA}\| \leq Me^{\omega t}, \quad t \geq 0,$$

for some $M \geq 1$ and $\omega \in \mathbb{R}$.

The Favard class of A is

$$F_A = \{p \in X : \limsup_{t \rightarrow 0^+} \frac{1}{t} \|e^{tA}p - p\| < +\infty\}.$$

which is a Banach space with the norm

$$\|p\|_{F_A} := \|p\| + \limsup_{t \rightarrow 0^+} \frac{1}{t} \|e^{tA}p - p\|.$$

Clearly, $D(A) \subset F_A$ and, if X is reflexive, $D(A) = F_A$.

We state a crucial property (see [5]) that we will repeatedly use in the sequel: if $f \in C([0, T]; F_A)$ then

$$\int_0^t e^{(t-s)A} f(s) ds \in D(A)$$

and

$$(2.2) \quad \|A \int_0^t e^{(t-s)A} f(s) ds\| \leq M \int_0^t e^{\omega(t-s)} \|f(s)\|_{F_A} ds$$

for all $0 \leq t \leq T$.

Let now $H : X \rightarrow F_A$ and $F : X \rightarrow X$ be locally Lipschitz continuous, i. e. for all $R > 0$ there exist $L_R, K_R > 0$ such that

$$(2.3) \quad \|H(p) - H(q)\|_{F_A} \leq L_R \|p - q\|, \quad \|F(p) - F(q)\| \leq K_R \|p - q\|$$

for all $p, q \in X$ such that $\|p\|, \|q\| \leq R$.

We are now ready to state the result (see [5]) about existence and uniqueness of solutions. Let $p^0 \in X$ be fixed and consider the abstract Cauchy problem

$$(2.4) \quad \begin{cases} p'(t) = A(p(t) + H(p(t))) + F(p(t)) \\ p(0) = p^0. \end{cases}$$

Theorem 2.1. *Let $A : D(A) \rightarrow X$ be a linear operator with $D(A) \subset X$ which generates a C_0 -semigroup e^{tA} . Let $H : X \rightarrow F_A$ and $F : X \rightarrow X$ satisfy (2.3). Then*

- a) *for each $p^0 \in X$ there exists a unique mild solution of (2.4) i.e. a continuous function $t \rightarrow p(t)$ satisfying the integral equation*

$$(2.5) \quad p(t) = e^{tA}p^0 + A \int_0^t e^{(t-s)A} H(p(s)) ds + \int_0^t e^{(t-s)A} F(p(s)) ds;$$

- b) *if $[0, t_{max})$ is the maximal interval of existence of the solution, then $t_{max} = +\infty$ or $\lim_{t \rightarrow t_{max}^-} \|p(t)\| = +\infty$;*
c) *if H and F are continuously differentiable and $(p^0 + H(p^0)) \in D(A)$ then $p(t)$ is a classical solution of (2.4), i.e. $p(t) + H(p(t)) \in D(A)$ for each $t \in [0, t_{max})$, $p(t)$ is differentiable and satisfies the equation (2.4) for each $0 \leq t < t_{max}$.*

Sketch of the proof. The proof is with minor modifications that in [5]. We give a sketch of the proof of part a), since the tools introduced will be useful later. For $R > 0$ introduce the projection $\pi_R : X \rightarrow X$

$$\pi_R(x) = \begin{cases} x & \text{if } \|x\| \leq R \\ \frac{x}{\|x\|} R & \text{if } \|x\| > R. \end{cases}$$

and define

$$(2.6) \quad H_R(x) := H(\pi_R(x)) \quad \text{and} \quad F_R(x) := F(\pi_R(x)).$$

The maps H_R and F_R are globally Lipschitz continuous, with Lipschitz constants $2L_R$ and $2K_R$ respectively. Then consider the integral operator $V_{p^0, R}$ defined on the Banach space $C([0, T], X)$:

$$(2.7) \quad (V_{p^0, R}q)(t) = e^{tA}p^0 + A \int_0^t e^{(t-s)A} H_R(q(s)) ds + \int_0^t e^{(t-s)A} F_R(q(s)) ds.$$

It is easy to see that, for T small enough, $V_{p^0, R}$ is a contraction so that a unique continuous solution $p_R(t)$ of

$$(2.8) \quad q(t) = e^{tA}p^0 + A \int_0^t e^{(t-s)A} H_R(q(s)) ds + \int_0^t e^{(t-s)A} F_R(q(s)) ds$$

exists. Repeating the same argument for $V_{p_R(T), R}$, $C([T, 2T], X)$ and so on, one sees that a continuous solution of (2.8) exists for $t \in [0, +\infty)$. Now, taking $R > \|p^0\|$, the solution will satisfy, for small t , $\|p_R(t)\| \leq R$, whence H_R and F_R can be replaced by H and F in (2.8) and $p_R(t)$ is the local solution of (2.5).

2.2. Continuous dependence on initial data. We prove here that the mild solution of the abstract Cauchy problem (2.4) depends continuously on the initial datum. Continuous dependence is part of the classical definition of well-posedness. In the following we denote by $p(t, p^0)$ the mild solution of (2.4) with initial point p^0 .

Theorem 2.2. *Let $p^0 \in X$ and let $(q_n)_{n \in \mathbb{N}}$ be a sequence in X converging to p^0 . Then for each $t > 0$ such that $p(t, p^0)$ exists, we have*

$$\lim_{n \rightarrow \infty} p(t, q_n) = p(t, p^0)$$

and the convergence is uniform for $t \in [0, T]$, where $T > 0$ is such that $p(T, p^0)$ exists.

Proof. Let $[0, T] \subset [0, t_{max})$, $R > 2 \max_{0 \leq t \leq T} \|p(t, p^0)\|$ and recall the definition of H_R and F_R in (2.6). If $p_R(t, q_n)$ and $p_R(t, p^0)$ are the mild solutions of the equation $p'(t) = A(I + H_R)p(t) + F_R(p(t))$ with initial values q_n and p^0 respectively, set

$$w_{R,n}(t) := p_R(t, q_n) - p_R(t, p^0).$$

If $w_n := q_n - p^0$ we can write

$$\begin{aligned} w_{R,n}(t) &= e^{tA}w_n + A \int_0^t e^{(t-s)A} (H_R(p_R(s, q_n)) - H_R(p_R(s, p^0))) ds \\ &\quad + \int_0^t e^{(t-s)A} (F_R(p_R(s, q_n)) - F_R(p_R(s, p^0))) ds. \end{aligned}$$

It follows that

$$\begin{aligned} \|w_{R,n}(t)\| &\leq M e^{\omega t} \|w_n\| + \int_0^t M e^{\omega(t-s)} |H_R(p_R(s, q_n)) - H_R(p_R(s, p^0))|_{F_A} ds \\ &\quad + \int_0^t M e^{\omega(t-s)} \|F_R(p_R(s, q_n)) - F_R(p_R(s, p^0))\| ds \\ &\leq M e^{\omega t} \|w_n\| + 2L_R M \int_0^t e^{\omega(t-s)} \|w_{R,n}(s)\| ds \\ &\quad + 2K_R M \int_0^t e^{\omega(t-s)} \|w_{R,n}(s)\| ds. \end{aligned}$$

From this, multiplying each member by $e^{-\omega t}$ and using the Gronwall Lemma, we obtain

$$(2.9) \quad \|w_{R,n}(t)\| \leq M \|w_n\| e^{(2M(L_R+K_R)+\omega)t} \leq M \|w_n\| e^{(2M(L_R+K_R)+\omega^+)T}$$

where $\omega^+ = \max(\omega, 0)$. Set $C_{R,T} := (2M(L_R + K_R) + \omega^+)T$. For n such that

$$\|w_n\| = \|q_n - p^0\| \leq \frac{R - 2 \max_{0 \leq t \leq T} \|p(t, p^0)\|}{M e^{C_{R,T}}}$$

it results $\|w_{R,n}(t)\| \leq R - 2 \max_{0 \leq t \leq T} \|p(t, p^0)\|$ and hence

$$\|p_R(t, q_n)\| \leq \|w_{R,n}(t)\| + \|p_R(t, p^0)\| \leq R - 2 \max_{0 \leq t \leq T} \|p(t, p^0)\| + \|p_R(t, p^0)\|.$$

Because of the choice of R , $p_R(t, p^0) \equiv p(t, p^0)$ in $[0, T]$ and therefore

$$\|p_R(t, p^0)\| \leq 2 \max_{0 \leq t \leq T} \|p(t, p^0)\|$$

whence $\|p_R(t, q_n)\| \leq R$ and finally $p_R(t, q_n) = p(t, q_n)$ in $[0, T]$. Replacing in (2.9) we get

$$\|p(t, q_n) - p(t, p^0)\| \leq M \|q_n - p^0\| e^{C_{R,T}},$$

which clearly proves the statement. \square

3. POSITIVE SOLUTIONS

Our model system (1.3) describes the dynamics of a host population infected by parasites; therefore, the only solutions that make biological sense are positive solutions. When using the abstract formulation (1.4), Banach lattices (see [2]) are the natural abstract framework. By definition a (real) Banach lattice is a real Banach space $(X, \|\cdot\|)$ endowed with an order relation, \leq , such that (X, \leq) is a lattice and the ordering is compatible with the Banach space structure of X .

The order is completely determined by *the positive cone of X* which is $X_+ = \{p \in X : p \geq 0\}$. This means that $p \geq q$ if and only if $p - q \in X_+$. It is easy to verify that X_+ is a closed, convex set. For instance, if $X = L^1(\Omega, \mu)$ and \leq is the natural order between functions, then $X_+ = \{f \in X : f(\omega) \geq 0, \mu - \text{a. e. in } \Omega\}$.

Definition 3.1. A linear operator $T : X \rightarrow X$ is called *positive* if $Tp \in X_+$ for all $p \in X_+$.

We are now able to state the main result of the section:

Theorem 3.2. *Let X be a Banach lattice and let A be the generator of a positive C_0 -semigroup on X i.e. $e^{tA}X_+ \subset X_+$ for all $t \geq 0$. Suppose that for each $R > 0$ there exists $\alpha \in \mathbb{R}$, $\alpha > 0$, such that*

$$(I + \alpha F_R)X_+ \subset X_+$$

and

$$A \int_0^t e^{(t-s)(A-\frac{1}{\alpha}I)} H_R(u(s)) ds \in X_+ \quad \text{for all } u \in C([0, T]; X_+),$$

where F and H satisfy (2.3), and H_R and F_R are defined in (2.6). Then, if $p^0 \in X_+$, $p(t, p^0) \in X_+$ for all $t \in [0, t_{max})$.

We need first the following Lemma:

Lemma 3.3. *Let X be a Banach space, let $\alpha > 0$, $R > 0$ and $p^0 \in X$, and let H_R and F_R be defined as in (2.6). A function $t \rightarrow p(t)$ satisfies the integral equation*

$$(3.1) \quad p(t) = e^{tA}p^0 + A \int_0^t e^{(t-s)A} H_R(p(s)) ds + \int_0^t e^{(t-s)A} F_R(p(s)) ds, \quad t \geq 0$$

if and only if it satisfies the integral equation

$$(3.2) \quad \begin{aligned} p(t) = & e^{t(A-\frac{1}{\alpha}I)}p^0 + A \int_0^t e^{(t-s)(A-\frac{1}{\alpha}I)} H_R(p(s)) ds \\ & + \frac{1}{\alpha} \int_0^t e^{(t-s)(A-\frac{1}{\alpha}I)} (I + \alpha F_R)(p(s)) ds, \quad t \geq 0. \end{aligned}$$

Proof. Let $p_R(t)$ be the unique solution of (3.1) and let $p_{R,\alpha}(t)$ be the unique solution of (3.2) (by the same arguments sketched in the proof of Theorem 2.1 it is easy to see that the equation (3.2) has a unique global solution). From Gronwall's lemma, it is easy to see that the functions $p_R(t)$, $p_{R,\alpha}(t)$, $f(t) := F_R(p_{R,\alpha}(t))$ and $h(t) := H_R(p_{R,\alpha}(t))$ all satisfy

$$\|p_R(t)\|, \|p_{R,\alpha}(t)\|, \|f(t)\|, \|h(t)\| \leq K e^{\eta t}$$

for suitable $K \geq 1$ and $\eta \geq 0$.

Hence p_R , $p_{R,\alpha}$, $f(t)$ and $h(t)$ are Laplace transformable for $\text{Re } \lambda > \eta$. From (3.2) it follows that

$$\begin{aligned} \widehat{p}_{R,\alpha}(\lambda) = & (\lambda + \frac{1}{\alpha} - A)^{-1} p^0 + A(\lambda + \frac{1}{\alpha} - A)^{-1} \widehat{h}(\lambda) \\ & + \frac{1}{\alpha} (\lambda + \frac{1}{\alpha} - A)^{-1} (\widehat{p}_{R,\alpha}(\lambda) + \alpha \widehat{f}(\lambda)), \end{aligned}$$

and applying $(\lambda - A)^{-1}$ to each member one obtains, using the resolvent identity,

$$\begin{aligned} 0 &= \alpha(\lambda - A)^{-1}p^0 + \alpha A(\lambda - A)^{-1}\widehat{h}(\lambda) + \alpha(\lambda - A)^{-1}\widehat{f}(\lambda) \\ &\quad - \alpha\left[(\lambda + \frac{1}{\alpha} - A)^{-1}p^0 + A(\lambda + \frac{1}{\alpha} - A)^{-1}\widehat{h}(\lambda)\right. \\ &\quad \left.+ \frac{1}{\alpha}(\lambda + \frac{1}{\alpha} - A)^{-1}(\widehat{p}_{R,\alpha}(\lambda) + \alpha\widehat{f}(\lambda))\right] \\ &= \alpha[(\lambda - A)^{-1}p^0 + A(\lambda - A)^{-1}\widehat{h}(\lambda) + (\lambda - A)^{-1}\widehat{f}(\lambda) - \widehat{p}_{R,\alpha}(\lambda)]. \end{aligned}$$

This implies

$$\widehat{p}_{R,\alpha}(\lambda) = (\lambda - A)^{-1}p^0 + A(\lambda - A)^{-1}\widehat{h}(\lambda) + (\lambda - A)^{-1}\widehat{f}(\lambda)$$

and hence

$$p_{R,\alpha}(t) = e^{tA}p^0 + A \int_0^t e^{(t-s)A}H(p_{R,\alpha}(s)) ds + \int_0^t e^{(t-s)A}F(p_{R,\alpha}(s)) ds.$$

The same steps in the opposite order show that the converse is also true and the claim is proved. \square

of Theorem 3.2. Fix $T < t_{max}$ and $R > \sup_{0 \leq t \leq T} \|p(t, p^0)\|$.

Choose $\alpha > 0$ such that $(I + \alpha F_R)u \geq \bar{0}$ if $u \geq 0$. Consider the non linear operator $V_{\alpha,R}$ on $W_T = C([0, T], X)$

$$\begin{aligned} [V_{\alpha,R}v](t) &:= e^{t(A - \frac{1}{\alpha}I)}p^0 + A \int_0^t e^{(t-s)(A - \frac{1}{\alpha}I)}H_R(v(s)) ds \\ &\quad + \frac{1}{\alpha} \int_0^t e^{(t-s)(A - \frac{1}{\alpha}I)}(I + \alpha F_R)v(s) ds. \end{aligned}$$

Because of the positivity of the C_0 -semigroup $e^{t(A - \frac{1}{\alpha}I)}$ and the choice of α , $V_{\alpha,R}$ is positive i.e. $V_{\alpha,R}(W_T^+) \subset W_T^+$ where $W_T^+ := C([0, T], X_+)$. Moreover, W_T^+ is closed in W_T and hence complete. Hence, the fixed point q_R of $V_{\alpha,R}$, that is the unique solution of (3.2), satisfies $q_R \in W_T^+$. By Theorem 3.3 q_R satisfies also (3.1). Furthermore, as far as $\|q_R(t)\| \leq R$, it satisfies

$$\begin{aligned} q_R(t) &= e^{tA}p^0 + A \int_0^t e^{(t-s)A}H(q_R(s)) ds \\ &\quad + \int_0^t e^{(t-s)A}F(q_R(s)) ds. \end{aligned}$$

and hence coincides with $p(t, p^0)$. Because of the choice of R it follows that $\|q_R(t)\| \leq R$ for each $t \in [0, T]$ whence

$$q_R(t) \equiv p(t, p^0)$$

on $[0, T]$ and therefore $p(t, p^0)$ is positive on the same interval.

Iterating this argument, $p(t, p^0)$ is shown to be positive on $[0, t_{max})$. \square

Remark 3.4. Note that, under the assumptions of Theorem 3.2, we only need that F and H are defined on X_+ in order to construct $p(t, p^0)$ for $p^0 \in X_+$.

4. APPLICATION TO THE MODEL FOR PARASITIC INFECTIONS

To prove the existence of a solution for (1.3) we transform it into an abstract Cauchy problem of the form (2.4) and then apply the results obtained in the previous sections.

The space in which the equation will be studied is

$$X := \{p = (p_i)_{i \in \mathbb{N}} : p_i \in L^1(0, +\infty) \forall i \geq 0, \sum_{i=1}^{+\infty} i \int_0^{+\infty} |p_i(a)| da < \infty\}$$

endowed with the norm

$$\|p\| := \int_0^{+\infty} |p_0(a)| da + \sum_{i=1}^{+\infty} i \int_0^{+\infty} |p_i(a)| da.$$

It is easy to see that $(X, \|\cdot\|)$ is a Banach space.

About the functions μ and β we assume the following (see for instance [14]):

- (H1) μ measurable, positive and there exist values μ_-, μ_+ such that $0 < \mu_- \leq \mu(a) \leq \mu_+$ for a.e. $a \in [0, +\infty)$
(H2) $\beta \in L^\infty[0, +\infty)$, $\beta(a) \geq 0$.

Finally, a minimal assumption on the function ψ that allows for global existence of solutions is

- (H3) $\psi \in C^1([0, +\infty))$, $\psi(s) \geq 0$, $\max_{s \in [0, +\infty)} \psi(s) = 1$.

Note that $\max \psi(s) = 1$ is simply a normalization, since any constant can be inserted in the function β .

If we assume that host population growth is of generalized logistic type, we can assume instead

- (H3') $\psi \in C^1([0, +\infty))$, $\psi(0) = 1$, $\psi'(s) < 0$, $\lim_{s \rightarrow +\infty} \psi(s) = 0$.

Another condition is needed to obtain a parasite-free stationary solution of (1.3). If $p = (p_0(a), p_1(a), \dots)$ is a stationary solution of (1.3) corresponding to $\varphi = 0$, then $p_i(a) \equiv 0$ for $i > 0$ and $p_0(a) = p_0(0)\pi(a)$ where $\pi(a) = e^{-\int_0^a \mu(s) ds}$. Setting

$$R_0 = \int_0^{+\infty} \beta(a)\pi(a) da,$$

it can be easily seen that there is a stationary solution with $\varphi = 0$ if and only if there exists $K > 0$ such that

$$\psi(K) = \frac{1}{R_0},$$

that is if and only if $R_0 > 1$, because of (H3'). In such a case it is unique. Under (H3'), if $R_0 \leq 1$, it is not difficult to show that the host population will decrease to 0 (see for instance [7]). Hence, a usual assumption will be

- (H4) $R_0 > 1$.

We show the well-posedness of system (1.3) by setting it in the abstract framework (1.5). With this aim, we define first the linear operator A on X :

$$(4.1) \quad \begin{aligned} D(A) &= \{p \in X : p_i \in W^{1,1}(0, +\infty), p_i(0) = 0 \forall i \geq 0, \text{ and such that} \\ &\text{there exists } N \in \mathbb{N} \text{ such that } p_i \equiv 0 \text{ for all } i > N\}. \\ (Ap)_i(a) &:= -p'_i(a) - (\mu(a) + i(\alpha + \sigma))p_i(a) + (i+1)\sigma p_{i+1}(a) \quad \text{for } i \geq 0, \end{aligned}$$

As we will prove below, A is closable and its closure \bar{A} generates a C_0 -semigroup on X .

Let now

$$E := \{p \in X : c + \sum_{i=0}^{+\infty} \int_0^{+\infty} p_i(s) ds \neq 0\}$$

and consider the non linear operator $F : E \rightarrow X$ defined by

$$\begin{aligned} (F(p))_0 &= -\frac{h \sum_{i=1}^{+\infty} i \int_0^{+\infty} p_i(a) da}{c + \sum_{i=0}^{+\infty} \int_0^{+\infty} p_i(a) da} p_0, \\ (F(p))_i &= \frac{h \sum_{i=1}^{+\infty} i \int_0^{+\infty} p_i(a) da}{c + \sum_{i=0}^{+\infty} \int_0^{+\infty} p_i(a) da} (p_{i-1} - p_i), \quad i \geq 1. \end{aligned}$$

Finally, the ‘multiplicative perturbation’ operator that takes account of the non-trivial boundary condition in 1.3 (see [5] for more details) is:

$$\begin{aligned} (Hp)_0(a) &= -\psi \left(\int_0^{+\infty} \sum_{i=0}^{+\infty} p_i(s) ds \right) \left(\int_0^{+\infty} \beta(s) \sum_{i=0}^{+\infty} p_i(s) \xi^i ds \right) \pi(a), \\ (Hp)_i &\equiv 0 \quad \text{for } i \geq 1. \end{aligned}$$

H is an operator on X such that $(p + Hp) \in D(A)$ if and only if the components of p are in $W^{1,1}$ and p satisfies the boundary conditions

$$\begin{aligned} p_0(0) &= \psi \left(\int_0^{+\infty} \sum_{i=0}^{+\infty} p_i(s) ds \right) \left(\int_0^{+\infty} \beta(s) \sum_{i=0}^{+\infty} p_i(s) \xi^i ds \right) \\ p_i(0) &= 0 \quad \text{for } i \geq 1 \end{aligned}$$

which are exactly the boundary conditions in (1.3).

Hence, the evolution equation (1.3) has been transformed into the abstract Cauchy problem

$$(4.2) \quad \begin{cases} p'(t) = A(p(t) + H(p(t))) + F(p(t)) \\ p(0) = p^0. \end{cases}$$

To prove that (4.2) is well-posed we start with

Theorem 4.1. *The linear operator A is closable in X , and \bar{A} generates a positive, strongly continuous semigroup of contractions.*

Proof. We will prove that A is dissipative, that $\overline{D(A)} = X$ and $\mathcal{R}(\lambda I - A)$ is dense in X for $\lambda > 0$.

In fact, by theorem 4.5 in [12], under these assumptions A is closable and \bar{A} is dissipative too.

Moreover, if A is dissipative and $\mathcal{R}(\lambda I - A)$ is dense in X , then $\mathcal{R}(\lambda I - \bar{A}) = X$. In fact, take $y \in X$, $(x_n)_{n \in \mathbb{N}}$ sequence in $D(A)$ such that $\lambda x_n - Ax_n \rightarrow y$. Since, because of the dissipativity of A , we have $\|(\lambda I - A)(x_n - x_m)\| \geq \lambda \|x_n - x_m\|$ and the left-hand side is a Cauchy sequence by assumption, it follows that the right-hand side is also a Cauchy sequence; therefore, there exists $x \in X$ such that $x_n \rightarrow x$; we can then conclude that $Ax_n \rightarrow \lambda x - y$ which implies, by the definition of closure, that $x \in \bar{A}$ and $\bar{A}x = \lambda x - y$. This means $(\lambda I - \bar{A})x = y$ so that $\mathcal{R}(\lambda I - \bar{A}) = X$.

At this point, applying Theorem 4.3 in [12] to \bar{A} , we can conclude that \bar{A} generates a C_0 -semigroup of contractions.

Finally, the positivity is shown by direct computation.

To prove that A is dissipative consider the *subdifferential of the norm* i.e. for $x \in X, x \neq 0$

$$(4.3) \quad \partial\|x\| = \{\varphi \in X^* : \langle \varphi, x \rangle = \|x\|, \|\varphi\| = 1\}$$

and

$$\partial\|0\| = \{\varphi \in X^* : \|\varphi\| \leq 1\}.$$

One has to show that for every $q \in D(A)$ there is a $q^* \in \partial\|q\|$ such that $\langle Aq, q^* \rangle \leq 0$ (the brackets denote the usual duality product). For $q = 0$ this is trivial. If $q \neq 0$ it is known (see, for instance, [3]) that, via the identification

$$X^* = \{\varphi = (\varphi_i)_{i \in \mathbb{N}} : \varphi_i \in L^\infty(0, +\infty), \sup_{i \in \mathbb{N}} \|\varphi_i\| < +\infty\},$$

$\varphi \in \partial\|q\|$ if and only if for each $i = 0, 1, 2, \dots$

$$(4.4) \quad \begin{aligned} \varphi_i(a) &= 1 & \text{if } a \in \Omega_i^+ &= \{s \in [0, +\infty) : q_i(s) > 0\} \\ \varphi_i(a) &= -1 & \text{if } a \in \Omega_i^- &= \{s \in [0, +\infty) : q_i(s) < 0\} \\ -1 \leq \varphi_i(a) \leq 1, & & \text{if } a \in \Omega_i^0 &= \{s \in [0, +\infty) : q_i(s) = 0\}. \end{aligned}$$

Hence

$$\begin{aligned}
\langle Aq, \varphi \rangle &= \sum_{i=1}^{+\infty} i \left[\int_{\Omega_i^+} (Aq)_i(a) da - \int_{\Omega_i^-} (Aq)_i(a) da \right] \\
&\quad + \int_{\Omega_0^+} (Aq)_0(a) da - \int_{\Omega_0^-} (Aq)_0(a) da \\
(4.5) \quad &= \sum_{i=1}^{+\infty} i \int_{\Omega_i^+} (-q'_i(a) - (\mu(a) + i(\alpha + \sigma))q_i(a) + \sigma(i+1)q_{i+1}(a)) da \\
&\quad - \sum_{i=1}^{+\infty} i \int_{\Omega_i^-} (-q'_i(a) - (\mu(a) + i(\alpha + \sigma))q_i(a) + \sigma(i+1)q_{i+1}(a)) da \\
&\quad + \int_{\Omega_0^+} (-q'_0(a) - \mu(a)q_0(a) + \sigma q_1(a)) da \\
&\quad - \int_{\Omega_0^-} (-q'_0(a) - \mu(a)q_0(a) + \sigma q_1(a)) da
\end{aligned}$$

where $\varphi \in \partial\|q\|$ has been chosen such that, for each i , $\varphi_i \equiv 0$ in Ω_i^0 . Now, since $q_i \in W^{1,1}(0, +\infty)$ for every i , Ω_i^+ is the union of a family, at most countable, of pairwise disjoint intervals, i.e.

$$\Omega_i^+ = \bigcup_{n=1}^{+\infty} (a_{n-1}^i, a_n^i)$$

with $q_i(a_j^i) = 0$ if $a_j^i \in \mathbb{R}$ and

$$\lim_{a \rightarrow a_j^i} q_i(a) = 0$$

if $a_j^i = +\infty$. In fact, for the latter assertion, observe that $q_i \in W^{1,1}(0, +\infty) \Rightarrow q_i \in \mathcal{BV}(0, +\infty) \cap L^1(0, +\infty)$; since $q_i \in L^1(0, +\infty)$, $\liminf_{a \rightarrow +\infty} |q_i(a)| = 0$; since $q_i \in \mathcal{BV}(0, +\infty)$, $\limsup_{a \rightarrow +\infty} |q_i(a)| = \liminf_{a \rightarrow +\infty} |q_i(a)|$. It follows $\lim_{a \rightarrow +\infty} q_i(a) = 0$, which is our claim.

Hence

$$\int_{\Omega_i^+} q'_i(a) da = 0;$$

in an analogous way, $\int_{\Omega_i^-} q_i'(a) da = 0$. Rearranging the sums in (4.5) (remember that all the sums are, in fact, finite) we get

$$\begin{aligned}
(4.6) \quad \langle Aq, \varphi \rangle &= - \sum_{i=1}^{+\infty} i \int_{\Omega_i^+} (\mu(a) + i\alpha) q_i(a) da + \sum_{i=1}^{+\infty} i \int_{\Omega_i^-} (\mu(a) + i\alpha) q_i(a) da \\
&+ \sigma \sum_{i=1}^{+\infty} \left[- \int_{\Omega_i^+} i^2 q_i(a) da + \int_{\Omega_i^-} i^2 q_i(a) da + \int_{\Omega_{i-1}^+} (i-1) i q_i(a) da \right. \\
&\quad \left. - \int_{\Omega_{i-1}^-} (i-1) i q_i(a) da \right] + \sigma \left(\int_{\Omega_0^+} q_1(a) da - \int_{\Omega_0^-} q_1(a) da \right) \\
&\quad - \int_{\Omega_0^+} \mu(a) q_0(a) da + \int_{\Omega_0^-} \mu(a) q_0(a) da \\
&= - \sum_{i=1}^{+\infty} i \int_0^{+\infty} (\mu(a) + i\alpha) |q_i(a)| da - \int_0^{+\infty} \mu(a) |q_0(a)| da \\
&\quad - \sigma \sum_{i=2}^{+\infty} \left[\int_{\Omega_i^+ \cap \Omega_{i-1}^+} i q_i(a) da + \int_{\Omega_i^+ \cap \Omega_{i-1}^-} i(2i-1) q_i(a) da - \int_{\Omega_i^- \cap \Omega_{i-1}^-} i q_i(a) da \right. \\
&\quad \left. - \int_{\Omega_i^- \cap \Omega_{i-1}^+} i(2i-1) q_i(a) da \right] - 2\sigma \left(\int_{\Omega_1^+ \cap \Omega_0^-} q_1(a) da - \int_{\Omega_1^- \cap \Omega_0^+} q_1(a) da \right) \leq 0.
\end{aligned}$$

Clearly, $\overline{D(A)} = X$ and hence, as argued above, A is closable and \bar{A} is dissipative. Now, to prove that $\mathcal{R}(\lambda I - A)$ is dense in X for all $\lambda > 0$, it is sufficient to prove that for each $p \in D(A)$ there exists $q \in D(A)$ such that $\lambda q - Aq = p$. Suppose that $p_i \equiv 0$ for $i > N$; then take $q = (q_i)_{i \in \mathbb{N}}$ such that $q_i \equiv 0$ for $i > N$ and q_N is the solution of

$$(4.7) \quad \begin{cases} q_N'(a) = -(\lambda + \mu(a) + N(\alpha + \sigma))q_N(a) + p_N(a) \\ q_N(0) = 0 \end{cases}$$

i.e.

$$(4.8) \quad q_N(a) = \int_0^a e^{-\int_s^a (\lambda + \mu(\tau) + N(\alpha + \sigma)) d\tau} p_N(s) ds.$$

Then, for $i < N$, q_i is the solution of

$$(4.9) \quad \begin{cases} q_i'(a) = -(\lambda + \mu(a) + i(\alpha + \sigma))q_i(a) + p_i(a) + \sigma(i+1)q_{i+1}(a) \\ q_i(0) = 0 \end{cases}$$

where q_{i+1} has been found in the previous steps.

Clearly, $q \in D(A)$, and by construction $\lambda q - Aq = p$ which proves our claim.

To see that the semigroup is positive, take $q^0 \in D(A) \cap X_+$ and suppose that $q_i^0 \equiv 0$ for all $i > N$. The solution of

$$(4.10) \quad \begin{cases} q'(t) = Aq(t) \\ q(0) = q^0 \end{cases}$$

can be constructed as follows. For $i > N$, $q_i(a, t) \equiv 0$ solve the equations. For $i = N$ the problem

$$\begin{cases} \frac{\partial}{\partial t} q_N(a, t) = -\frac{\partial}{\partial a} q_N(a, t) - (\mu + N(\alpha + \sigma))q_N(a, t) \\ q_N(a, 0) = q_N^0(a) \end{cases}$$

has the solution defined by

$$\begin{cases} q_N(a, t) = q_N(a - t, 0)e^{-\int_{a-t}^a \mu(s) + N(\alpha + \sigma) ds} & a > t \geq 0 \\ q_N(a, t) = 0 & t \geq a \geq 0. \end{cases}$$

For $i < N$ the problem

$$\begin{cases} \frac{\partial}{\partial t} q_i(a, t) = -\frac{\partial}{\partial a} q_i(a, t) - (\mu(a) + i(\alpha + \sigma))q_i(a, t) + \sigma(i + 1)q_{i+1}(a, t) \\ q_i(a, 0) = q_i^0(a) \end{cases}$$

has the solution defined by

$$\begin{cases} q_i(a, t) = q_i(a - t, 0)e^{-\int_{a-t}^a \mu(s) + N(\alpha + \sigma) ds} \\ \quad + (i + 1) \int_0^t \sigma e^{-\int_{a-t+s}^a \mu(r) + N(\alpha + \sigma) dr} q_{i+1}(a - t + s, s) ds & a > t \geq 0 \\ q_i(a, t) = 0 & t \geq a \geq 0. \end{cases}$$

Clearly the solution $q(t) \equiv (q_i(\cdot, t))_{i \in \mathbb{N}} \in X_+$. By density, the same will be true for $e^{t\bar{A}}q^0$ for all $q^0 \in X_+$, that is the semigroup generated by \bar{A} is positive. \square

From now on, we will write A meaning, in fact, its closure \bar{A} whenever this will not cause ambiguity.

Proposition 4.2. $H(p) \in F_A$ for all $p \in X$.

Proof. It is $H(p) = (C(p)\pi(\cdot), 0, 0, \dots)$, where $C(\cdot)$ is a real function, precisely

$$C(p) = -\psi \left(\int_0^{+\infty} \sum_{i=0}^{+\infty} p_i(a) da \right) \left(\int_0^{+\infty} \beta(a) \sum_{i=0}^{+\infty} p_i(a) \xi^i da \right).$$

Moreover, if $p = (p_0, 0, 0, \dots)$, $e^{tA}p$ is represented by the well known [I] semi-group of age-structured populations without fertility, namely

$$(e^{tA}p)_0 = \begin{cases} p_0(a - t) \frac{\pi(a)}{\pi(a-t)} & \text{if } a > t \\ 0 & \text{if } a < t \end{cases}$$

and $(e^{tA}p)_i \equiv 0$ for $i \geq 1$.

Hence, for each $t > 0$, we have

$$(4.11) \quad \frac{1}{t} \|e^{tA}(Hp) - Hp\| = \frac{1}{t} \int_0^t |C(p)\pi(a)| da$$

whence

$$\limsup_{t \rightarrow 0^+} \frac{1}{t} \|e^{tA}(Hp) - Hp\| = \lim_{t \rightarrow 0^+} \frac{1}{t} \int_0^t |C(p)\pi(a)| da = |C(p)|$$

and therefore $H(p) \in F_A$. □

Before stating the main result we need two more lemmas.

Lemma 4.3. *Let $\alpha > 0$. The operator U_α on $W_T = C([0, T], X)$ defined by*

$$[U_\alpha u](t) := A \int_0^t e^{(A - \frac{1}{\alpha})(t-s)} H(u(s)) ds$$

is positive, i.e. it takes positive functions into positive functions.

Proof. Set

$$I_t(u) := \int_0^t e^{-\frac{1}{\alpha}(t-s)} e^{(t-s)A} H(u(s)) ds.$$

It is easy to see (see for instance [7]) that

$$e^{-\frac{1}{\alpha}(t-s)} [e^{(t-s)A} H(u(s))]_0(a) = \begin{cases} e^{-\frac{1}{\alpha}(t-s)} C(u(s))\pi(a) & \text{if } a \geq t - s \\ 0 & \text{otherwise,} \end{cases}$$

and

$$e^{-\frac{1}{\alpha}(t-s)} [e^{(t-s)A} H(u(s))]_i(a) \equiv 0 \quad \text{if } i \geq 1.$$

Hence, $I_t(u)$ has a unique component not identically zero, which is

$$[I_t(u)]_0(a) = \begin{cases} e^{-\frac{1}{\alpha}t}\pi(a) \int_0^t e^{\frac{1}{\alpha}s} C(u(s)) ds & \text{if } t \leq a \\ e^{-\frac{1}{\alpha}t}\pi(a) \int_{t-a}^t e^{\frac{1}{\alpha}s} C(u(s)) ds & \text{if } t > a. \end{cases}$$

Finally

$$[A(I_t(u))]_0(a) = \begin{cases} 0 & \text{if } t \leq a. \\ -e^{-\frac{1}{\alpha}a}\pi(a)C(u(t-a)) & \text{if } t > a, \end{cases}$$

and $[A(I_t(u))]_i \equiv 0$ if $i \geq 1$. If $u(s) \geq 0$ for each $s \in [0, T]$ then $C(u(s)) \leq 0$ and $[A(I_t(u))]_0 \geq 0$, which proves the claim. □

Lemma 4.4. *For each $R > 0$ there exists $\alpha > 0$ such that $(I + \alpha F_R)X_+ \subset X_+$.*

Proof. Take $u \geq 0$; then, setting $\bar{u} = \pi_R(u)$, we see that $(I + \alpha F_R)u \geq 0$ if and only if

$$\frac{\alpha h \sum_{j=1}^{+\infty} j \int_0^{+\infty} \bar{u}_j}{c + \sum_{j=0}^{+\infty} \int_0^{+\infty} \bar{u}_j} (\bar{u}_{i-1} - \bar{u}_i) + u_i \geq 0$$

for each $i \geq 0$, always setting $\bar{u}_{-1} = 0$. Recalling that $0 \leq \bar{u}_i \leq u_i$, we see that this inequality is true for all i if $1 - \alpha\varphi(\bar{u}) \geq 0$, where

$$\varphi(\bar{u}) = \frac{h \sum_{j=1}^{+\infty} j \int_0^{+\infty} \bar{u}_j(s) ds}{c + \sum_{j=0}^{+\infty} \int_0^{+\infty} \bar{u}_j(s) ds}$$

Since it can be easily seen that $\varphi(\bar{u}) \leq \frac{hR}{c}$, the thesis holds if $\alpha \leq \frac{c}{hR}$. \square

Finally, we are able to state

Theorem 4.5. *If (H1)-(H3) hold, the Cauchy problem on X*

$$(4.12) \quad \begin{cases} p'(t) = A(p(t) + H(p(t))) + F(p(t)) \\ p(0) = p^0 \end{cases}$$

where X , A , H and F have been defined above, has, if $p^0 \in X_+$, a unique mild solution in X_+ . If moreover $p^0 + H(p^0) \in D(A)$, then the mild solution is classical.

Proof. It follows from Theorems 2.1 and 3.2 (see also Remark 3.4).

In fact, it can be easily seen that the maps F and H are Lipschitz continuous and differentiable on X_+ because of the hypotheses on ψ and β . Moreover, Lemmas 4.3 (the same proof, with the necessary and obvious adjustments, works with H_R instead of H) and 4.4 show that the assumptions of Theorem 3.2 hold. \square

The remaining of the section is devoted to prove that the solution yielded by Theorem 4.5 is, in fact, global.

Proposition 4.6. *Let (H1)-(H2)-(H3) hold. Let $p(t) = (p_i(\cdot, t))_{i \in \mathbb{N}}$ be a positive solution of (4.12) defined on $[0, t_{max})$. Then there exists $L > 0$ such that $\|p(t)\| \leq \|p(0)\|e^{Lt}$ for each $t \in [0, t_{max})$.*

Proof. First, we prove that the *a priori* estimate holds if the initial datum is taken in a smaller domain, then, by a density argument, we conclude that the same is true for all $p^0 \in X$.

Consider the Banach space

$$X_1 := \left\{ p = (p_i)_{i \in \mathbb{N}} : p_i \in L^1(0, +\infty) \forall i \geq 0, \sum_{i=1}^{+\infty} i^2 \int_0^{+\infty} |p_i(a)| da < \infty \right\}$$

endowed with the norm

$$\|p\|_1 := \int_0^{+\infty} |p_0(a)| da + \sum_{i=1}^{+\infty} i^2 \int_0^{+\infty} |p_i(a)| da.$$

The operator A defined in (4.1) satisfies Theorem 4.1 also in X_1 : one needs only to modify (4.6) in a straightforward way. Hence A_1 , the closure of A in X_1 , generates a positive, strongly continuous semigroups of contractions. Consider now

$$(4.13) \quad \begin{cases} p'(t) = A_1(p(t) + H_1(p(t))) + F_1(p(t)) \\ p(0) = p^0. \end{cases}$$

where $F_1 := F|_{X_1 \cap E}$ and $H_1 := H|_{X_1}$.

It is not difficult to prove that H_1 and F_1 are locally Lipschitz continuous with respect to $\|\cdot\|_1$ and $|\cdot|_{F(\bar{A}_1)}$ and are continuously differentiable on $(X_1)_+$. Moreover, Proposition 4.2, Lemma 4.3, Lemma 4.4 can be rephrased for the space X_1 and the operators A_1, F_1, H_1 . The conclusion is that problem (4.13) is well-posed on $(X_1)_+$.

Now, if $p(t) = (p_i(a, t))_{i \in \mathbb{N}}$ is a classical positive solution of (4.12) with the additional hypothesis that $p^0 + H(p^0) \in D(A_1)$ then $p(t)$ is a solution of (4.13). Therefore $p(t) \in X_1$ for all t .

For a positive solution, $\|p(t)\| = L(p(t))$, where L is the bounded linear operator, defined by

$$Lp := \int_0^{+\infty} p_0(a) da + \sum_{i=1}^{+\infty} i \int_0^{+\infty} p_i(a) da.$$

Since L is a bounded linear operator on X and $p \in C^1([0, T], X)$, we have

$$(4.14) \quad \begin{aligned} \frac{d}{dt} \|p(t)\| &= (L(p(t)))' = L(p'(t)) \\ &= \int_0^{+\infty} \frac{\partial}{\partial t} p_0(a, t) da + \sum_{i=1}^{+\infty} i \int_0^{+\infty} \frac{\partial}{\partial t} p_i(a, t) da. \end{aligned}$$

Now, for $i = 0, 1, 2, \dots$ we have

$$(4.15) \quad \begin{aligned} \int_0^{+\infty} \frac{\partial}{\partial t} p_i(a, t) da &\leq - \int_0^{+\infty} \frac{\partial}{\partial a} p_i(a, t) da \\ &\quad - \int_0^{+\infty} (\mu_- + \varphi(t) + i(\alpha + \sigma)) p_i(a, t) da \\ &\quad + \int_0^{+\infty} \sigma(i+1) p_{i+1}(a, t) da + \int_0^{+\infty} \varphi(t) p_{i-1}(a, t) da. \end{aligned}$$

setting, as usual, $p_{-1} \equiv 0$. As already shown, $p_i(a, t)$ are, for all t , absolutely continuous function in the variable a , satisfying $\lim_{a \rightarrow \infty} p_i(a, t) = 0$. Hence, from (4.15) we obtain

$$(4.16) \quad \int_0^{+\infty} \frac{\partial}{\partial t} p_i(a, t) da \leq p_i(0, t) - (\mu_- + \varphi(t) + i(\alpha + \sigma))P_i(t) \\ + \sigma(i+1)P_{i+1}(t) + \varphi(t)P_{i-1}(t)$$

where

$$P_i(t) = \int_0^{\infty} p_i(a, t) da.$$

Inserting (4.16) into (4.14), we have

$$(4.17) \quad \frac{d}{dt} \|p(t)\| \leq - \sum_{i=1}^{+\infty} (\mu_- + \varphi(t) + i(\alpha + \sigma))iP_i(t) + \sum_{i=1}^{+\infty} \sigma i(i+1)P_{i+1}(t) \\ + \varphi(t) \sum_{i=1}^{+\infty} iP_{i-1}(t) + p_0(0, t) - (\mu_- + \varphi(t))P_0(t) + \sigma P_1(t) \\ = -\mu_- \sum_{i=1}^{+\infty} iP_i(t) - \varphi(t) \sum_{i=1}^{+\infty} iP_i(t) - \alpha \sum_{i=1}^{+\infty} i^2 P_i(t) - \sigma \sum_{i=1}^{+\infty} i^2 P_i(t) \\ + \sigma \sum_{i=1}^{+\infty} (i+1)^2 P_{i+1}(t) - \sigma \sum_{i=1}^{+\infty} (i+1)P_{i+1}(t) + \varphi(t) \sum_{i=1}^{+\infty} iP_{i-1}(t) \\ - (\mu_- + \varphi(t))P_0(t) + \sigma P_1(t) + p_0(0, t) \\ \leq -\mu_- \|p(t)\| - \alpha \sum_{i=1}^{+\infty} i^2 P_i(t) - \sigma \sum_{i=1}^{+\infty} (i+1)P_{i+1}(t) + \varphi(t) \sum_{i=1}^{+\infty} P_i(t) + p_0(0, t).$$

Note that all the series converge, and all rearrangements are justified because, for each t , $p(t) \in X_1$ whence $\sum_{i=1}^{+\infty} i^2 P_i(t) < \infty$.

Thus

$$\frac{d}{dt} \|p(t)\| \leq -\mu_- \|p(t)\| - \alpha \sum_{i=1}^{+\infty} iP_i(t) - \sigma \sum_{i=1}^{+\infty} (i+1)P_{i+1}(t) \\ + \frac{h \sum_{i=1}^{+\infty} iP_i(t)}{c + \sum_{i=0}^{+\infty} P_i(t)} \left(\sum_{i=1}^{+\infty} P_i(t) \right) + \|\beta\|_{L^\infty} \sum_{i=0}^{+\infty} P_i(t) \\ \leq [h + \|\beta\|_{L^\infty} - \mu_-] \|p(t)\|$$

and then $\|p(t)\| \leq \|p(0)\| e^{(h+\|\beta\|-\mu_-)t}$.

By a density argument the same estimate holds for all $p^0 \in X_+$. \square

Corollary 4.7. *If $p^0 \in X_+$, then the mild solution of (4.12) is global.*

Proof. Apply Theorem 2.1, part b). \square

Finally, we wish to show that, under assumption (H3'), the positive solutions are ultimately bounded. Precisely

Theorem 4.8. *Let (H1)-(H2)-(H3') hold; assume moreover*

$$(H5) \quad \sup \{a : \beta(a) > 0\} < +\infty.$$

Then there exists M such that $\forall p^0 \in X_+$, $N(t) \leq M$ and $P(t) \leq M$ for all $t > T$ for some suitable T .

Proof. Choose initially p^0 such that $p^0 + H(p^0) \in D(A_1)$.

Take

$$u(a, t) = \sum_{i=0}^{\infty} p_i(a, t)$$

the age-density of total host population. With some algebra, we have

$$\frac{\partial}{\partial t} u(a, t) = -\mu(a)u(a, t) - \alpha \sum_{i=0}^{\infty} i p_i(a, t) = -\tilde{\mu}(a, t)u(a, t)$$

with

$$(4.18) \quad \tilde{\mu}(a, t) = \begin{cases} \mu(a) + \alpha \frac{\sum_{i=0}^{\infty} i p_i(a, t)}{u(a, t)} & \text{if } u(a, t) > 0 \\ \mu(a) & \text{if } u(a, t) = 0. \end{cases}$$

Analogously, one can write

$$u(0, t) = \int_0^{\infty} \tilde{\beta}(a, t, S(t))u(a, t) da$$

with

$$(4.19) \quad \tilde{\beta}(a, t, s) = \begin{cases} \psi(s)\beta(a) \frac{\sum_{i=0}^{\infty} i^s p_i(a, t)}{u(a, t)} & \text{if } u(a, t) > 0 \\ \psi(s)\beta(a) & \text{if } u(a, t) = 0 \end{cases}$$

and $S(t) = N(t)$.

One can then apply Theorem 1 of [8] to obtain $N(t) \leq M$ for $t > T$. In that Theorem the fertility and mortality functions are not supposed to depend directly on time t , but it is straightforward modifying its proof to cover this case, since the assumptions (16) and (17) of that Theorem are satisfied. Moreover, assumption (H5) can be used in place of the maximal age $a_{\dagger} < +\infty$ used in [8].

Now, we compute $P'(t)$ as in (4.17), obtaining

$$P'(t) \leq -\mu_- P(t) - \alpha \sum_{i=1}^{+\infty} i^2 P_i(t) - \sigma P(t) + \varphi(t)N(t).$$

From Holder's inequality, we have

$$\sum_{i=0}^{+\infty} i^2 P_i(t) \geq \frac{(\sum_{i=0}^{+\infty} i P_i(t))^2}{\sum_{i=0}^{+\infty} P_i(t)} = \frac{P^2(t)}{N(t)}.$$

Using also $\varphi(t)N(t) \leq hP(t)$, we obtain

$$P'(t) \leq (h - \mu_-)P(t) - \alpha \frac{P^2(t)}{N(t)} \leq P(t)(h - \mu_- - \frac{\alpha}{M}P(t)).$$

From this, one immediately sees $\limsup_{t \rightarrow \infty} P(t) \leq M(h - \mu_-)/\alpha$, which is the thesis.

By density, the same will hold for all $p^0 \in X_+$. □

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