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# Modelling physiologically structured populations: renewal equations and partial differential equations

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*Abstract.* We analyse the long term behaviour of the measure-valued solutions of a class of linear renewal equations modelling physiologically structured populations. The renewal equations that we consider are characterised by a regularisation property of the kernel. This regularisation property allows to deduce the large time behaviour of the measure-valued solutions from the asymptotic behaviour of their absolutely continuous, with respect to the Lebesgue measure, component. We apply the results to a model of cell growth and fission and to a model of waning and boosting of immunity. For both models we relate the renewal equation to the partial differential equation (PDE) formulation and draw conclusions about the asymptotic behaviour of the solutions of the PDEs.

#### 1. Introduction

Models of physiologically structured populations can take various forms. If the individual states are discrete stages in which individuals sojourn for an exponentially distributed amount of time, then it is natural to formulate the model at the population level as a system of ordinary differential equations describing the rate of change of the number of individuals in the different stages [18,42]. If the individual states form a continuum, like in e.g. age-size structured populations, there are several popular modelling approaches.

A very natural, and historically the oldest, approach is to formulate an integral equation of renewal type for the population birth rate. The method is based on the observation that those who are born at the current time are the children of individuals who were themselves born in the past, have survived up to the current time and give birth at the current time. This approach was formalised by Lotka [31] and Sharpe and Lotka [39] for age structured populations, using ideas going back to Euler [17].

Another way to model the dynamics of structured populations is to first write down a partial differential equation (PDE) of transport-degradation type describing development (movement in the individual state space) and survival. After that, the PDE is augmented by a rule for reproduction. This can either lead to extra non-local terms in the PDE, like in models of individuals reproducing by fission, or to non-local

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boundary conditions, like in age-size structured models in which newborns enter the individual state space at the boundary where age is zero. The PDE-approach was first introduced by McKendrick [33] for age-structured populations and later adapted to age-size-structured populations by Tsuchiya et al. [44], Bell and Anderson [3] and others. For a data oriented discrete time variant, see [16] and [9].

Here we focus on the integral equation for the population birth rate, which in general is a measure representing the rate at which individuals are born in different subsets of the individual state space. If there are no dependencies between individuals such as competition for resources, that is, if the environmental condition is given, then the integral equation is linear and of renewal type. Here we assume that the environmental condition is constant in time.

In a recent paper, [19], we considered the question when such a renewal equation can be reduced to a one dimensional renewal equation in the sense that the measurevalued solution of the original equation can be recovered from the solution of the one dimensional reduction. In the present paper we analyse the renewal equation when a different, less restrictive, assumption on the kernel is satisfied and prove asynchronous exponential growth/decline for the solution of the renewal equation.

Our interest in measure-valued solutions is motivated by the fact that it allows to consider in a unified way the case in which  $\Omega$  is a discrete set and the case in which we have a continuum of states. Moreover, considering measure-valued solutions for REs allows us to draw the connection with measure-valued solutions of PDEs, that have gained much interest in the last years, see for instance [15].

We apply our results to two concrete population models: a model of cell growth and fission (into equal or unequal parts) and a model of waning and boosting of the immunity level. As anticipated above, these models can be also formulated as PDEs, see (6.1), (6.2), (6.11) and could also be analysed in the PDE framework as has been done in [5,8,36].

The aim of this paper is twofold. On one hand we reiterate the message presented in [19], i.e., renewal equations are suitable when dealing with measure-valued solutions. The reason is that the existence and uniqueness of their solution can be proven constructively as in the case of scalar equations and, moreover, since renewal equations are integral equations, no regularity assumption with respect to the time variable is required for the concept of solution. This is in contrast with what happens in the PDE framework, where it is typically necessary to work with weak solutions in the measure sense, i.e., weak solutions of the dual equation, see (7.4).

The second aim of the paper is to provide applicable techniques, based on the work presented in [26] and [28], to study the asymptotic behaviour of the measure-valued solutions of renewal equations.

In the case of age-structured populations the relationship between the renewal equation and PDE approaches is well understood and discussed in an abstract setting in [13]. In the case of size-structured populations the relationship between the two formulations has been investigated in [7] and [2]. In the closing section of the present paper we show that the measure-valued solutions of the renewal equation yield a solution of a corresponding PDE and we deduce the asymptotic behaviour of the solution of the PDE from the behaviour of the solution of the RE.

The paper is organised as follows: in Sect. 2 we provide conditions on the kernel that guarantee the existence of a unique solution for the renewal equation. In Sect. 3 we introduce the main assumption of this work: the kernel has a regularising effect on the initial condition. We also motivate heuristically the assumption.

In Sect. 4 we prove asynchronous exponential growth for the solution of the renewal equation when the kernel satisfies the assumption presented in Sect. 3. We do this by adapting the methods presented in [26] and [28]. The aim of Sect. 5 is to show that kernels satisfying the regularisation assumption arise in applications. We analyse the corresponding models in Sect. 6. Finally, as anticipated above, Sect. 7 is devoted to the connection between REs and PDEs.

In Appendix A we collect explanations of the notational conventions, while in Appendix B we collect results on the existence of a unique solution for the PDE that corresponds to the renewal equation we study.

# 2. The renewal equation: existence and uniqueness of the solution

In this paper we study linear physiologically structured population models that can be formalised via a renewal equation with a measure-valued solution. More precisely, we consider a population of individuals characterised by a structuring variable, *i*-state. We assume that the individual state evolves in time due to different individual level mechanisms that might be continuous and deterministic, as is growth, or discontinuous and stochastic, as is fission.

We denote with  $\Omega$  the set of the possible *i*-states and we assume that  $\Omega$  is a Borel subset of  $\mathbb{R}^n$ . The set of the possible states at birth is  $\Omega_0 \subset \Omega$ .

We denote with  $B(t, \omega)$  the population birth rate, that is the rate at which individuals appear in the population with state in the set  $\omega \in \mathscr{B}(\Omega_0)$  at time *t*. Note that when an individual jumps from state A to another state B, we will say that an individual with state A has died and that an individual with state B is born. Likewise, in the case of cell fission, we consider the disappearance of the mother as 'death' and the appearance of the two daughters as 'birth'.

If we assume that the population distribution at time zero is a given datum  $M_0 \in \mathcal{M}_{+,b}(\Omega)$ , then we deduce that *B* solves

$$B(t,\omega) = \int_0^t \int_{\Omega_0} K(a,\xi,\omega) B(t-a,d\xi) da + B_0(t,\omega) \quad t > 0, \, \omega \in \mathscr{B}(\Omega_0) \quad (2.1)$$

where  $K(t, \xi, \omega)$  is interpreted as the rate at which an individual, having state  $\xi$  time *t* ago, gives birth to an individual with state in the set  $\omega$  and

$$B_0(t,\omega) := \int_{\Omega} K(t,x,\omega) M_0(dx).$$
(2.2)

Here we repeat the definition of locally bounded kernels, and of their convolution, from [19], but we refer to the Appendix of that paper for the proofs of the results presented below.

**Definition 2.1.** (*Locally bounded kernel*) A locally bounded kernel is a positive function  $K : \mathbb{R}_+ \times \Omega \times \mathscr{B}(\Omega_0) \to \mathbb{R}_+$  with the following properties

- 1. for every  $(a, \xi) \in \mathbb{R}_+ \times \Omega$ ,  $K(a, \xi, \cdot) \in M_+(\Omega_0)$  (space of positive Borel measures)
- 2. for every  $\omega \in \mathscr{B}(\Omega_0)$ , the function

$$(a,\xi) \mapsto K(a,\xi,\omega), \quad (a,\xi) \in \mathbb{R}^+ \times \Omega$$

is measurable (with respect to the product Borel  $\sigma$ -algebra).

3. for any T > 0

$$\sup_{(a,\xi)\in[0,T]\times\Omega}K(a,\xi,\Omega_0)<\infty.$$

The middle argument  $\xi$  of *K* ranges over all of  $\Omega$  only in connection with the initial condition, cf. (2.2). In connection with births it ranges over  $\Omega_0$ . We therefore define  $\mathbb{B}_{loc}$ , the *set of the locally bounded kernels*, as the set of kernels defined on  $\mathbb{R}_+ \times \Omega_0 \times \mathscr{B}(\Omega_0)$  such that the properties of Definition 2.1 hold with  $\xi$  restricted to  $\Omega_0$ .

**Definition 2.2.** (*Convolution product of kernels*) We define the convolution product of  $K_1, K_2 \in \mathbb{B}_{loc}$ , as

$$(K_2 * K_1)(t, x, \omega) := \int_0^t \int_{\Omega_0} K_2(t - s, \xi, \omega) K_1(s, x, d\xi) ds.$$
(2.3)

**Definition 2.3.** (*Semiring*) A semiring R is a set endowed with two binary operations, addition + and multiplication \*, such that

- (R, +) is a commutative monoid with identity element **0**: i.e. for every element  $a, b, c \in R$  we have that (a + b) + c = a + (b + c), for every  $a, b \in R$  we have that a + b = b + a and for every  $a \in R$  we have that  $a + \mathbf{0} = a$ ;
- (R, \*) is a semigroup: for every  $a, b, c \in R$  we have that (a\*b)\*c = a\*(b\*c);
- multiplication from the right and from the left is distributive over the addition,
- multiplication by **0** annihilates *R*: for every  $a \in R$  we have that  $a * \mathbf{0} = \mathbf{0} * a = \mathbf{0}$ .

**Lemma 2.4.** (Properties of the convolution) The convolution product \* of two locally bounded kernels is a locally bounded kernel. The set  $\mathbb{B}_{loc}$ , equipped with the sum and with the convolution product \*, is a semiring.

Unlike the classical convolution of scalar functions, the convolution \* defined by (2.2) is not commutative. Moreover,  $(\mathbb{B}_{loc}, *)$  is a semigroup, but not a monoid. The reason is that the candidate identity element **1** is a Dirac measure in the time/age variable, indeed  $\mathbf{1}(t, x, \omega) = \delta_0(t)\chi_{\omega}(x)$ . Hence **1** does not belong to  $\mathbb{B}_{loc}$ .

**Definition 2.5.**  $\mathscr{X}$  denotes the set of functions  $f : \mathbb{R}_+ \times \mathscr{B}(\Omega_0) \to \mathbb{R}_+$  such that for every  $a \in \mathbb{R}_+$ ,  $f(a, \cdot)$  is a measure, the function  $f(\cdot, \omega)$  is measurable for every  $\omega \in \mathscr{B}(\Omega_0)$  and  $f(\cdot, \Omega_0)$  is locally integrable.

**Definition 2.6.** Given  $K \in \mathbb{B}_{loc}$  and  $f \in \mathcal{X}$ , we denote with  $\mathcal{L}_K f$  the convolution of *K* and *f*, defined by

$$(\mathscr{L}_K f)(t,\omega) := \int_0^t \int_{\Omega_0} K(t-\sigma, x, \omega) f(\sigma, dx) d\sigma \quad t \ge 0 \quad \omega \in \mathscr{B}(\Omega_0).$$
(2.4)

**Lemma 2.7.** If  $K \in \mathbb{B}_{loc}$ , then the operator  $\mathscr{L}_K$  is a linear operator from  $\mathscr{X}$  to itself. If  $K_1, K_2 \in \mathbb{B}_{loc}$ , then  $\mathscr{L}_{K_2}\mathscr{L}_{K_1} = \mathscr{L}_{K_2 * K_1}$ .

We now interpret (2.1) as the equation  $B = \mathscr{L}_K B + B_0$  with given  $B_0 \in \mathscr{X}$  and unknown  $B \in \mathscr{X}$ .

**Proposition 2.8.** Let  $K \in \mathbb{B}_{loc}$  and  $B_0 \in \mathscr{X}$ . Then, there exists a unique solution B of equation (2.1) and it is given by

$$B = B_0 + \mathscr{L}_R B_0 \tag{2.5}$$

where  $R \in \mathbb{B}_{loc}$  is the resolvent of the kernel K defined by  $R = \sum_{n=1}^{\infty} K^{*n}$  where  $K^{*1} = K$  and for every  $n \ge 2$ 

$$K^{*n} = K^{*(n-1)} * K.$$

We deduce that, if *K* is a locally bounded kernel and if  $B_0$  is given by (2.2), where  $M_0 \in \mathscr{M}_{+,b}(\Omega)$ , then  $B_0 \in \mathscr{X}$  and equation (2.1) has a unique solution.

#### 3. Reduction to densities

In this subsection we present the assumptions on the kernel K that allow us to study the asymptotic behaviour of the solution of equation (2.1) by studying the asymptotic behaviour of the density of its non-singular component. We start with an heuristic explanation of the simplification achieved in this manner.

We can rewrite equation (2.1) in the following translation invariant form

$$B(t,\omega) = \int_0^\infty \int_{\Omega_0} K(a,\xi,\omega) B(t-a,d\xi) da$$
(3.1)

where for every  $\omega \in \mathscr{B}(\Omega_0)$ ,  $B(\theta, \omega)d\theta := \Phi(d\theta, \omega)$  if  $\theta < 0$  with  $\Phi$  a given measure. We allow  $\Phi$  to be a measure with respect to the time-of-birth variable simply because it does not harm. The fact that equation (3.1) is translation invariant and linear suggests to look for exponential solutions of the form:

$$B(t,\omega) := e^{\lambda t} \Psi(\omega) \text{ for every } t \in \mathbb{R}.$$
(3.2)

We want to investigate whether such exponential solutions exist and whether they are attractive, i.e., describe the long-term behaviour of B.

To guarantee the convergence of the relevant integrals we make the following assumption.

**Assumption 3.1.** There exists a  $z_0 < 0$  and a constant C > 0 such that for every  $t \ge 0$ 

$$\sup_{x \in \Omega_0} K(t, x, \Omega_0) \le C e^{z_0 t}.$$
(3.3)

We say that a locally bounded kernel that satisfies Assumption 3.1 is a  $z_0$ -bounded kernel.

Substituting the Ansatz (3.2) in (3.1) we obtain the following non-linear eigenproblem

$$\Psi(\omega) = \int_0^\infty \int_{\Omega_0} e^{-\lambda a} K(a,\xi,\omega) \Psi(d\xi) da.$$
(3.4)

So we need to study the properties of the operator

$$\Psi \mapsto \int_0^\infty \int_{\Omega_0} e^{-\lambda a} K(a,\xi,\cdot) \Psi(d\xi) da.$$

that maps  $\mathcal{M}_{+,b}(\Omega_0)$  into itself. In particular we would like to prove its compactness, but this is a very difficult task when we deal with spaces of measures, see for instance [43].

Therefore we introduce regularity assumptions on *K* that allow us to reduce the non-linear eigenproblem (3.4) to measures that are absolutely continuous with respect to the Lebesgue measure, so to an associated non-linear eigenproblem in  $L^1(\Omega_0)$ . It is easiest to assume that for each *t* and *x* the measure K(t, x, .) has a density. But as we shall see in Sect. 5, there are natural examples in which the 'smoothing' needs one more step.

**Assumption 3.2.** For every  $x \in \Omega_0$ , every  $t \ge 0$  the measure

$$\omega \mapsto \int_0^t \int_{\Omega_0} K(t-a,\xi,\omega) K(a,x,d\xi) da$$
(3.5)

is absolutely continuous with respect to the Lebesgue measure. Moreover, for every  $t \ge 0$  and for every  $f \in L^1(\Omega_0)$  the measure

$$\omega \mapsto \int_{\Omega_0} K(t, x, \omega) f(x) dx \tag{3.6}$$

is absolutely continuous with respect to the Lebesgue measure.

**Definition 3.3.** We say that *K* is a  $z_0$ -bounded regularizing kernel if it is a  $z_0$ -bounded kernel that satisfies Assumption 3.2.

The interpretation of the absolute continuity with respect to the Lebesgue measure of (3.5) is that, when we focus on an individual with state x and look t time later at the distribution of the state-at-birth over  $\Omega_0$  of grandchildren born at that time, it has a density. So we require that the distribution concentrated in x is, by the combination of growth, survival and twice reproduction, transformed into an absolutely continuous distribution.

On the other hand, the absolute continuity, with respect to the Lebesgue measure, of (3.6), guarantees that, if the distribution of the states at birth of a certain generation is absolutely continuous with respect to the Lebesgue measure, then the same is true for the future generations.

We refer to Appendix A for an explanation of the notation used in the formulation of the following theorem (whose proof is given at the end of the current section).

**Theorem 3.4.** Let K be a  $z_0$ -bounded regularizing kernel and let  $B_0$  be given by (2.2) as a function of K and  $M_0 \in \mathcal{M}_{+,b}(\Omega)$ . Then the solution B of (2.1) satisfies

$$\|B(t, \cdot)^{s}\| \le c_{1}e^{z_{0}t} + c_{2}te^{tz_{0}} \quad t > 0$$
(3.7)

where  $\|\cdot\| = \|\cdot\|_{TV} = \|\cdot\|_{\flat}$  and  $c_1, c_2 > 0$ .

Since the operator  $\mathscr{L}_K$  is linear, equation (2.1) can be rewritten as

$$B^{AC} + B^s = \mathscr{L}_K B^{AC} + \mathscr{L}_K B^s + B_0^{AC} + B_0^s$$
(3.8)

Equation (3.8) can be decoupled in a system of two equations

$$B^{AC} = \mathscr{L}_K B^{AC} + \left(\mathscr{L}_K B^s\right)^{AC} + B_0^{AC}$$
(3.9)

and

$$B^{s} = \left(\mathscr{L}_{K}B^{s}\right)^{s} + B_{0}^{s}.$$
(3.10)

Thanks to Theorem 3.4 we can focus on the asymptotic behaviour of the density of  $B^{AC}$  to gain information regarding *B*.

We next present a definition and two lemmas which will be applied in the proof of Theorem 3.4.

**Definition 3.5.**  $\mathscr{I}$  is the set of the locally bounded kernels *K* such that

$$K(t, x, \cdot) \in \mathcal{M}_{+,AC}(\Omega_0)$$

for every  $t \ge 0$  and  $x \in \Omega_0$ .

**Definition 3.6.** (Right semi-ideal) Let *R* be a semiring with the binary operations + and \*. A set  $\mathscr{J} \subset R$  is a right semi-ideal if  $(\mathscr{J}, +)$  is a monoid and for every  $i \in \mathscr{J}$  and every  $K \in R$  we have that  $j * K \in \mathscr{J}$ .

**Lemma 3.7.** The set  $\mathscr{I}$  is a right semi-ideal. Moreover, if  $K \in \mathscr{I}$ , then for every  $t \geq 0$  and every  $f \in \mathscr{X}$ , we have that  $(\mathscr{L}_K f)(t, \cdot) \in \mathscr{M}_{+,AC}(\Omega_0)$ .

*Proof.* Assume that  $K_2 \in \mathscr{I}$  and that  $K_1 \in \mathbb{B}_{loc}$ . Consider a set A that has Lebesgue measure equal to zero. Since  $K_2 \in \mathscr{I}$ , we deduce that, for every  $t \ge 0$  and  $x \in \Omega_0$ ,

$$K_2(t, x, A) = 0.$$

By Definition 2.2 and formula (2.3), we deduce that, for every  $t \ge 0$  and  $x \in \Omega_0$ 

$$(K_2 * K_1)(t, x, A) = 0.$$

We conclude that for every  $t \ge 0$  and  $x \in \Omega_0$  the measure  $(K_2 * K_1)(t, x, \cdot)$  is absolutely continuous with respect to the Lebesgue measure, hence  $K_2 * K_1 \in \mathscr{I}$ . The second statement of the proof follows analogously from formula (2.4)

**Lemma 3.8.** If K satisfies Assumption 3.2, then  $\sum_{n=2}^{\infty} K^{*n} \in \mathscr{I}$ .

*Proof.* Thanks to Assumption 3.2 we know that  $K * K \in \mathscr{I}$ . Since  $\mathscr{I}$  is a right-ideal we deduce that, if  $K^{*n} \in \mathscr{I}$ , then  $K^{*n} * K = K^{*(n+1)} \in \mathscr{I}$ . We conclude by induction that  $\sum_{n=2}^{\infty} K^{*n} \in \mathscr{I}$ .

Proof of Theorem 3.4. Since B solves (2.1), then

$$B = B_0 + \mathscr{L}_R B_0 = B_0 + \mathscr{L}_K B_0 + \mathscr{L}_{\sum_{n=2}^{\infty} K^{*n}} B_0.$$

Thanks to Lemma 3.8 we deduce that

$$B^s = B_0^s + \mathscr{L}_K B_0^s.$$

As a consequence of the fact that for every  $t \ge 0$ ,  $B_0(t, \Omega_0) \le c_1 e^{z_0 t}$  and (3.3), we deduce that there exists  $c_2 > 0$  such that

$$\mathscr{L}_K B_0(t, \Omega_0) \le c_2 t e^{z_0 t}$$
 for every  $t \ge 0$ ,

hence  $B^{s}(t, \Omega_0) \le c_1 e^{z_0 t} + c_2 t e^{z_0 t}$ .

#### 4. Asymptotic behaviour of the solution of the renewal equation

In this section we denote with X the Banach space  $L^1(\Omega_0)$  endowed with the  $L^1$  norm  $\|\cdot\|_1$ . Moreover we denote with  $X_+$  the cone of the positive functions in  $L^1(\Omega_0)$  and we call the bounded linear operator  $L: X \to X$  positive if  $L: X_+ \to X_+$ .

To study the asymptotic behaviour of the solution B of (2.1) we adopt the following strategy:

- in Sect. 4.1 we introduce the renewal equation for the density of  $B^{AC}$  and we prove that it has a unique solution;
- in Sect. 4.2 we perform the Laplace transform to all the terms in the renewal equation for the density of  $B^{AC}$ . We derive in this way a non-linear eigenproblem;
- in Sect. 4.3 we present some results on positive operators that are important to study the non-linear eigenproblem derived in (4.2);

 $\square$ 

- in Sect. 4.4 we prove that there exists a unique, up to renormalisation, real eigencouple solving the non-linear eigenproblem derived in Sect. 4.2;
- in Sect. 4.5 we adapt the approach presented by Heijmans in [26] to prove that the solution of the non-linear eigenproblem is attractive, i.e., we deduce the asymptotic behaviour of the density of  $B^{AC}$ ;
- in Sect. 4.6 we sketch a different approach to derive the asymptotic behaviour of the density of  $B^{AC}$ ;
- in Sect. 4.7 we show that the behaviour of the density of  $B^{AC}$  determines the behaviour of B.
- 4.1. Renewal equation for the density

**Definition 4.1.** A positive locally bounded operator kernel is a map  $\tilde{K} : \mathbb{R}_+ \to \mathscr{L}(X)$  such that

- $\tilde{K}(a)$  is a positive operator for every  $a \ge 0$ ;
- the map  $a \mapsto \tilde{K}(a) f$  is Bochner measurable for every  $f \in X$ ;
- for every  $T \ge 0$

$$\sup_{a \in [0,T]} \|\tilde{K}(a)\|_{op} = \sup_{a \in [0,T]} \sup_{\{f \in X : \|f\|_1 \le 1\}} \|\tilde{K}(a)f\|_1 < \infty.$$
(4.1)

Since in this paper we will only deal with operator kernels that are positive and locally bounded, in the following we use the term *operator kernel* to refer to locally bounded operator kernels.

**Lemma 4.2.** Let  $\tilde{K}$  be an operator kernel. Let  $b_0 : \mathbb{R}_+ \to X$  be Bochner measurable and locally bounded. Then the equation

$$b(t) = \int_0^t \tilde{K}(t-a)b(a)da + b_0(t), \quad t \ge 0$$
(4.2)

-

has a unique solution  $b : \mathbb{R}^*_+ \to X$ , which is locally bounded and Bochner measurable.

*Proof.* The main step of the proof consists in proving the existence of the resolvent of  $\tilde{K}$ . To this end, we aim at proving that

$$\sup_{a \in [0,T]} \sup_{\{f \in X: \|f\|_1 \le 1\}} \|\tilde{R}(a)f\|_1 = \sup_{a \in [0,T]} \sup_{\{f \in X: \|f\|_1 \le 1\}} \|\sum_{n=1}^{\infty} \tilde{K}^{\star n}(a)f\|_1 < \infty$$

where for every  $f \in X$  and every  $a \ge 0$ 

$$K^{\star 1}(a)f := \tilde{K}(a)f$$

and for every  $n \ge 2$ 

$$\tilde{K}^{\star n}(a)f := \int_0^a \tilde{K}^{\star (n-1)}(a-s)\tilde{K}(s)fds.$$

To ensure that the resolvent is well defined, we need to prove that, if  $K_i$  are operator kernels, then  $K_1 \star K_2 : \mathbb{R}_+ \to \mathscr{L}(X)$ , defined by

$$K_1 \star K_2 : t \mapsto \left( f \mapsto \int_0^t K_1(t-a)K_2(a)fda \right)$$

is also an operator kernel. Inequality (4.1) follows by the boundedness properties of  $K_1$  and  $K_2$ , while the Bochner measurability can be proven by an adaptation of the proof of the measurability of the classical convolution product. See the proof of Theorem 1 in [22] for more details.

Hence, if

$$\sup_{\{f \in X: \|f\|_1 \le 1\}} \left\| \int_0^T \tilde{K}(s) f ds \right\|_1 < 1$$

then for every  $0 \le a \le T$ 

$$\sup_{\{f \in X: \|f\|_{1} \le 1\}} \|\tilde{R}(a)f\|_{1} = \sup_{\{f \in X: \|f\|_{1} \le 1\}} \left\| \sum_{n=1}^{\infty} \tilde{K}^{\star n}(a)f \right\|_{1}$$
$$\leq \sum_{n=1}^{\infty} \left( \sup_{\{f \in X: \|f\|_{1} \le 1\}} \left\| \int_{0}^{T} \tilde{K}(s)fds \right\|_{1} \right)^{n} < \infty.$$

If, instead,

$$\sup_{\{f \in X: \|f\|_1 \le 1\}} \left\| \int_0^T \tilde{K}(a) f da \right\|_1 \ge 1$$

the above argument can be adapted by considering a scaled version of  $\tilde{K}$ ,  $\tilde{K}_{\lambda}(a) := e^{-\lambda a} \tilde{K}(a)$ , with  $\lambda$  chosen such that

$$\sup_{\{f\in X:\|f\|_1\leq 1\}}\left\|\int_0^T \tilde{K}_{\lambda}(a)fda\right\|_1<1.$$

The uniqueness of the solution of equation (4.2) follows by standard arguments of renewal theory. See for instance [22] or [23, pp. 233–234].  $\Box$ 

4.2. Laplace transformed equation

In this section, we make the following assumptions on  $\tilde{K}$  and  $b_0$ .

Assumption 4.3.  $\tilde{K}$  is an operator kernel. Moreover, there exists a  $z_0 < 0$  and a constant C > 0 such that for every  $t \ge 0$ 

$$\|\tilde{K}(t)f\|_{1} \le Ce^{z_{0}t} \|f\|_{1}.$$
(4.3)

**Assumption 4.4.**  $b_0 : \mathbb{R}_+ \to X$  is a Bochner measurable function and there exists a c > 0 such that for every  $t \ge 0$ 

$$\|b_0(t)\|_1 \le ce^{z_0t} + c_1te^{z_0t} + c_2t^2e^{z_0t}.$$
(4.4)

We denote with b the solution of equation (4.2).

**Lemma 4.5.** There exists  $a \ \beta \in \mathbb{R}$  such that  $b(t)e^{-\lambda t}$  is integrable over  $\mathbb{R}_+$  for every  $\lambda > \beta$ .

*Proof.* This proof is an adaptation of the proof of Lemma 3.4 in [26]. Thanks to the fact that  $\tilde{K}$  satisfies (4.3) and  $b_0$  satisfies (4.4), we know that there exists a  $\beta \in \mathbb{R}$  such that both

$$\int_0^\infty e^{-\beta a} \sup_{\{f \in X : \|f\|_1 = 1\}} \left\| \tilde{K}(a) f \right\|_1 da = k_1 < 1$$

and

$$\sup_{t \ge 0} e^{-\beta t} \|b_0(t)\|_1 = k_2 < \infty$$

hold. Since b satisfies (4.2), then

$$e^{-\beta t} \|b(t)\|_{1} \le e^{-\beta t} \left\| \int_{0}^{t} \tilde{K}(a)b(t-a)da \right\|_{1} + e^{-\beta t} \|b_{0}(t)\|_{1}$$
$$\le \left\| \int_{0}^{t} e^{-\beta a} \tilde{K}(a)e^{-\beta(t-a)}b(t-a)da \right\|_{1} + k_{2}$$

Consider the map  $M : \mathbb{R}_+ \to \mathbb{R}_+$  defined by  $M(t) := \max_{a \in [0,t]} e^{-\beta a} ||b(a)||_1$  then we deduce that for every t > 0

$$M(t) \le M(t)k_1 + k_2$$

this implies that  $M(t) \le \frac{k_2}{1-k_1}$ . We deduce that  $||b(t)||_1 \le ce^{\beta t}$  for a positive constant c > 0, and the desired conclusion follows.

As a consequence the Laplace transform of *b*,

$$\hat{b}(\lambda) := \int_0^\infty e^{-\lambda t} b(t) dt$$

is well defined for every  $\lambda \in \mathbb{C}$  with  $\Re \lambda > \beta$ .

The *next generation operator* corresponding to the operator kernel  $\tilde{K}$  is the operator  $\mathbb{K}_0: X \to X$  defined by

$$\mathbb{K}_0 f := \int_0^\infty \tilde{K}(a) f da.$$
(4.5)

Notice that the integral in (4.5) is guaranteed to converge thanks to the fact that  $\tilde{K}$  satisfies (4.3).

Motivated by the interpretation in the context of population models, we call

$$R_0 := \rho(\mathbb{K}_0), \tag{4.6}$$

where  $\rho(\mathbb{K}_0)$  denotes the spectral radius of  $\mathbb{K}_0$ , *basic reproduction number*.

We denote with  $\mathbb{K}_{\lambda}$  the *discounted next generation operator* 

$$\mathbb{K}_{\lambda}f := \int_{0}^{\infty} e^{-\lambda a} \tilde{K}(a) f da.$$
(4.7)

Notice that if  $\lambda \in \mathbb{C}$  then  $\mathbb{K}_{\lambda}$  is a complex-valued function. This is the reason why we introduce the concept of complexification of a Banach space and of a linear operator.

We denote with  $X^{\mathbb{C}}$  the set of the functions  $f : \Omega_0 \to \mathbb{C}$  such that  $f = f_1 + if_2$  for some  $f_1 \in X$  and  $f_2 \in X$ .

**Definition 4.6.** The complexification of a linear operator  $T : X \to X$  is the operator  $T : X^{\mathbb{C}} \to X^{\mathbb{C}}$  defined by

$$T(f+ig) = Tf + iTg.$$

The operator  $\mathbb{K}_{\lambda}$  is well defined for every  $\lambda \in \mathbb{C}$  with  $\Re \lambda > z_0$ . The same holds for

$$\hat{b_0}(\lambda) := \int_0^\infty e^{-\lambda t} b_0(t) dt.$$

The Laplace transformed version of equation (4.2), is

$$\hat{b}(\lambda) = \hat{b_0}(\lambda) + \mathbb{K}_{\lambda}\hat{b}(\lambda) \quad \Re \lambda > z_0.$$
(4.8)

Let

$$\Sigma := \{\lambda \in \Delta : 1 \in \sigma(\mathbb{K}_{\lambda})\}$$
(4.9)

where

$$\Delta := \{\lambda \in \mathbb{C} : \Re \lambda > z_0\}$$
(4.10)

For  $\lambda \in \mathbb{C} \setminus \Sigma$  it is possible to write

$$\hat{b}(\lambda) = (I - \mathbb{K}_{\lambda})^{-1} \hat{b}_0(\lambda).$$
(4.11)

As will be explained later, applying the inverse Laplace transform formula to  $\hat{b}$ , we deduce the asymptotic behaviour of b.

It is then clear that the first fundamental step to deduce the asymptotic behaviour of  $\hat{b}$  is to study the non-linear eigenproblem

$$f = \mathbb{K}_{\lambda} f, \tag{4.12}$$

which is, in a sense, the differentiated version of (3.4).

If the non-linear eigenproblem (4.12) has a unique, upon normalisation of f, real solution  $(\lambda, f) = (r, \psi_r)$ , then r is called *Malthusian parameter*, while the eigenvector  $\psi_r$  is called the *stable distribution*.

4.3. Compact and non-supporting positive operators

The aim of this section is to present the results on positive compact and nonsupporting operators that we need to study the non-linear eigenproblem (4.12). To this end we introduce the following notation:  $X_{+}^{*}$  is the positive cone in the dual of  $X^{*}$ , represented by the set  $L_{+}^{\infty}(\Omega_{0})$ .

We start this section by introducing the concept of non-supporting operators.

**Definition 4.7.** (Non-supporting operator) Let  $L : X \to X$  be a positive bounded linear operator. The operator L is non-supporting with respect to  $X_+$  if for every  $\psi \in X_+, \psi \neq 0$  and  $F \in X_+^*, F \neq 0$ , there exists an integer p such that for every  $n \ge p$  we have that  $\langle F, L^n \psi \rangle > 0$ .

The following result is fundamental for our purposes as it provides important information regarding the spectral radius of positive non-supporting operators. We do not write the statement in its most general form, i.e., for a generic Banach space E with certain properties, but we state the result for  $E = X = L^1(\Omega_0)$ .

**Theorem 4.8.** ([32] and [38]) Let  $T : X \to X$  be positive and non-supporting (cf. Definition 4.7) and suppose that  $\rho(T)$  is a pole of the resolvent, then

- 1.  $\rho(T) > 0$  and  $\rho(T)$  is an algebraically simple eigenvalue of T.
- 2. The corresponding eigenvector  $\psi$  is almost everywhere strictly positive.
- 3. The corresponding dual eigenvector F is strictly positive, i.e. $\langle F, \phi \rangle > 0$  for every  $\phi \in X_+$  with  $\phi \neq 0$ .
- 4. If  $\{\lambda \in \sigma(T) : |\lambda| = \rho(T)\}$  consists only of poles of the resolvent, then it consists only of  $\lambda = \rho(T)$  and all the remaining elements  $\lambda \in \sigma(T)$  satisfy  $|\lambda| < \rho(T)$ .

The following result, proven by Marek, [32, Theorem 4.3 and Theorem 4.5], allows us to compare the spectral radius of two positive operators by comparing the operators. Again, we do not write the statement in its most general form, but we state the result for  $E = X = L^1(\Omega_0)$  and for the classes of operators we are interested in.

**Proposition 4.9.** Suppose that  $S, T : X \to X$  are positive, bounded, linear operators. *Then, the following holds:* 

- 1. *if*  $S \leq T$ , *that is if*  $T S : X_+ \to X_+$ , *then*  $\rho(S) \leq \rho(T)$ ;
- 2. *if* T, S are non-supporting and compact and  $S \le T$  with  $S \ne T$ , then  $\rho(S) < \rho(T)$ .

4.4. The Malthusian parameter r

In this section we make again Assumption 4.3 on  $\tilde{K}$  and Assumption 4.4 on  $b_0$ . We denote with  $\mathbb{K}_{\lambda}$  the discounted next generation operator, (4.7). We recall that  $\Delta$  is given by (4.10).

The aim of this section is to prove that there exists a unique, up to renormalisation, real solution to the non-linear eigenproblem (4.12).

**Theorem 4.10.** Assume that for every  $\lambda \in \Delta \cap \mathbb{R}$  the positive operator  $\mathbb{K}_{\lambda}$  is nonsupporting and compact. Then, there exists a unique real eigencouple  $(r, \psi_r)$ , with  $\psi_r \in X_+$  and  $\|\psi_r\|_1 = 1$ , that solves equation (4.12). If  $R_0 > 1$  then r > 0, if  $R_0 = 1$ then r = 0, if  $R_0 < 1$  then r < 0.

To prove Theorem 4.10 we follow the approach presented by Heijmans in [26]. The main steps of the proof consist in

- 1. proving that  $\rho(\mathbb{K}_{\lambda})$  is a positive eigenvalue of  $\mathbb{K}_{\lambda}$  and that its corresponding eigenfunction is strictly positive: to this end we apply Theorem 4.8, hence we need the operator  $\mathbb{K}_{\lambda}$  to be compact and non-supporting;
- 2. proving that the function  $\lambda \mapsto \rho(\mathbb{K}_{\lambda})$  is strictly decreasing and continuous and that  $\lim_{\lambda \to z_0} \rho(\mathbb{K}_{\lambda}) \ge 1$  while  $\lim_{\lambda \to \infty} \rho(\mathbb{K}_{\lambda}) = 0$ . To this end we will employ step 1 and Proposition 4.9.

Step 1 is made in Lemma 4.11 and Step 2 is made in Proposition 4.12 and Proposition 4.13.

**Lemma 4.11.** Assume that the operator  $\mathbb{K}_{\lambda}$  is compact and non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ . Then

- 1. the spectral radius of  $\mathbb{K}_{\lambda}$ , denoted with  $\rho(\mathbb{K}_{\lambda})$ , is a positive, algebraically simple eigenvalue of  $\mathbb{K}_{\lambda}$ ;
- 2. the corresponding eigenvector  $\psi_{\lambda} \in X$ , with normalisation  $\|\psi_{\lambda}\|_{1} = 1$ , satisfies  $\psi_{\lambda}(x) > 0$  for a.e.  $x \in \Omega_{0}$
- 3. the dual eigenfunctional  $F_{\lambda} \in X^*$ , such that  $\mathbb{K}^*_{\lambda}F_{\lambda} = \rho(\mathbb{K}_{\lambda})F_{\lambda}$  where  $\mathbb{K}^*_{\lambda}$  is the dual operator of  $\mathbb{K}_{\lambda}$ , is strictly positive, i.e.  $\langle F_{\lambda}, \phi \rangle > 0$  for every  $\phi \in X_+$  with  $\phi \neq 0$ .

*Proof.* By the fact that  $\mathbb{K}_{\lambda}$  is positive we deduce that  $\rho(\mathbb{K}_{\lambda}) \in \sigma(\mathbb{K}_{\lambda})$ . Since  $\mathbb{K}_{\lambda}$  is also compact we deduce that the spectral radius is a pole of the resolvent. Hence, if we additionally assume that  $\mathbb{K}_{\lambda}$  is non-supporting, we can apply Theorem 4.8 and deduce the desired conclusion.

**Proposition 4.12.** Assume  $\mathbb{K}_{\lambda}$  to be compact and non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ . The map  $\lambda \mapsto \rho(\mathbb{K}_{\lambda})$  is decreasing and continuous for  $\lambda \in [z_0, \infty)$ .

*Proof.* To prove that the function  $\lambda \mapsto \rho(\mathbb{K}_{\lambda})$  is decreasing it is enough to notice that if  $\lambda_2 > \lambda_1$ , then for every  $f \in X_+$  we have that  $(\mathbb{K}_{\lambda_1} - \mathbb{K}_{\lambda_2}) f$  belongs to  $X_+$ . Hence, by Proposition 4.9 we deduce that  $0 < \rho(\mathbb{K}_{\lambda_2}) < \rho(\mathbb{K}_{\lambda_1})$  by Theorem 4.8.

To prove the continuity notice that thanks to Lemma 4.11 we have that for every  $\lambda > z_0$  it holds that  $\frac{\langle \mathbb{K}^*_{\lambda}F_{\lambda},\psi_{\mu}\rangle}{\langle F_{\lambda},\psi_{\mu}\rangle} = \frac{\rho(\mathbb{K}_{\lambda})\langle F_{\lambda},\psi_{\mu}\rangle}{\langle F_{\lambda},\psi_{\mu}\rangle} = \rho(\mathbb{K}_{\lambda})$  and similarly that  $\frac{\langle F_{\lambda}\mathbb{K}_{\mu},\psi_{\mu}\rangle}{\langle F_{\lambda},\psi_{\mu}\rangle} = \frac{\rho(\mathbb{K}_{\mu})\langle F_{\lambda},\psi_{\mu}\rangle}{\langle F_{\lambda},\psi_{\mu}\rangle} = \rho(\mathbb{K}_{\mu})$ . Hence

$$\rho(\mathbb{K}_{\lambda}) - \rho(\mathbb{K}_{\mu}) = \frac{\langle \mathbb{K}_{\lambda}^{*} F_{\lambda}, \psi_{\mu} \rangle}{\langle F_{\lambda}, \psi_{\mu} \rangle} - \frac{\langle F_{\lambda} \mathbb{K}_{\mu}, \psi_{\mu} \rangle}{\langle F_{\lambda}, \psi_{\mu} \rangle} = \frac{\langle \left(\mathbb{K}_{\lambda}^{*} - \mathbb{K}_{\mu}^{*}\right) F_{\lambda}, \psi_{\mu} \rangle}{\langle F_{\lambda}, \psi_{\mu} \rangle}$$
$$\leq \|\mathbb{K}_{\lambda}^{*} - \mathbb{K}_{\mu}^{*}\|_{X^{*}} = \|\mathbb{K}_{\lambda} - \mathbb{K}_{\mu}\|_{1}.$$

 $\square$ 

Therefore, if we prove that  $\lim_{\lambda \to \mu} \|\mathbb{K}_{\lambda} - \mathbb{K}_{\mu}\|_1 = 0$ , then we deduce that  $\lambda \mapsto \rho(\mathbb{K}_{\lambda})$  is continuous. Since for every  $x_1, x_2 \ge 0$  we have  $|e^{-x_1} - e^{-x_2}| \le |x_1 - x_2|$ , then

$$\begin{split} &\int_{\Omega_0} |\mathbb{K}_{\lambda} f(x) - \mathbb{K}_{\mu} f(x)| dx \leq \int_{\Omega_0} \int_0^\infty |e^{-\lambda a} - e^{-\mu a}| \left| \tilde{K}(a) f \right|(x) dx \\ &\leq \int_0^\infty |e^{-\lambda a} - e^{-\mu a}| \|\tilde{K}(a) f\|_1 da \leq |\lambda - \mu| \|f\|_X \int_0^\infty a e^{z_0 a} da. \end{split}$$

Hence  $\lambda \mapsto \mathbb{K}_{\lambda}$  is continuous and the desired conclusion follows.

**Proposition 4.13.** Let  $\mathbb{K}_{\lambda}$  be compact and non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ . If  $R_0 \geq 1$ , then there exists a unique  $r \geq 0$  such that

$$\rho(\mathbb{K}_r) = 1. \tag{4.13}$$

If  $R_0 < 1$  and there exists a  $z \in [z_0, 0)$  such that  $\rho(\mathbb{K}_z) \ge 1$ , then there exists a unique r < 0 such that (4.13) holds.

*Proof.* The map  $\lambda \mapsto \rho(\mathbb{K}_{\lambda})$  is decreasing and continuous. First of all, in both cases,  $R_0 < 1$  and  $R_0 \ge 1$ , we have that  $\rho(\mathbb{K}_{\lambda}) \to 0$  as  $\lambda \to \infty$ . To see this, it is enough to notice that

$$0 \leq \rho(\mathbb{K}_{\lambda}) \leq \|\mathbb{K}_{\lambda}\|_{op} \to 0 \text{ as } \lambda \to \infty.$$

If  $R_0 \ge 1$ , then, by the comparison theorem of linear operators, i.e., Proposition 4.9, the definition of  $R_0$  and the continuity of  $\lambda \mapsto \rho(\mathbb{K}_{\lambda})$  we deduce that there exists a  $r \ge 0$  such that (4.13) holds.

When  $R_0 < 1$  the proof is similar.

*Proof of Theorem 4.10.* The proof is a direct consequence of Proposition 4.13 and of the fact that the spectral radius of  $\mathbb{K}_{\lambda}$  is an eigenvalue when positive.

4.5. Large time behaviour of the density

Most of the results of this section hold thanks to the assumption that the discounted next generation operator  $\mathbb{K}_{\lambda}$  is non-supporting for real values of  $\lambda$ .

The aim of this section is to prove that the unique real eigensolution of (4.12) is attracting. Namely we aim at proving the following theorem.

**Theorem 4.14.** Assume that for every  $\lambda \in \Delta \cap \mathbb{R}$  the operator  $\mathbb{K}_{\lambda}$  is non-supporting and that its complexification  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \Delta$ . Additionally, assume that if  $\lambda \in \Sigma$ , where  $\Sigma$  is given by (4.9), and  $\lambda \neq r$ , then  $\Re \lambda < r$ . Let  $(r, \psi_r)$  be the unique real normalised eigencouple solving (4.12). Then there exists v > 0 such that

$$||e^{-rt}b(t) - c\psi_r(\cdot)||_1 \le Le^{-vt}, \quad t > 0$$

for some constants L, c > 0.

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To prove Theorem 4.14 we follow the approach presented by Heijmans in [26]. We need to prove that the exponential solution of the form (3.2) with  $\lambda = r$  and  $\psi = \psi_r$ , is attracting. We can divide the proof in the following main steps.

- 1. We prove that  $(I \mathbb{K}_{\lambda})^{-1}$  is meromorphic on the half-plane  $\Delta$  and that it has a pole of order 1 in  $\lambda = r$ . The residue has the form:  $R_{-1}\psi = C(\psi)\psi_r$  where  $C(\psi) > 0$ .
- 2. We prove that there exists a spectral gap: there exists an  $\varepsilon$ , with  $0 < \varepsilon < r$ , such that  $\Re \lambda \leq r \varepsilon$  for every  $\lambda \in \Sigma$ . To this end we apply the Riemann Lebesgue Lemma (i.e. Lemma 4.18), and we exploit the fact that for every  $\lambda \in \Sigma$  we have that  $\Re \lambda < r$ . The results proven in step 1 will also be used.
- 3. We apply the Laplace transform inversion theorem (i.e. Lemma 4.22), to deduce the behaviour of b. To this end we apply some results of complex analysis (such as the Cauchy Theorem) and the results of the previous steps.

Step 1 is made in Proposition 4.15 and 4.19. Step 2 is made in Lemma 4.17. Finally step 3 is made in Proposition 4.21 and Theorem 4.14.

**Proposition 4.15.** Assume that the positive operator  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \Delta$ . The function  $\lambda \mapsto (I - \mathbb{K}_{\lambda})^{-1}$  is meromorphic on  $\Delta$ .

To prove this proposition we use the following result due to Steinberg and proven in [41].

**Theorem 4.16.** Let  $\Gamma$  be a subset of the complex plane which is open and connected. If  $\{T(\lambda) : \lambda \in \Gamma\}$  is an analytic family of compact operators on  $X^{\mathbb{C}}$ , then either  $I - T(\lambda)$  is nowhere invertible in  $\Gamma$  or  $(I - T(\lambda))^{-1}$  is meromorphic in  $\Gamma$ .

*Proof of Proposition 4.15.* From the definition of  $\mathbb{K}_{\lambda}$  we know that

 $\|\mathbb{K}_{\lambda}\|_{op} \leq \|\mathbb{K}_{\Re\lambda}\|_{op} \to 0 \text{ as } \Re\lambda \to \infty.$ 

Hence  $(I - \mathbb{K}_{\lambda}^{\mathbb{C}})$  is invertible for  $\Re \lambda$  large enough. Since  $\mathbb{K}_{\lambda}$  is compact for each real  $\lambda$  with  $\lambda > z_0$  and since  $\lambda \mapsto \mathbb{K}_{\lambda}$  is analytic, we can apply Theorem 4.16 to deduce that  $\lambda \mapsto (I - \mathbb{K}_{\lambda})^{-1}$  is meromorphic.

**Lemma 4.17.** Let  $\mathbb{K}_{\lambda}$  be non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$  and compact for every  $\lambda \in \Delta$ . Let r be the Malthusian parameter. Moreover, assume that if  $\lambda \in \Sigma$ , where  $\Sigma$  is given by (4.9), and  $\lambda \neq r$ , then  $\Re \lambda < r$ . There exists an  $\varepsilon > 0$  such that for every  $\lambda \in \Sigma$  with  $\lambda \neq r$ ,  $\Re \lambda \leq r - \varepsilon$ .

The following lemma is taken from [27], see Theorem 6.4.2, and will be applied to prove Lemma 4.17.

**Lemma 4.18.** (*Riemann-Lebesgue*) Let  $f \in L^1((0, \infty), X^{\mathbb{C}})$  and let  $\hat{f}$  be its Laplace transform. Then  $\lim_{|\eta|\to\infty} \hat{f}(\xi + i\eta) = 0$ , uniformly for  $\xi$  in bounded closed subintervals of  $(0, \infty)$ .

*Proof of Lemma 4.17.* Thanks to Lemma 4.18 we have that for every  $\overline{r} < r$  there exists an  $\eta_0 > 0$  such that  $\|\mathbb{K}_{s+i\eta}\|_{op} < 1$ , hence  $(I - \mathbb{K}_{s+i\eta})^{-1}$  is analytic, for every  $s \in [\overline{r}, r]$  and  $|\eta| > \eta_0$ . Since the function  $(I - \mathbb{K}_{\lambda})^{-1}$  is meromorphic, we deduce that the number of its poles contained in the compact set  $\{\lambda \in \mathbb{C} | Im\lambda| \le \eta_0 \text{ and } \Re\lambda \in [\overline{r}, r]\}$  is finite. This implies that the set  $\Sigma \cap \{\lambda \in \mathbb{C} \ \Re\lambda \in [\overline{r}, r]\}$  has a finite number of elements. Thanks to the assumption of Lemma 4.17, the only  $\lambda \in \Sigma$  with  $\Re\lambda = r$  is  $\lambda = r$ . From this we deduce that there exists an  $\varepsilon > 0$  such that  $\Re\lambda \le r - \varepsilon$  for every  $\lambda \in \Sigma$  with  $\lambda \neq r$ .

Since, from Proposition 4.15, we know that  $\mathbb{K}_{\lambda}$  is analytic in a neighbourhood of *r* we can write its Taylor expansion:

$$\mathbb{K}_{\lambda} = \sum_{n=0}^{\infty} (\lambda - r)^n K_n.$$
(4.14)

Moreover, the map  $\mathscr{R}_{\lambda} = (I - \mathbb{K}_{\lambda})^{-1}$  can be represented by a Laurent series around the pole *r* of order  $p \ge 1$ :

$$\mathscr{R}_{\lambda} = \sum_{n=-p}^{\infty} \left(\lambda - r\right)^{n} R_{n}.$$
(4.15)

**Proposition 4.19.** Let  $\mathbb{K}_{\lambda}$  be non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$  and let  $\mathbb{K}_{\lambda}$  be compact for every  $\lambda \in \Delta$ . Moreover assume that if  $\lambda \in \Sigma$  and  $\lambda \neq r$ , then  $\Re \lambda < r$ . Let r be the Malthusian parameter,  $\psi_r$  be the stable distribution,  $F_r$  be the corresponding dual eigenfunction. The function  $\lambda \mapsto (I - \mathbb{K}_{\lambda})^{-1}$  has a pole of order one in  $\lambda = r$  and the residue,  $R_{-1}$ , is given by

$$R_{-1}\psi = \frac{\langle F_r, \psi \rangle}{\langle F_r, -K_1\psi_r \rangle}\psi_r, \quad \psi \in X.$$

*Proof.* The proof of this proposition is the same as the proof of Theorem 7.1 in [26]. The fact that

$$\mathscr{R}_{\lambda}(I - \mathbb{K}_{\lambda}) = (I - \mathbb{K}_{\lambda})\mathscr{R}_{\lambda} = I, \qquad (4.16)$$

implies, together with (4.14) and (4.15) that

$$R_{-p}(I - K_0) = (I - K_0)R_{-p} = 0.$$
(4.17)

From (4.17) and from the fact that  $K_0 = \mathbb{K}_r$  we deduce that the range of  $R_{-p}$  is equal to  $\{\gamma \psi_r : \gamma \in \mathbb{C}\}$ . Similarly we deduce that the range of  $R_{-p}^*$ , which is the dual operator of  $R_{-p}$ , is equal to  $\{\gamma F_r : \gamma \in \mathbb{C}\}$ . As a consequence there exist  $\Phi$  and H solving

$$R_{-p}\Phi = \psi_r \text{ and } R^*_{-p}H = F_r \tag{4.18}$$

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respectively.

From the identity (4.16) and formula (4.15) and (4.14) we can also deduce that if p > 1, then

$$-R_{-p}K_1 + R_{-p+1}(I - K_0) = 0.$$

While, if p = 1 we have that

$$-R_{-1}K_1 + R_0(I - K_0) = I.$$

Combining these two last equations with (4.17) we deduce that if p > 1 then

$$R_{-p}K_1R_{-p} = 0 (4.19)$$

while if p = 1

$$R_{-1}K_1R_{-1} = -R_{-1}. (4.20)$$

As a consequence of (4.19) and (4.18), if p > 1, then

$$\langle F_r, K_1\psi_r\rangle = \langle R_{-p}^*H, K_1R_{-p}\Phi\rangle = \langle H, R_{-p}K_1R_{-p}\Phi\rangle = 0,$$

which is a contradiction with the fact that  $F_r$  strictly positive and  $-K_1\psi_r = \left[-\frac{d}{d\lambda}\mathbb{K}_{\lambda}\right]_r$  $\psi_r$  is positive. Hence p = 1.

Now let  $R_{-1}\psi = f(\psi)\psi_r$  for some linear functional f. Using the fact that  $F_r = R_{-1}^*H_r$  and (4.20) we deduce that

$$\begin{aligned} \langle F_r, \psi \rangle &= \langle R_{-1}^*H, \psi \rangle = \langle H, R_{-1}\psi \rangle = \langle H, -R_{-1}K_1R_{-1}\psi \rangle = \\ \langle R_{-1}^*H, -K_1(f(\psi)\psi_r) \rangle &= f(\psi)\langle R_{-1}^*H, -K_1\psi_r \rangle = f(\psi)\langle F_r, -K_1\psi_r \rangle \end{aligned}$$

it follows that  $f(\psi) = \frac{\langle F_r, \psi \rangle}{\langle F_r, -K_1 \psi_r \rangle}$ .

**Definition 4.20.** The Hardy-Lebesgue class  $H_1(\alpha, X^{\mathbb{C}})$  is the class of functions  $g : \mathbb{C} \to X$ , which are analytic in  $\Re \lambda > \alpha$  and satisfy the following conditions

$$\sup_{\xi > \alpha} \int_{-\infty}^{\infty} \|g(\xi + i\eta)\|_1 d\eta < \infty$$
(4.21)

and  $g(\alpha + i\eta) = \lim_{\xi \to \alpha} g(\xi + i\eta)$  exists a.e. and is an element of  $L^1((-\infty, \infty), X)$ .

**Proposition 4.21.** Let  $\mathbb{K}_{\lambda}$  be compact for every  $\lambda \in \Delta$  and  $\mathbb{K}_{\lambda}$  non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ . Moreover, assume that if  $\lambda \in \Sigma$  and  $\lambda \neq r$ , then  $\Re \lambda < r$ . Let r be the Malthusian parameter. Then  $\hat{b} \in H_1(\alpha, X^{\mathbb{C}})$  if  $\alpha > r$ .

*Proof of Proposition 4.21.* For each fixed  $\xi > z_0$  the map

$$\eta \mapsto \hat{b_0}(\xi + i\eta)$$

belongs to  $L^1((-\infty, \infty), X^{\mathbb{C}})$ , see for instance Theorem 6.3.2 in [27]. From Lemma 4.18 we know that there exists a  $\eta_0$  such that if  $|\eta| \ge \eta_0$  then

$$\left\| \left( I - \mathbb{K}_{\xi+i\eta} \right)^{-1} \right\|_{op} \le 2.$$

Since when  $\xi > r$  the function  $\eta \mapsto (I - \mathbb{K}_{\xi + i\eta})^{-1}$  is continuous on the compact set  $[-\eta_0, \eta_0]$  it follows that, if  $\xi > r$  there exists a constant  $C(\xi) > 0$  such that

$$\left\| \left( I - \mathbb{K}_{\xi + i\eta} \right)^{-1} \right\|_{op} \le C(\xi)$$

for all  $\eta \in \mathbb{R}$ . Since  $\hat{b}$  is given by (4.11) we deduce, that

$$\|\hat{b}(\xi + i\eta)\|_1 \le C(\xi) \|\hat{b}_0(\xi + i\eta)\|_1$$
 for  $\xi > r$  and  $\eta \in \mathbb{R}$ .

As a consequence of the positivity of b and  $\hat{b_0}$ , we have that for every  $\xi \ge \alpha > r$ 

$$\|\hat{b}(\xi + i\eta)\|_{1} \le \|\hat{b}(\alpha + i\eta)\|_{1} \le C(\alpha)\|\hat{b}_{0}(\alpha + i\eta)\|_{1}$$
(4.22)

Hence  $\|\hat{b}(\xi + i\eta)\|_1$  is integrable with respect to  $\eta$  over  $(-\infty, \infty)$  and thanks to (4.22) we deduce that  $\hat{b}$  satisfies (4.21).

Since the maps  $\lambda \mapsto (I - \mathbb{K}_{\lambda})^{-1}$  and  $\lambda \mapsto \hat{b}_{0}(\lambda)$  are analytic when  $\Re \lambda > r$  we deduce that the map  $\lambda \mapsto \hat{b}(\lambda)$  is analytic for  $\Re \lambda > r$ . Hence the limit of  $\hat{b}(\xi + i\eta)$  as  $\xi \to \alpha$  exists and is equal to  $\hat{b}(\alpha + i\eta)$ . The fact that  $\hat{b}(\alpha + i \cdot) \in L^{1}((-\infty, \infty), X^{\mathbb{C}})$  follows from inequality (4.22).

The following lemma, useful for the proof of Theorem 4.14, is taken from [20].

**Lemma 4.22.** Let  $\hat{g} \in H_1(\alpha, X^{\mathbb{C}})$ , (cf. Definition 4.20) then the function

$$f(t) = \frac{1}{2\pi i} \lim_{T \to \infty} \int_{\gamma - iT}^{\gamma + iT} e^{\lambda t} \hat{g}(\lambda) d\lambda \quad \gamma \ge \alpha$$

is well defined for every  $t \in \mathbb{R}$ , and does not depend on  $\gamma$ . Moreover, f(t) = 0 if t < 0, while f is continuous in t for t > 0. Finally  $\hat{f}(\lambda) = \hat{g}(\lambda)$ .

*Proof of Theorem 4.14.* Also in this case, the proof is very similar to a proof in [26], viz. the proof of Corollary 8.3. We write the main steps here.

Since the function  $\hat{b}$  belongs to  $H_1(\alpha, X^{\mathbb{C}})$  for every  $\alpha > r$ , we deduce, by Lemma 4.22 and by the uniqueness of the Laplace transform [27, Theorem 6.2.3] that

$$b(t) = \frac{1}{2\pi i} \int_{\alpha - i\infty}^{\alpha + i\infty} e^{\lambda t} \hat{b}(\lambda) d\lambda.$$
(4.23)

Consider  $0 < v < \varepsilon$  where  $\varepsilon$  is given by Lemma 4.17 and notice that

$$\int_{\alpha-iT}^{\alpha+iT} e^{\lambda t} \hat{b}(\lambda) = \oint_{\Gamma} e^{\lambda t} \hat{b}(\lambda) d\lambda - \lim_{T \to \infty} \int_{\Gamma_3} e^{\lambda t} \hat{b}(\lambda) d\lambda - \lim_{T \to \infty} \int_{\Gamma_2} e^{\lambda t} \hat{b}(\lambda) d\lambda$$

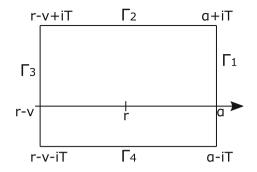


Figure 1. Graphic representation of the set  $\Gamma$ 

$$-\lim_{T\to\infty}\int_{\Gamma_4} e^{\lambda t}\hat{b}(\lambda)d\lambda \tag{4.24}$$

where  $\Gamma := \bigcup_{i=1}^{4} \Gamma_i$  and  $\Gamma_1$  is the segment in the complex plan connecting the point  $\alpha - iT$  to  $\alpha + iT$ ,  $\Gamma_2$  is the segment connecting  $\alpha + iT$  with r - v + iT,  $\Gamma_3$  is the segment connecting r - v + iT with r - v - iT and, finally,  $\Gamma_4$  is the segment connecting r - v - iT with  $\alpha - iT$ .

From the Cauchy theorem for vector valued functions ([27]), equality (4.24) and Lemma 4.18 and the Laplace inversion formula (4.23), we deduce that

$$b(t) = \frac{1}{2\pi i} \oint_{\Gamma} e^{\lambda t} \hat{b}(\lambda) d\lambda + \frac{1}{2\pi i} \lim_{T \to \infty} \int_{r-v-iT}^{r-v+iT} e^{\lambda t} \hat{b}(\lambda) d\lambda.$$

By the residue theorem we have that

$$\frac{1}{2\pi i} \oint_{\Gamma} e^{\lambda t} \hat{b}(\lambda) d\lambda = Res_{\lambda=r} e^{\lambda t} \hat{b}(\lambda) = e^{rt} R_{-1} \hat{b}_0(r) = e^{rt} \frac{\langle F_r, \hat{b}_0(r) \rangle}{\langle F_r, -K_1 \psi_r \rangle} \psi_r.$$

We conclude the proof by noting that

$$\left\|\frac{1}{2\pi i}\lim_{T\to\infty}\int_{r-\nu-iT}^{r-\nu+iT}e^{\lambda t}\hat{b}(\lambda)d\lambda\right\|_{1}\leq Me^{(r-\nu)t}$$

with

$$M = \frac{1}{2\pi} \int_{-\infty}^{\infty} \left\| \hat{b}(r - v + i\eta) \right\|_{1} d\eta$$

and explaining why

$$\int_{-\infty}^{\infty} \left\| \hat{b}(r-v+i\eta) \right\|_1 d\eta < \infty.$$

As in the proof of Proposition 4.21 we know that thanks to Lemma 4.18, there exists a  $\eta_0 > 0$  and a constant C > 0 such that

$$||(I - \mathbb{K}_{r-v+i\eta})^{-1}||_{op} \le C$$

for every  $\eta$  with  $|\eta| > \eta_0$ . On the other hand since the function  $\eta \mapsto (I - \mathbb{K}_{r-\nu+i\eta})^{-1}$  is continuous on the compact set  $[-\eta_0, \eta_0]$  we deduce that for every  $\eta \in \mathbb{R}$ 

$$||(I - \mathbb{K}_{r-v+i\eta})^{-1}||_{op} \le C.$$

By equality (4.11) we deduce that

$$\|\hat{b}(r-v+i\eta)\|_{1} \le C \|\hat{b}_{0}(r-v+i\eta)\|_{1}.$$

Since from the proof of Proposition 4.21 we know that for every  $\xi > z_0$  the function  $\eta \mapsto \hat{b}_0(\xi + i\eta)$  belongs to  $L^1((-\infty, \infty), X^{\mathbb{C}}))$  we deduce, possibly adjusting *C*, that the function  $\eta \mapsto \hat{b}(r - v + i\eta)$  belongs to  $L^1((-\infty, \infty), X^{\mathbb{C}}))$ .

We next present here two sufficient conditions on  $\tilde{K}$  that guarantee that for every  $\lambda \in \Sigma$ , with  $r \neq \lambda$ , we have that  $\Re \lambda < r$ . As will be shown in Sect. 5, either Assumption 4.23 or Assumption 4.24 can be easily checked for all the model examples we consider.

**Assumption 4.23.** There exists a measurable function  $\gamma : \mathbb{R}_+ \times \Omega_0 \to \mathbb{R}$  such that for every  $x \in \Omega_0$  the function  $a \mapsto \gamma(a, x)$  is piecewise monotone and there exists a measurable function  $c : \mathbb{R}_+ \times \Omega_0 \to \mathbb{R}_+$  such that

$$\widetilde{K}(a)\varphi(\cdot) = c(a, \cdot)\varphi(\gamma(a, \cdot)) \quad \forall \varphi \in X_+ \text{ and } \forall a \in \mathbb{R}_+.$$

**Assumption 4.24.** There exists a function  $\tilde{k} : \mathbb{R}_+ \times \Omega_0 \times \Omega_0 \mapsto \mathbb{R}_+$ , that is measurable in each variable and such that

$$\sup_{a\in[0,T]}\sup_{x\in\Omega_0}\int_{\Omega_0}\tilde{k}(a,x,y)dy<\infty$$

and such that

$$(\tilde{K}(a)\varphi)(y) := \int_{\Omega_0} \tilde{k}(a, x, y)\varphi(x)dx \quad \forall \varphi \in X \text{ and } \forall a \in \mathbb{R}_+.$$

The aim of the following proposition is to show that each of the preceding two assumptions guarantees that  $\Re \lambda < r$  for every  $\lambda \in \Sigma$  with  $\lambda \neq r$ .

**Proposition 4.25.** Let  $\mathbb{K}_{\lambda}$  be compact for every  $\lambda \in \Delta$  and non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ . Let  $\tilde{K}$  satisfy either Assumption 4.23 or Assumption 4.24. Let r be the Malthusian parameter. If  $\lambda \in \Sigma$ , where  $\Sigma$  is given by (4.9), and  $\lambda \neq r$ , then  $\Re \lambda < r$ .

To prove Proposition 4.25 we need the following Theorem, which corresponds to Theorem 1.39 in [37].

**Theorem 4.26.** Let  $\varphi \in X^{\mathbb{C}}$  and assume that

$$\int_{\Omega_0} |\varphi(x)| dx = \left| \int_{\Omega_0} \varphi(x) dx \right|$$

then there exists a constant  $\beta$  such that  $\beta \varphi = |\varphi|$  a.e. on  $\Omega_0$ .

*Proof of Proposition 4.25.* The proof is an adaptation of the proof of Theorem 6.13 in [26].

Assume that there exists a  $\lambda \in \Sigma$  with  $\lambda \neq r$  such that  $\mathbb{K}_{\lambda} \psi = \psi$  for some  $\psi \in X^{\mathbb{C}}$ . It follows that

$$|\psi| = |\mathbb{K}_{\lambda}\psi| \le \mathbb{K}_{\Re\lambda}|\psi|. \tag{4.25}$$

Taking duality parings with  $F_{\Re\lambda}$  on both sides of the inequality we deduce that

$$\langle F_{\mathfrak{R}\lambda}, |\psi| \rangle \leq \rho(\mathbb{K}_{\mathfrak{R}\lambda}) \langle F_{\mathfrak{R}\lambda}, |\psi| \rangle.$$

This implies that  $\rho(\mathbb{K}_{\Re_{\lambda}}) \ge 1 = \rho(\mathbb{K}_r)$ . Since, by Proposition 4.12 we know that the function  $\mu \to \rho(\mathbb{K}_{\mu})$  is decreasing when  $\mu$  varies in  $\mathbb{R}$  we deduce that  $\Re \lambda \le r$ .

Assume now that  $\Re \lambda = r$ , hence, since  $\lambda \neq r$ , it must hold that  $Im\lambda > 0$ . From (4.25) we know that  $\mathbb{K}_r |\psi| \ge |\psi|$ . If we assume that  $\mathbb{K}_r |\psi| \neq |\psi|$  then taking duality parings with  $F_r$  we deduce that  $\langle F_r, |\psi| \rangle > \langle F_r, |\psi| \rangle$ . This is a contradiction, hence it must hold that  $\mathbb{K}_r |\psi| = |\psi|$ . Since  $(r, \psi_r)$  is the unique (up to normalization) solution of the non-linear eigenproblem (4.12), we deduce that there exists an  $\ell : \Omega_0 \to \mathbb{R}$  such that  $\psi(x) = e^{i\ell(x)}\psi_r(x)$  and, as a consequence of (4.25), we have that  $\mathbb{K}_r\psi_r = |\mathbb{K}_\lambda\psi|$  i.e.

$$\int_0^\infty e^{-ra} \tilde{K}(a) \psi_r da = \left| \int_0^\infty e^{-ra} e^{iaIm\lambda} \tilde{K}(a) e^{i\ell(\cdot)} \psi_r da \right|$$
(4.26)

If we make Assumption 4.23 this implies that

$$\int_0^\infty e^{-ra} \tilde{K}(a) \psi_r da = \left| \int_0^\infty e^{-ra} e^{iaIm\lambda} e^{i\ell(\gamma(a,\cdot))} \tilde{K}(a) \psi_r da \right|$$

Since

$$\int_0^\infty e^{-ra} \tilde{K}(a) \psi_r da = \int_0^\infty \left| e^{-ra} e^{iaIm\lambda} e^{i\ell(\gamma(a,\cdot))} \tilde{K}(a) \psi_r \right| da$$

we deduce, by Theorem 4.26, that there exist a  $\beta \in \mathbb{R}$  such that

$$aIm\lambda + \ell(\gamma(a, x)) = \beta.$$

As a consequence we have that

$$e^{i\ell(x)}\psi_r(x) = \int_0^\infty e^{-(\Re\lambda + iIm\lambda)a}\tilde{K}(a)\psi(x)da$$
$$= \int_0^\infty e^{-a\Re\lambda}e^{i\beta - i\ell(\gamma(a,x))}\tilde{K}(a)\psi(x)da$$
$$= e^{i\beta}\int_0^\infty e^{-a\Re\lambda}\tilde{K}(a)\psi_r(x)da = e^{i\beta}\psi_r(x).$$

This implies that  $\ell(x) = \beta \pmod{2\pi}$  for a.e.  $x \in \Omega_0$  and hence, the piecewise monotonicity of  $\gamma(\cdot, x)$  implies that  $Im\lambda = 0$ . This is a contradiction and the desired conclusion follows.

If, instead, we make Assumption 4.24 equality (4.26) implies that

$$\int_0^\infty e^{-ra} \int_{\Omega_0} \tilde{k}(a, y, x) \psi_r(y) dy da$$
$$= \left| \int_0^\infty e^{-ra} \int_{\Omega_0} e^{iaIm\lambda + i\ell(y)} \tilde{k}(a, y, x) \psi_r(y) dy da \right|$$

Since

$$\int_0^\infty e^{-ra} \int_{\Omega_0} \tilde{k}(a, y, x) \psi_r(y) dy da$$
  
= 
$$\int_0^\infty \int_{\Omega_0} \left| e^{-ra} e^{iaIm\lambda + i\ell(y)} \tilde{k}(a, y, x) \psi_r(y) \right| dy da,$$

we deduce by Theorem 4.18 that there exists a  $\beta \in \mathbb{R}$  such that

$$aIm\lambda + \ell(x) = \beta.$$

As a consequence we have that

$$e^{i\ell(x)}\psi_r(x) = \int_0^\infty e^{-(\Re\lambda + iIm\lambda)a}\tilde{K}(a)\psi(x)da$$
$$= \int_0^\infty e^{-a\Re\lambda}e^{i\beta - i\ell(x)}\tilde{K}(a)\psi(x)da$$
$$= e^{i\beta}\int_0^\infty e^{-a\Re\lambda}\tilde{K}(a)\psi_r(x)da = e^{i\beta}\psi_r(x).$$

This implies that  $\ell(x) = \beta \pmod{2\pi}$  for a.e.  $x \in \Omega_0$  and hence that  $Im\lambda = 0$ . This is a contradiction and the desired conclusion follows.

#### 4.6. An alternative approach

In this section we present an alternative approach for proving Theorem 4.14. We make the same assumptions on  $\tilde{K}$  and  $b_0$  as made in Sect. 4.5 and we keep the same notation.

We plan to deduce the asymptotic behaviour of the solution of equation (4.2) by obtaining estimates on the resolvent operator from the following theorem, which is Theorem 2 in [22].

**Theorem 4.27.** Let  $w \in \mathbb{R}$  and let  $\tilde{K} \in L^1_{-w}(\mathbb{R}_+, \mathscr{L}(X^{\mathbb{C}}))$  be an operator kernel. Then its resolvent  $\tilde{R}$  belongs to  $L^1_{-w}(\mathbb{R}_+, \mathscr{L}(X^{\mathbb{C}}))$  if and only if  $I - \mathbb{K}_{\lambda}$  is invertible for every  $\lambda \in \mathbb{C}$  such that  $\Re \lambda \geq w$ .

To be able to apply this theorem, we have to assume that the function  $a \mapsto \tilde{K}(a)$  is measurable with respect to the topology induced by the operator norm on  $\mathscr{L}(X)$ . This measurability assumption is stronger than the measurability assumption we ask for the operator kernels in Sect. 4.1.

**Theorem 4.28.** Assume that for every  $\lambda \in \Delta \cap \mathbb{R}$  the operator  $\mathbb{K}_{\lambda}$  is non-supporting and that its complexification  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \Sigma$ . Additionally assume that  $\tilde{K} : \mathbb{R}_+ \to \mathscr{L}(X^{\mathbb{C}})$  is measurable and satisfies either Assumption 4.23 or Assumption 4.24. Let  $(r, \psi_r)$  be the eigencouple solving (4.12). Then there exists v > 0 such that

$$||e^{-rt}b(t) - c\psi_r(\cdot)||_1 \le Le^{-vt}, \quad t > 0$$

for some constants L, c > 0.

*Proof.* We already know that for every  $\lambda \in \mathbb{C}$  with  $\Re \lambda \geq \sigma > r$  the operator  $I - \mathbb{K}_{\lambda}$  is invertible. Moreover  $\tilde{K} \in L^{1}_{-\sigma}(\mathbb{R}_{+}, \mathscr{L}(X^{\mathbb{C}}))$  for any  $\sigma > r$ . Hence we deduce from Theorem 4.27 that  $\tilde{R} \in L^{1}_{-\sigma}(\mathbb{R}_{+}, \mathscr{L}(X^{\mathbb{C}}))$ . We denote the Laplace transform of  $\tilde{R}$  as follows

$$\mathbb{R}_{\lambda} := \int_{0}^{\infty} e^{-\lambda a} \tilde{R}(a) da < \infty \quad \Re \lambda > \sigma.$$

Similarly as in Proposition 4.21 we deduce that  $(I - \mathbb{K}_{\lambda})^{-1}\mathbb{K}_{\lambda}\hat{b_0}(\lambda) \in H(\sigma, X^{\mathbb{C}})$  for  $\sigma > r$ . Hence, from the Laplace inversion formula we deduce that

$$\int_0^t \tilde{R}(a)b_0(t-a)da = \frac{1}{2\pi i} \lim_{T \to \infty} \int_{\sigma-iT}^{\sigma+iT} e^{\lambda t} \left(I - \mathbb{K}_{\lambda}\right)^{-1} \mathbb{K}_{\lambda} \hat{b_0}(\lambda) d\lambda$$

if  $\sigma > r$ .

Consider a  $w \in \mathbb{R}$  with w < r such that the operator  $(I - \mathbb{K}_{\lambda})$  is invertible for every  $\lambda \in \mathbb{C}$  with  $w \leq \Re \lambda < r$ . This w exists thanks to Lemma 4.17. Define the operator Q as

$$\int_0^t Q(a)b_0(t-a)da := \frac{1}{2\pi i} \lim_{T \to \infty} \int_{w-iT}^{w+iT} e^{\lambda t} \left(I - \mathbb{K}_{\lambda}\right)^{-1} \mathbb{K}_{\lambda} \hat{b_0}(\lambda) d\lambda.$$

Similarly as in the proof of Theorem 4.14 we can deduce, by the residue theorem, that

$$\int_0^t \tilde{R}(a)b_0(t-a)da - \int_0^t Q(a)b_0(t-a)da = e^{rt}R_{-1}\mathbb{K}_r\hat{b_0}(r)$$

As a consequence

$$b(t) = \int_0^t \tilde{R}(a)b_0(t-a)da + b_0(t)$$
  
=  $\int_0^t Q(a)b_0(t-a)da + e^{rt}R_{-1}\mathbb{K}_r\hat{b_0}(r) + b_0(t)$   
=  $\int_0^t Q(a)b_0(t-a)da + e^{rt}\frac{\langle F_r, \mathbb{K}_r\hat{b_0}(r)\rangle}{\langle F_r, -K_1\psi_r\rangle}\psi_r + b_0(t)$ 

Notice that by the definition of  $F_r$  we have that

$$\frac{\langle F_r, \mathbb{K}_r \hat{b_0}(r) \rangle}{\langle F_r, -K_1 \psi_r \rangle} = \frac{\langle \mathbb{K}_r^* F_r, \hat{b_0}(r) \rangle}{\langle F_r, -K_1 \psi_r \rangle} = \frac{\langle F_r, \hat{b_0}(r) \rangle}{\langle F_r, -K_1 \psi_r \rangle}$$

Moreover, by the definition of Q we have  $\|\int_0^t Q(a)b_0(t-a)da\|_1 \le ce^{wt}$  where the constant c is equal to

$$c := \int_{-\infty}^{\infty} \| (I - \mathbb{K}_{w+i\eta})^{-1} \mathbb{K}_{w+i\eta} \hat{b_0}(w+i\eta) \|_1 d\eta$$

The fact that  $c < \infty$  follows by an adaptation of the final part of the proof of Theorem 4.14. Hence, using (4.4), it follows that

$$\left\| e^{-rt} b(t) - \frac{\langle F_r, \hat{b_0}(r) \rangle}{\langle F_r, -K_1 \psi_r \rangle} \psi_r \right\|_1 \le c_1 e^{(w-r)t} + e^{-rt} \|b_0(t)\|_1 \le c_2 e^{-vt},$$

for some positive constants  $v, c_1, c_2$ .

This approach is not very different from the approach developed in Sect. 4.5, but here we have to make stronger measurability assumptions on  $\tilde{K}$ . These correspond to stronger assumptions on the model parameters and therefore we decided to focus on Heijmans' approach.

# 4.7. Asymptotic behaviour of the measure-valued solution

In this section we deduce the asymptotic behaviour of the measure B from the behaviour of the density of its absolutely continuous component. This type of technique has been applied in [12] and in [36].

**Lemma 4.29.** Let K be a  $z_0$ -bounded regularizing kernel and let  $B_0$  be given by (2.2) as a function of K and  $M_0 \in \mathcal{M}_{+,b}(\Omega)$ . Let  $\tilde{K} : \mathbb{R}^*_+ \to \mathcal{L}(X)$  be the operator defined by

$$K(a) f = d_{K,f}(a) \text{ for every } a \ge 0 \text{ and } f \in X$$

$$(4.27)$$

where  $d_{K,f}(a) \in X$  is the density of the measure (3.6) with t replaced by a. Let us denote with B the solution of equation (2.1). Then

$$B^{AC}(t,\omega) = \int_{\omega} b(t)(x)dx \quad \forall \omega \in \mathscr{B}(\Omega_0)$$
(4.28)

where b is the solution of (4.2) with respect to  $\tilde{K}$  and the function  $b_0 : \mathbb{R}_+ \to X$ mapping t to the density of  $B_0^{AC}(t, \cdot) + \mathscr{L}_K(B^s)^{AC}(t, \cdot)$ .

*Proof.* First of all we need to check that  $\tilde{K}$  is an operator kernel, so in particular that for every  $f \in X$  the map

$$a \mapsto K(a)f \tag{4.29}$$

is Bochner measurable. Since X is separable, Bochner measurability and weak measurability coincide. So it suffices to show that the map (4.29) is weakly measurable, i.e. that for every  $g \in L^{\infty}(\Omega_0)$  the map

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$$a \mapsto \int_{\Omega} g(x)\tilde{K}(a)f(x)dx = \int_{\Omega} g(x)d_{K,f}(a)(x)dx$$

is measurable. This is a consequence of the fact that for every  $\omega$  the map

$$a \mapsto \int_{\omega} d_{K,f}(a)(x) dx = \int_{\Omega} K(a, y, \omega) f(y) dy$$

is measurable. We refer to [19] for the details. Similarly one shows that  $b_0 : \mathbb{R}_+ \to X$  is Bochner measurable.

Moreover, thanks to the fact that K is a locally bounded kernel

$$\sup_{a\in[0,T]}\sup_{f\in X}\|\tilde{K}(a)f\|_1<\infty.$$

Hence, thanks to Lemma 4.2, equation (4.2), with respect to  $\tilde{K}$  and  $b_0$  has a unique solution *b*. Integrating all the terms in the equation over the set  $\omega$  we deduce that

$$\tilde{B}(t,\omega) := \int_{\omega} b(t)(x) dx$$

is a solution of (3.9). By uniqueness it follows that  $\tilde{B} = B^{AC}$ 

**Theorem 4.30.** Let K be a  $z_0$ -bounded regularizing kernel such that the operator  $\mathbb{K}_{\lambda}$ , defined by (4.7) with  $\tilde{K}$  given by (4.27), is compact for every  $\lambda \in \Delta$  and nonsupporting for every  $\Delta \cap \mathbb{R}$ . Assume also that  $\tilde{K}$  satisfies either Assumption 4.23 or Assumption 4.24. Let us denote with B the solution of equation (2.1) and let  $\Psi_r(dx) = \psi_r(x)dx$ , with  $\psi_r$  the stable distribution, and r the Malthusian parameter. Then there exist constants M, k > 0 such that

$$\left\|e^{-rt}B(t,\cdot) - c\Psi_r(\cdot)\right\| \le Me^{-kt} \quad \forall t > 0.$$
(4.30)

where c > 0 is the same constant as in Theorem 4.14 and  $\|\cdot\| = \|\cdot\|_{TV} = \|\cdot\|_{b}$ .

*Proof.* Since the density of  $B^{AC}(t, \cdot)$ , b(t), solves (4.2) with respect to the  $\tilde{K}$  and  $b_0$  given by Lemma 4.29, we deduce that

$$\begin{split} \left\| e^{-rt} B(t, \cdot) - c \Psi_r(\cdot) \right\| &\leq \left\| e^{-rt} B(t, \cdot) - e^{-rt} B^{AC}(t, \cdot) + e^{-rt} B^{AC}(t, \cdot) - c \Psi_r(\cdot) \right\| \\ &\leq \left\| e^{-rt} B(t, \cdot) - e^{-rt} B^{AC}(t, \cdot) \right\| + \left\| e^{-rt} B^{AC}(t, \cdot) - c \Psi_r(\cdot) \right\| \\ &\leq e^{-rt} \left\| B^s(t, \cdot) \right\| + \left\| e^{-rt} b(t, \cdot) - c \psi_r(\cdot) \right\|_1 \leq e^{-rt} \left\| B^s(t, \cdot) \right\| + L e^{-vt} \\ &\leq c_1 e^{(z_0 - r)t} + c_2 t e^{(z_0 - r)t} + L e^{-vt}, \end{split}$$

where in the last inequality we have applied (3.7). From this chain of inequalities we deduce that (4.30) holds.  $\Box$ 

We stress that in Corollary 4.30 we prove balanced exponential growth and we also provide an exponential estimate of the remainder, as is done in [5] to which we refer for yet another approach.

# 5. Kernels arising from structured population models

The aim of this section is to present three classes of  $z_0$ -bounded regularizing kernels that, as we shall show in the next sections satisfy the assumptions of Theorems 4.10 and 4.14, i.e. the corresponding operator kernel  $\tilde{K}$  satisfies either Assumption 4.23 or Assumption 4.24 and the corresponding operator  $\mathbb{K}_{\lambda}$  is non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$  and compact for every  $\lambda \in \Delta$ .

Since the classes of kernels that we present are motivated by structured population models, we interpret the mathematical assumptions by describing their meaning in the context of the corresponding models. To help the reader we also provide the more classical PDE formulation of the models in the next section. In all of this section we assume that the *i*-state space  $\Omega$  is a subset of  $\mathbb{R}^+_+$ .

5.1. The kernel as a modelling ingredient

The main modelling ingredient of the renewal equation is the kernel, which summarises the effect of the individual level mechanisms determining the population evolution. The individual level mechanisms modelled via the renewal equation (2.1)are

- deterministic smooth development of the individual state, as growth or waning.
- giving birth, with offspring appearing at a different position (i.e. having a different state), or jumping to another position, in which case we say that the individual in the old state died while an individual in the new state was born. We assume that this happens at a position dependent rate  $\Lambda$ .

Therefore we assume that the kernel is

$$K(a,\xi,\omega) := \mathscr{F}(a,\xi)\Lambda(X(a,\xi))\nu(X(a,\xi),\omega)$$
(5.1)

where

- $X(a, \xi)$  is the state of an individual that survived up to the current time and that, *a* time ago, had state  $\xi$ .
- $\mathscr{F}(a,\xi)$  is the probability that an individual that *a* time ago had state  $\xi$  survives up to the present time.
- $-\nu(z,\omega)$  denotes the expected number of individuals born with size in  $\omega$  when an individual with size *z* reproduces or jumps.

We want to find sufficient conditions on  $\mathscr{F}$ , X and  $\nu$  that guarantee that K is a  $z_0$ -bounded regularizing kernel, that the corresponding operator kernel  $\tilde{K}$  satisfies either Assumption 4.23 or Assumption 4.24 and that the corresponding operator  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \Delta$  and non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ . To this end we start by writing the following basic assumptions on  $\mathscr{F}$ , X,  $\nu$  implying that K is a  $z_0$ -bounded kernel.

# Assumption 5.1. Assume that

- the map  $(a, \xi) \mapsto \mathscr{F}(a, \xi)$  is measurable;

- the map  $(a, \xi) \mapsto X(a, \xi)$  is measurable;
- for every  $\omega \in \mathscr{B}(\Omega_0)$  the map  $x \mapsto v(x, \omega)$  is measurable and

$$\sup_{x\in\Omega}\nu(x,\,\Omega_0)\leq M$$

for some M > 0;

- there exists a  $z_0 < 0$  and a constant c > 0 such that

$$\sup_{x \in \Omega_0} \mathscr{F}(t, x) \Lambda(X(t, x)) \le c e^{z_0 t}, \quad t \ge 0;$$
(5.2)

If Assumption 5.1 holds, then the kernel *K*, defined by (5.1), is a  $z_0$ -bounded kernel. What additional assumptions on  $\nu$  and *X* guarantee that *K* is also a regularizing kernel?

**Proposition 5.2.** Let  $\mathcal{F}$ , v, X satisfy Assumption 5.1.

If, additionally,  $v(x, \cdot) \in \mathcal{M}_{+,AC}(\Omega_0)$ , then the kernel K defined by (5.1) is a  $z_0$ -bounded regularizing kernel.

*Proof.* The absolute continuity, with respect to the Lebesgue measure, of the measures (3.6) and (3.5) is a consequence of the fact that  $K(a, x, \cdot) \in \mathscr{I}$ , with  $\mathscr{I}$  defined in Definition 3.5, for every a > 0 and  $x \in \Omega_0$ .

We aim at finding milder conditions on v that still guarantee that the kernel *K* is regularizing. Motivated by biological applications (see the upcoming sections) we focus on the following type of measures

$$\nu(x,\omega) = \beta(x)\delta_{q(x)}(\omega) \quad x \in \Omega, \ \omega \in \mathscr{B}(\Omega_0).$$
(5.3)

where q and  $\beta$  are suitable functions.

We first present an example of a measure  $\nu$ , satisfying (5.3), and a function *X*, that give rise to a kernel *K* which is **not** regularizing.

Example 5.3. If

$$v(x,\omega) = 2\delta_{\frac{x}{2}}(\omega)$$

and if we assume that the development is exponential, i.e.  $X(a, \xi) = \xi e^a$ , then Assumption 3.2 does not hold. Hence *K* is not a regularizing kernel. Indeed,

$$2\int_{0}^{t}\int_{\Omega}K(s,x,d\xi)\mathscr{F}(t-s,\xi)\delta_{\frac{1}{2}X(t-s,\xi)}(\omega)\Lambda(X(t-s,\xi))ds$$
  
=  $4\int_{0}^{t}\int_{\Omega}\mathscr{F}(s,x)\Lambda(xe^{s})\delta_{\frac{x}{2}e^{s}}(d\xi)\mathscr{F}(t-s,\xi)\delta_{\frac{1}{2}\xi e^{t-s}}(\omega)\Lambda(X(t-s,\xi))ds$   
=  $4\delta_{\frac{x}{4}e^{t}}(\omega)\int_{0}^{t}\mathscr{F}(s,x)\Lambda(xe^{s})\mathscr{F}\left(t-s,\frac{x}{2}e^{s}\right)\Lambda\left(X\left(t-s,\frac{x}{2}e^{s}\right)\right)ds.$ 

The take home message of this example is that it is not only the shape of v that determines whether the kernel is regularizing or not, but also the development rate.

We now state sufficient assumptions on q,  $\beta$ ,  $\mathscr{F}$  and X that guarantee that the kernel K defined by (5.1) is a  $z_0$ -bounded regularizing kernel.

**Proposition 5.4.** Let  $\mathscr{F}$ , v, X satisfy Assumption 5.1. Assume that v is of the form (5.3) for a measurable function  $\beta : \Omega \to \mathbb{R}_+$  and a measurable function  $q : \Omega \to \mathbb{R}_+$ . Additionally, assume that q is such that the function

$$F_a: x \mapsto q(X(a, x)) \tag{5.4}$$

is invertible and such that if  $|\omega| = 0$ , then  $|F_a^{-1}(\omega)| = 0$ , where we are denoting with  $|\cdot|$  the Lebesgue measure, see Appendix A. Finally assume that q and X are such that the function

$$p_{t,x}: a \mapsto q(X(t-a, q(X(a, x))))$$
(5.5)

is invertible and such that  $|\omega| = 0$  implies  $|p_{t,x}^{-1}(\omega)| = 0$ . Then the kernel K defined by (5.1) is a  $z_0$ -bounded regularizing kernel.

*Proof.* The kernel K is  $z_0$ -bounded because  $\mathscr{F}$ , X and  $\nu$  satisfy Assumption 5.1.

We now prove that, for every f, the measure (3.6) is absolutely continuous with respect to the Lebesgue measure. For notational convenience we rewrite K as

$$K(a, x, \omega) = j(a, x)\delta_{q(X(a, x))}(\omega).$$

Let  $A \in \mathscr{B}(\Omega)$  be a set of zero Lebesgue measure, then

$$\begin{split} &\int_{\Omega_0} f(x) K(a, x, A) dx = \int_{\Omega_0} f(x) j(a, x) \delta_{q(X(a, x))}(A) dx \\ &= \int_{F_a^{-1}(A)} f(x) j(a, x) dx = 0. \end{split}$$

We now prove that also (3.5) is an absolutely continuous measure with respect to the Lebesgue measure. Indeed

$$\begin{split} &K^{*2}(T, x, A) \\ &= \int_0^T \int_{\Omega} K(s, x, d\xi) j(T - s, \xi) \delta_{q(X(T - s, \xi))}(A) ds \\ &= \int_0^T j(s, x) j(T - s, q(X(s, x))) \delta_{PT, x(s)}(A) ds \\ &= \int_{[0, T] \cap p_{T, x}^{-1}(A)} j(s, x) j(T - s, q(X(s, x))) ds. \end{split}$$

The assumptions on  $p_{T,x}$  then guarantee that  $K^{*2}(T, x, \cdot)$  is absolutely continuous with respect to the Lebesgue measure.

## 6. Asymptotic behaviour of the population birth rate for the model examples

We now motivate the above assumptions on  $\nu$  by presenting the models that we are going to study with the results presented in Sect. 4.

6.1. Two applications to structured population models

# 6.1.1. Cell growth and fission

The first example is the model of cell growth and fission that is classically formulated via the PDE

$$\partial_t n(t, x) + \partial_x \left( g(x)n(t, x) \right) = -\left[ \Lambda(x) + \mu(x) \right] n(t, x) + 4\Lambda(2x)n(t, 2x)$$
(6.1)

or alternatively via the PDE

$$\partial_t n(t, x) + \partial_x \left( g(x)n(t, x) \right) = -\left[ \Lambda(x) + \mu(x) \right] n(t, x) + \int_{\Omega} h(y, x) \Lambda(y)n(t, y) dy,$$
(6.2)

These PDEs describe the evolution in time of a population of cells, structured by size, growing at rate g, dying at rate  $\mu$  and dividing into two smaller cells at rate  $\Lambda$ . The type of equation depends on how the cells divide. More precisely, if cells divide into equal parts, then the density of cells of size x at time t, n(t, x), is the solution of equation (6.1). If, instead, the expected number of cells with size in [y, y + dy], produced by the division of a cell of size x, is equal to h(x, y)dy, then n(t, x) is the solution of equation (6.2).

The model described above fits into the class of models introduced in Sect. 5.1. Hence, the population birth rate, which in this case is the rate at which individuals are born due to fission, has to satisfy (2.1), with *K* given by (5.1) and  $X(a, \xi)$  is the solution at time *a* of the following ODE

$$\frac{dx}{dt} = g(x) \quad x(0) = \xi, \tag{6.3}$$

while

$$\mathscr{F}(t,\xi) := \exp\left(-\int_0^t \tilde{\mu}(X(s,\xi))ds\right) = \exp\left(-\int_{\xi}^{X(t,\xi)} \frac{\tilde{\mu}(x)}{g(x)}dx\right)$$
(6.4)

where  $\tilde{\mu}(x) = \mu(x) + \Lambda(x)$ , and with

$$\nu(x,\omega) = \int_{\omega} h(x, y) dy$$
 or  $\nu(x, \omega) = 2\delta_{\frac{x}{2}}(\omega).$ 

Now the question is, what are the assumptions on the parameters g,  $\Lambda$  and  $\nu$  that ensure that K is a  $z_0$ -bounded regularizing kernel, that the corresponding operator  $\tilde{K}$ 

satisfies Assumption 4.23 or Assumption 4.24 and that  $\mathbb{K}_{\lambda}$  is non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ , compact for every  $\lambda \in \Delta$ ? In other words, what are the assumptions on the parameters that allow us to study the evolution of the population by using the results presented in Sect. 4? Below we present two collections of assumptions, one for the case of fission into equal sizes and one for the case of fission into unequal sizes. We start with the latter.

Assumption 6.1. (Unequal fission model) We assume that

1. 
$$\Omega = \mathbb{R}^*_+;$$

2. the growth rate  $g : \Omega \to \mathbb{R}^*_+$  is a continuous function such that for every  $z \in \Omega$ 

$$\int_{z}^{\infty} \frac{1}{g(s)} ds = \infty; \tag{6.5}$$

- 3. the fission rate  $\Lambda : (0, \infty) \to \mathbb{R}_+$  is a measurable function such that either  $supp(\Lambda) = [M, \infty)$ , where M > 0, or  $supp(\Lambda) = \mathbb{R}^*_+$ , and such that  $\lim_{z\to\infty} \Lambda(z)$  exists and is strictly positive;
- 4. the death rate  $\mu : \Omega \to \mathbb{R}_+$  is measurable;
- 5. for every  $y \in \Omega$

$$\nu(y,\cdot) \in \mathscr{M}_{+,AC}(\Omega),\tag{6.6}$$

with density  $h(y, \cdot)$  such that h(y, x) = 0 when y < x and h(y, x) > 0 if y > x

$$\int_0^y h(y, x) dx = 2, \quad h(y, x) = h(y, y - x); \tag{6.7}$$

6. the set of the states at birth is

$$\Omega_0 := \bigcup_{y \in supp(\Lambda)} supp(h(y, \cdot)) = (0, \infty).$$

We assume that for every  $\varepsilon > 0$  there exists a  $\delta_{\varepsilon} > 0$  such that for every  $0 < \delta < \delta_{\varepsilon}$  we have

$$\left| \int_{\Omega_0} \left( h(y, x) - h(y, x + \delta) \right) dx \right| < \frac{\varepsilon}{y} \quad \text{for every } y > 0 \tag{6.8}$$

where  $h(y, x + \delta) := 0$  if  $x + \delta \notin \Omega_0$ .

7. Finally we assume that

$$\int_0^1 \frac{\Lambda(y)}{yg(y)} dy < \infty.$$
(6.9)

We now explain the interpretation of these requirements on  $g, h, \Lambda$ . By the definition of g,

$$\tau(x, y) := \int_x^y \frac{1}{g(z)} dz$$

is the time that it takes to develop from size x to size y. Hence, the fact that g satisfies (6.5) implies that the time that it takes to grow up to size equal to sup  $\Omega$  is equal to infinity. This, together with the assumption on the limiting large size behaviour of the fission rate, guarantees that the probability that a cell reaches size equal to infinity is zero.

The first assumption on h in (6.7) guarantees that a cell always divides into two cells. The second assumption in the same line is a consequence of the fact that mass is conserved during fission and hence a cell of size x that divides into a cell of size y produces also a cell of size equal to x - y.

In many works the *i*-state space  $\Omega$  is assumed to be a compact subset of  $\mathbb{R}^*_+$ , see for instance [14] and [25]. Here we relax this assumption and assume that  $\Omega = \mathbb{R}^*_+$ . The price of this generalisation is that we need to impose assumptions on the model parameters g,  $\Lambda$ , h that exclude gelation (i.e. escape of mass at infinity, in the "fragmentation" terminology) and shattering (i.e. escape of mass at zero). This is why we introduce conditions (6.8) and (6.9). These tightness assumptions guarantee the compactness of the operator  $\mathbb{K}_{\lambda}$ , as we will see in Sect. 6.2.1, proof of Proposition 6.8.

Condition (6.8) holds for a broad class of self-similar kernels. In particular it holds for uniform fragmentation,  $h(y, x) = \frac{2}{y}\chi_{(0,x)}$ , but also for some of the self-similar kernels considered in [40]. Indeed assume that

$$h(y,x) = \frac{2}{y}p\left(\frac{x}{y}\right)$$

where  $p : [0, 1] \mapsto \mathbb{R}_+$  is s.t.  $p \in L^{\infty}([0, 1])$  with  $\int_0^1 p(z)dz = 1$  and p(1-z) = p(z) for every  $z \in [0, 1]$ . Then

$$\begin{aligned} \left| \int_{\Omega_0} \left[ h(y,x) - h(y,x+\delta) \right] dx \right| &\leq \left| \int_0^{y-\delta} \left[ h(y,x) - h(y,x+\delta) \right] dx \right| \\ &+ \left| \int_{y-\delta}^y h(y,x) dx \right| \leq \frac{2}{y} \left| \int_0^{y-\delta} \left[ p\left(\frac{x}{y}\right) - p\left(\frac{x+\delta}{y}\right) \right] dx \right| \\ &+ \frac{2}{y} \left| \int_{y-\delta}^y p\left(\frac{x}{y}\right) dx \right| \leq 2 \left| \int_0^{1-\frac{\delta}{y}} \left[ p\left(z\right) - p\left(z+\frac{\delta}{y}\right) \right] dz \right| \\ &+ 2 \left| \int_{1-\frac{\delta}{y}}^1 p\left(z\right) dz \right| \\ &\leq 2 \left| \int_0^{1-\frac{\delta}{y}} p\left(z\right) dz - \int_{\frac{\delta}{y}}^1 p\left(z\right) dz \right| + \frac{2}{y} \delta \|p\|_{L^\infty} \\ &\leq 2 \left| \int_{1-\frac{\delta}{y}}^1 p\left(z\right) dz \right| + 2 \left| \int_0^{\frac{\delta}{y}} p\left(z\right) dz \right| + \frac{2}{y} \delta \|p\|_{L^\infty} \leq \frac{6}{y} \delta \|p\|_{L^\infty}. \end{aligned}$$

Hence h satisfies (6.8).

Finally condition (6.9) guarantees that  $\Lambda(y) \to 0$  as  $y \to 0$  quickly, namely faster that y itself. We expect that it is possible to weaken considerably the condition

h(x, y) > 0 if x > y. This condition is however attractive, because it allows for a straightforward proof of the non-supportingness of the operator  $\mathbb{K}_{\lambda}$ .

For the model in which cells divide into equal parts we make the following assumptions.

Assumption 6.2. (Equal fission model) In this case we assume that

- 1.  $\Omega = \Omega_0 := (0, \infty),$
- 2. g satisfies point 2 of Assumption 6.1, is Lipschitz continuous and g(2x) < 2g(x)for every  $x \in \Omega$  and  $0 < \sup_{x \in \Omega} \frac{1}{g(x)} < \infty$ ,
- 3.  $\Lambda$  satisfies point 3 of Assumption 6.1,
- 4.  $\mu$  satisfies point 4 of Assumption 6.1,
- 5. for every  $y \in \Omega$  we have that

$$\nu(y,\omega) = 2\delta_{y/2}(\omega) \quad \omega \in \mathscr{B}(\Omega_0). \tag{6.10}$$

The requirements on the parameters listed in Assumption 6.2 are needed to deduce the asymptotic behaviour of the population with the method presented in Sect. 4.7. Indeed the assumptions on the growth rate *g* exclude the possibility of having cyclic solutions, see [4,34], being a sufficient assumption to guarantee that the operator  $\mathbb{K}_{\lambda}$ is compact and non-supporting, as we will see in Sect. 6.2.1.

**Lemma 6.3.** Let either Assumption 6.1 or Assumption 6.2 hold. Then the kernel K defined by (5.1) is a  $z_0$ -bounded regularizing kernel for some  $z_0 < 0$ .

*Proof.* Thanks to (6.5),

$$K(t, x, \Omega_0) \sim e^{-\lim_{z\to\infty} \Lambda(z)t}$$

as time tends to infinity. Hence for every  $z_0 > -\lim_{z\to\infty} \Lambda(z)$  we have that *K* satisfies (3.3). If  $\nu$  satisfies Assumption 6.1, then this concludes the proof thanks to Proposition 5.2.

Assume, instead, that v is given by (6.10) and that g(2x) < 2g(x). Then the function  $p_{T,x}$  introduced in Proposition 5.4 is equal to

$$p_{T,x}:s\mapsto \frac{1}{2}X\left(T-s,\frac{1}{2}X(s,x)\right).$$

This map is differentiable and by the chain rule

$$2p'_{T,x}(s) = -\partial_1 X\left(T - s, \frac{1}{2}X(s, x)\right) + \partial_2 X\left(T - s, \frac{1}{2}X(s, x)\right) \frac{1}{2}\frac{d}{ds}X(s, x)$$

Using (6.3) we deduce that for every  $a > 0, \xi > 0$  and s > 0

$$\frac{dX(a, (X(s,\xi)))}{ds} = \partial_2 X(a, X(s,\xi)) g(X(s,\xi)).$$

On the other hand

$$\frac{dX(a, (X(s,\xi)))}{ds} = \frac{dX(a+s,\xi)}{ds} = g(X(a+s,\xi)).$$

Hence substituting s = 0 we deduce that

$$\partial_2 X(a,\xi) = \frac{g(X(a,\xi))}{g(\xi)}.$$

Therefore using g(2x) < g(x) we deduce that

$$2p'_{T,x}(s) = -g\left(X\left(T-s,\frac{1}{2}X(s,x)\right)\right) + \frac{g(X\left(T-s,\frac{1}{2}X(s,x)\right))}{g\left(\frac{1}{2}X(s,x)\right)}\frac{1}{2}g(X(s,x))$$
$$= -g\left(X\left(T-s,\frac{1}{2}X(s,x)\right)\right)\left(1 - \frac{g(X(s,x))}{2g\left(\frac{1}{2}X(s,x)\right)}\right) < 0.$$

As a consequence  $p_{T,x}$  is monotone, hence invertible and such that |A| = 0 implies  $|p_{T,x}^{-1}(A)| = 0$ 

The function  $F_a$ , given by (5.4), is invertible and such that if |A| = 0, then  $|F_a^{-1}(A)| = 0$  as the map  $x \mapsto X(a, x)$  is monotone.

#### 6.1.2. Waning and boosting

Consider a population of individuals structured by their level of immunity against a pathogen. Assume that the level of immunity decreases with rate g and is boosted by infection and that the force of infection equals a constant  $\gamma$ . We assume that the time that it takes the immune systems to clear the infection is negligible compared to the time in between two infections and consider, accordingly, boosting as instantaneous.

Assume that the immunity level after the boosting is determined by the immunity level before the boosting event via the boosting function f. We assume that f is as in Fig. 2 and we denote with  $f_1$  the restriction of f to the set  $(0, x_c)$  and with  $f_2$  the restriction to f on  $(x_c, M]$ . The density of individuals with immunity level x at time t, n(t, x), satisfies the following PDE

$$\partial_t n(t, x) + \partial_x \left( g(x)n(t, x) \right) = -\gamma n(t, x) + Sn(t, x) \tag{6.11}$$

where

$$S\varphi(x) = \begin{cases} 0 & x < m \\ -\gamma \frac{1}{f'(f_1^{-1}(x))} \varphi(f_1^{-1}(x)) + \gamma \frac{1}{f'(f_2^{-1}(x))} \varphi(f_2^{-1}(x)) & m < x < r \ (6.12) \\ \gamma \frac{1}{f'(f_2^{-1}(x))} \varphi(f_2^{-1}(x)) & r < x < M. \end{cases}$$

The term Sn(t, x) in equation (6.11) represents the individuals that (re)appear in the population at time t with state x after boosting. Since the function f has a local minimum, an individual with immunity level  $x \in [m, r]$  can be obtained as the result of

the boosting of an individual in any one of the sets  $(0, x_c), (x_c, M)$  while an individual with state at birth  $x \in [r, M]$  is produced by the boosting of an individual with state in  $(x_c, M)$ .

The backward reformulation of equation (6.11) is

$$\partial_t m(t,x) - g(x)\partial_x m(t,x) = -\gamma m(t,x) + S^* m(t,x)$$
(6.13)

where  $S^*$  is the (pre)dual operator of S and is given by

$$S^*\varphi(x) = \gamma\varphi(f(x)).$$

This model fits into the class of models described in Sect. 5.1. Hence, the population birth rate *B*, which in this case is the rate at which individuals appear in the population with a higher immunity level due to boosting, is the solution of equation (2.1) with a kernel *K* given by formula (5.1). The factor  $X(a, \xi)$  in (5.1) is the solution of the ODE (6.3), with *g* the rate of waning. The factor  $\Lambda(x) = \gamma > 0$  is the boosting rate. Since we assume the death rate to be equal to zero, we have that the term  $\mathscr{F}$  in (5.1) is equal to

$$\mathscr{F}(t,\xi) := e^{-\gamma t} \tag{6.14}$$

and

$$\nu(y,\omega) := \delta_{f(y)}(\omega) \tag{6.15}$$

for every *i*-state *y* and for every set of states at birth  $\omega$ .

We have chosen a specific form of f in order to make the computations in Sect. 6.2.3 not too demanding for the reader. For sure the result holds for a much wider class of boosting functions f (see for instance [12], but note that in that paper there is no proof that convergence is exponential). We now specify the assumptions on the parameters that guarantee that we can apply the results presented in Sect. 4.

Assumption 6.4. (Waning and boosting model, see Fig. 2) We assume that

- 1.  $\Omega = (0, M];$
- 2. the boosting function  $f : \Omega \to [m, M] =: \Omega_0$  is such that  $f(x) = f_1(x)$  if  $x \in (0, x_c]$  while  $f(x) = f_2(x)$  if  $x \in (x_c, M]$  where

$$f_1(x) = -\alpha_1 x + q_1$$
 and  $f_2(x) = \alpha_2 x + q_2$ 

with

$$\begin{aligned} \alpha_1 &= \frac{r - m}{x_c}, \quad q_1 = r \text{ where } 0 < m < M, 0 < r < M \\ \alpha_2 &= \frac{M - m}{M - x_c}, \quad q_2 = m - x_c \frac{M - m}{M - x_c}; \end{aligned}$$

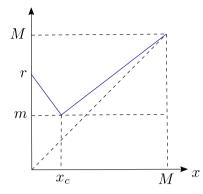


Figure 2. Boosting function

3.  $g: \Omega \to (-\infty, 0)$  is a continuous function and such that

$$\frac{\alpha_2 g(y)}{g(f(y))} < 1 \quad \text{for a.e. } y \in \Omega_0.$$
(6.16)

The conditions on the parameters g, v,  $\Lambda$  listed in Assumption 6.4 guarantee that the model is well defined and allow to apply the results of Sect. 4.7 as we will see in Sect. 6.2.3.

In this work we focus on Assumption 6.4 and we assume that the set of the possible immunity levels is a compact set, but this assumption can be relaxed as for instance in [12].

Condition (6.16) is sufficient to guarantee that the kernel *K* defined by (5.1) is regularizing. The meaning of this assumption is the following. The immunity level of an individual who boosts at time *t* and then wanes for a time interval of length *dt* is lower than the immunity level of an individual who wanes for *dt* and then boosts at time t + dt. This assumption can be seen as a congener of the assumption g(2x) < 2g(x) in the case of fission into equal sizes. We refer to [12] for more explanations.

**Lemma 6.5.** Let g,  $\mu$ ,  $\Lambda$ ,  $\nu$  satisfy Assumption 6.4. Then the kernel K defined by (5.1) is  $a - \gamma$ -bounded regularizing kernel.

*Proof.* The fact that K is a  $-\gamma$  kernel follows simply by noting that

$$\mathscr{F}(a, x)\Lambda(X(a, x)) = \gamma e^{-\gamma a}.$$

We next investigate whether K is a regularizing kernel. To this end we notice that the function  $F_a$  introduced in Proposition 5.4,

$$F_a: x \mapsto f(X(a, x))$$

is invertible because it is piecewise monotone.

On the other hand, the function  $p_{T,x}$  now reads

$$p_{T,x}: a \mapsto f(X(T-a, f(X(a, x))))$$

As in the proof of Lemma 6.3, using the chain rule, condition (6.16) and the definition of *X* as the solution of the ODE (6.3) we prove that

$$p'_{T,x}(a) = -f'(X(T-a, f(X(a, x))))g(X(T-a, f(X(a, x)))) + \left[1 - \frac{f'(X(a, x))g(X(a, x))}{g(f(X(a, x)))}\right] \quad a.e. \ a > 0.$$

Thanks to (6.16) we deduce that  $p_{T,x}$  is piecewise monotone. Hence the desired conclusion follows.

6.2. Asymptotic behaviour for the model examples

In this section we apply the results presented in Sect. 4 to the model examples. To this end we proceed as follows

- 1. we use Lemma 4.29 to associate to the kernel K an operator kernel  $\tilde{K}$ ;
- 2. we define the discounted next generation operator  $\mathbb{K}_{\lambda}$  as a function of  $\tilde{K}$ , using (4.7);
- 3. then we check that the operator  $\mathbb{K}_{\lambda}$  is compact and non supporting.

### 6.2.1. Cell growth and fission (into unequal parts)

In this section we assume that the parameters g,  $\mu$ ,  $\Lambda$ ,  $\nu$  satisfy Assumption 6.1. Hence there exists a  $z_0$  such that the kernel K, given by (5.1), is a  $z_0$ -regularizing kernel.

It remains to prove that, under the assumptions of the unequal fission model,  $\mathbb{K}_{\lambda}$  satisfies the assumptions of Theorem 4.14. Recall that  $K \in \mathscr{I}$ . We denote with *k* its density, given by

$$k(a, x, y) := \mathscr{F}(a, x)\Lambda(X(a, x))h(X(a, x), y).$$
(6.17)

The operator  $\tilde{K}$  introduced in (4.27), is given by

$$\left(\tilde{K}(a)\varphi\right)(y) := \int_{\Omega_0} k(a, x, y)\varphi(x)dx \quad a \ge 0, \quad y \in \Omega_0$$
(6.18)

and as a direct consequence we have the following result.

**Lemma 6.6.** The kernel  $\tilde{K}$  satisfies Assumption 4.24.

The following theorem, see e.g [30], is fundamental to prove the compactness of the operator  $\mathbb{K}_{\lambda}$  in the model examples.

**Theorem 6.7.** (*Fréchet-Kolmogorov*) Let  $T : X^{\mathbb{C}} \to X^{\mathbb{C}}$  be linear and bounded. If for every  $\varepsilon > 0$  there exists a  $\delta > 0$  such that for every  $0 < |h| < \delta$ 

$$\int_{\Omega_0} |T\varphi(x+h) - T\varphi(x)| \, dx \le \varepsilon \|\varphi\|_1$$

for every  $\varphi \in X^{\mathbb{C}}$ , where  $T\varphi(x+h) = 0$  if  $x + h \notin \Omega_0$ , then the operator T is compact.

**Proposition 6.8.** The operator  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \Delta$  and the operator  $\mathbb{K}_{\lambda}$  is non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ .

*Proof.* To prove compactness we apply Theorem 6.7. Recalling Assumption 6.8 we deduce that for every  $\varepsilon > 0$  there exists a  $\delta_{\varepsilon} > 0$  such that for every  $\delta < \delta_{\varepsilon}$  and for every  $\varphi \in X_+$ 

$$\begin{split} &\int_{\Omega_0} \left| \left( \mathbb{K}_{\lambda} \varphi \right) (x+\delta) - \left( \mathbb{K}_{\lambda} \varphi \right) (x) \right| dx \\ &\leq \int_0^\infty \int_{\Omega_0} \varphi(y) e^{-a \Re \lambda} \mathscr{F}(a, y) \Lambda(X(a, y)) \cdot \\ &\cdot \left| \int_{\Omega_0} h(X(a, y), x+\delta) - h(X(a, y), x) dx \right| dy da \\ &\leq \varepsilon \int_0^\infty \int_0^\infty \varphi(y) e^{-a \Re \lambda} \mathscr{F}(a, y) \frac{\Lambda(X(a, y))}{X(a, y)} dy da, \end{split}$$

where for the last inequality we have used (6.8).

Using Fubini's theorem and performing the change of variables X(a, y) = x we deduce that

$$\begin{split} &\int_0^\infty \int_0^\infty \varphi(y) e^{-a\Re\lambda} \mathscr{F}(a, y) \frac{\Lambda(X(a, y))}{X(a, y)} dy da \\ &= \int_0^\infty \int_0^\infty \varphi(y) e^{-a\Re\lambda} \mathscr{F}(a, y) \frac{\Lambda(X(a, y))}{X(a, y)} da dy \\ &= \int_0^\infty \int_y^\infty \varphi(y) e^{-\tau(y, x)\Re\lambda} \hat{\mathscr{F}}(y, x) \frac{\Lambda(x)}{xg(x)} dx dy \\ &\leq \int_0^1 \int_0^x \varphi(y) e^{-\tau(y, x)\Re\lambda} \hat{\mathscr{F}}(y, x) \frac{\Lambda(x)}{xg(x)} dy dx \\ &+ \int_1^\infty \int_0^x \varphi(y) e^{-\tau(y, x)\Re\lambda} \hat{\mathscr{F}}(y, x) \frac{\Lambda(x)}{xg(x)} dy dx \end{split}$$

Now, using Fubini's theorem, the change of variables x = X(a, y) and the bound (5.2), we estimate the second term in the following way

$$\begin{split} &\int_{1}^{\infty} \int_{0}^{x} \varphi(y) e^{-\tau(y,x)\Re\lambda} \hat{\mathscr{F}}(y,x) \frac{\Lambda(x)}{xg(x)} dy dx \\ &\leq \int_{1}^{\infty} \int_{0}^{x} \varphi(y) e^{-\tau(y,x)\Re\lambda} \hat{\mathscr{F}}(y,x) \frac{\Lambda(x)}{g(x)} dy dx \\ &\leq \int_{0}^{\infty} \int_{0}^{x} \varphi(y) e^{-\tau(y,x)\Re\lambda} \hat{\mathscr{F}}(y,x) \frac{\Lambda(x)}{g(x)} dy dx \\ &\leq \int_{0}^{\infty} \int_{y}^{\infty} \varphi(y) e^{-\tau(y,x)\Re\lambda} \hat{\mathscr{F}}(y,x) \frac{\Lambda(x)}{g(x)} dx dy \\ &\leq \int_{0}^{\infty} \int_{0}^{\infty} \varphi(y) e^{-a\Re\lambda} \hat{\mathscr{F}}(a,y) \Lambda(X(a,y)) dady \end{split}$$

$$\leq C \int_0^\infty e^{(-\Re\lambda+z_0)a} da \int_0^\infty \varphi(y) dy \leq \frac{C}{\Re\lambda-z_0} \|\varphi\|_1$$

On the other hand, thanks to (6.9)

$$\int_0^1 \int_0^x \varphi(y) e^{-\tau(y,x)\Re\lambda} \hat{\mathscr{F}}(y,x) \frac{\Lambda(x)}{xg(x)} dy dx \le e^{-\tau(0,1)\Re\lambda} \|\varphi\|_1 \int_0^1 \frac{\Lambda(x)}{xg(x)} dx.$$

It follows that for every  $\varepsilon > 0$  there exists a  $\delta$  such that

$$\|(\mathbb{K}_{\lambda}\varphi)(\cdot+\delta) - (\mathbb{K}_{\lambda}\varphi)(\cdot)\|_{1} \le \varepsilon \|\varphi\|_{1}.$$

Applying Lemma 6.7 we conclude that  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \mathbb{C}$  with  $\Re \lambda > z_0$ .

We now prove that  $\mathbb{K}_{\lambda}$  is non-supporting. To this end we firstly prove a stronger property. Indeed, thanks to (6.8) we can prove that  $\mathbb{K}_{\lambda}\varphi(x) > 0$  for every  $x \in \Omega_0$ , because for every  $\varphi \in L^1_+(\Omega_0)$  and every  $x \in \Omega_0$ 

$$(\mathbb{K}_{\lambda}\varphi)(x) = \int_{0}^{\infty} \int_{0}^{\infty} \varphi(y) e^{-\lambda a} \mathscr{F}(a, y) \Lambda(X(a, y)) h(X(a, y), x) dady$$
$$= \int_{0}^{\infty} \varphi(y) \int_{y}^{\infty} e^{-\lambda \tau(y, z)} \widehat{\mathscr{F}}(z, y) \frac{\Lambda(z)}{g(z)} h(z, x) dz dy$$

Since we assume that h(z, x) > 0 for every z > x, then

$$\int_{y}^{\infty}\hat{\mathscr{F}}(y,z)e^{-\lambda\tau(y,z)}\frac{\Lambda(z)}{g(z)}h(z,x)dz>0.$$

Since  $\varphi$  belongs to  $X_+$  there exists a set of positive Lebesgue measure  $U \subset \Omega_0$ , on which  $\varphi$  is strictly positive. The integration is over  $\Omega_0$ . We conclude that  $(\mathbb{K}_\lambda \varphi)(x) > 0$  for every  $x \in \Omega_0$ .

**Proposition 6.9.** Let  $g, \mu, \Lambda, v$  be such that Assumption 6.1 holds. Let  $r, \psi_r$  be respectively the Malthusian parameter and the stable distribution. The solution B of (2.1) satisfies

$$\|e^{-rt}B(t,\cdot)-c\Psi_r\| \le Me^{-vt}$$

where  $\Psi_r(dx) = \psi(x)dx$  and c, M > 0 and v > 0 and the norm  $\|\cdot\| = \|\cdot\|_{TV} = \|\cdot\|_{\mathfrak{d}}$ . Moreover

$$sign(r) = sign(R_0 - 1)$$

where  $R_0$  is defined in (4.6) and

$$\mathbb{K}_0\mu(\cdot) = \int_0^\infty \int_{\Omega_0} k(t, x, \cdot)\mu(dx)dt.$$

# 6.2.2. Cell growth and fission (into equal parts)

In this section we assume that the parameters g,  $\mu$ ,  $\Lambda$ ,  $\nu$  are such that Assumption 6.2 holds. Also in this case we have to check whether the assumptions of Lemma 4.29 hold. In this case

$$(\tilde{K}(s)\varphi)(z) := 4 \frac{g(X(-s,2z))}{g(2z)} \mathscr{F}(s,X(-s,2z)) \Lambda(2z)\varphi(X(-s,2z)) \quad (6.19)$$

for every z > 0 such that  $s < \tau(0, 2z)$  while  $(\tilde{K}(s)\varphi)(z) = 0$  otherwise. Indeed

$$\int_{\Omega} K(s, x, \omega)\varphi(x)dx = 2\int_{0}^{\infty} \mathscr{F}(s, x)\Lambda(X(s, x))\delta_{\frac{1}{2}X(s, x)}(\omega)\varphi(x)dx$$
$$= 4\int_{\omega} \chi_{[0,\tau(0,2y)]}(s)\mathscr{F}(s, X(-s, 2y))\Lambda(y)\varphi(x)\frac{g(X(-s, 2y))}{g(2y)}dy$$

**Lemma 6.10.** The kernel  $\tilde{K}$  satisfies Assumption 4.23.

*Proof.* The statement follows by the definition of  $\tilde{K}$ .

The following theorem can be found in [29] and will be important to prove the compactness of the operator  $\mathbb{K}_{\lambda}$ .

**Theorem 6.11.** Let  $T : X^{\mathbb{C}} \to X^{\mathbb{C}}$  be linear and bounded and of the form

$$(T\varphi)(x) = \int_{\Omega_0} h(x, y)\varphi(y)dy.$$

Suppose that there exists an  $h_+$  such that

$$|h(x, y)| \le h_+(x, y) \quad x, y \in \Omega_0$$

and that the operator  $T_+: X_+ \to X_+$ 

$$(T_+\varphi)(x) := \int_{\Omega_0} h_+(x, y)\varphi(y)dy$$

is compact. Then T is compact.

**Lemma 6.12.** The operator  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \Delta$  and  $\mathbb{K}_{\lambda}$  is non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ .

*Proof.* Using (6.19) and (5.2), we deduce that for every  $\varphi \in X_+$ 

$$\begin{aligned} |(\mathbb{K}_{\lambda}\varphi)(y)| \\ &\leq 4 \int_{0}^{\tau(0,2y)} e^{-s\Re\lambda} \frac{g(X(-s,2y))}{g(2y)} \mathscr{F}(s,X(-s,2y))\Lambda(2y)\varphi(X(-s,2y))ds \\ &\leq c \int_{0}^{\tau(0,2y)} e^{-s\Re\lambda} e^{z_{0}s} \frac{g(X(-s,2y))}{g(2y)} \varphi(X(-s,2y))ds \end{aligned}$$

Let p > 0. The operator  $\mathbb{K}^+(p)$  defined by

$$\left(\mathbb{K}^{+}(p)\varphi\right)(y) = \int_{0}^{\tau(0,2y)} e^{-ps} \frac{g(X(-s,2y))}{g(2y)} \varphi(X(-s,2y)) ds$$

is a linear bounded map from  $X_+$  to  $X_+$ . Indeed, thanks to the second assumption in (6.9), if we assume that  $\varphi \in X_+$ , then

$$\begin{split} &\int_0^\infty \left( \mathbb{K}^+(p)\varphi \right)(y)dy = \int_0^\infty \int_0^{\tau(0,2y)} e^{-ps}\varphi(X(-s,2y)) \frac{g(X(-s,2y))}{g(2y)} dsdy \\ &= \int_0^\infty \int_0^{2y} e^{-p\tau(z,2y)} \frac{\varphi(z)}{g(2y)} dzdy \le \int_0^\infty \int_{z/2}^\infty \frac{e^{-p\tau(z,2y)}}{g(2y)} dy\varphi(z)dz \\ &= \frac{1}{p} \|\varphi\|_1 \end{split}$$

We want to prove that  $\mathbb{K}_{\lambda}$  it is compact. To this end, we apply Lemma 6.7. Consider  $\delta > 0$ , then

$$\begin{split} \left| \mathbb{X}^{+}(p)\varphi(\delta+y) - \mathbb{X}^{+}(p)\varphi(y) \right| \\ &\leq \left| \int_{0}^{\tau(0,2y+2\delta)} e^{-ps} \frac{g(X(-s,2y+2\delta))}{g(2y+2\delta)} \varphi(X(-s,2y+2\delta)) ds \right| \\ &- \int_{0}^{\tau(0,2y)} e^{-ps} \frac{g(X(-s,2y))}{g(2y)} \varphi(X(-s,2y)) ds \right| \\ &\leq \left| \int_{0}^{2y+2\delta} e^{-p\tau(z,2y+2\delta)} \frac{\varphi(z)}{g(2y+2\delta)} dz - \int_{0}^{2y} e^{-p\tau(z,2y)} \frac{\varphi(z)}{g(2y)} dz \right| \\ &\leq \left| \int_{2y}^{2y+2\delta} e^{-p\tau(z,2y+2\delta)} \frac{\varphi(z)}{g(2y+2\delta)} dz \right| \\ &+ \int_{0}^{2y} \left| \frac{e^{-p\tau(z,2y)}}{g(2y)} - \frac{e^{-p\tau(z,2y+2\delta)}}{g(2y+2\delta)} \right| \varphi(z) dz. \end{split}$$

Moreover

$$\int_{2y}^{2y+2\delta} \left| e^{-p\tau(z,2y+2\delta)} \frac{\varphi(z)}{g(2y+2\delta)} \right| dz$$
  
$$\leq \sup_{x \in \Omega} \frac{1}{g(x)} e^{-p\tau(2y,2y+2\delta)} \int_{2y}^{2y+2\delta} e^{-p\tau(z,2y)} \varphi(z) dz.$$

Consequently,

$$\|\mathbb{K}^+(p)\varphi(\cdot+\delta) - \mathbb{K}^+(p)\varphi(\cdot)\|_1$$

$$\leq \sup_{x \in \Omega} \frac{1}{g(x)} \int_{0}^{\infty} e^{-p\tau(2y,2y+2\delta)} \int_{2y}^{2y+2\delta} e^{-p\tau(z,2y)} \varphi(z) dz dy \\ + \int_{0}^{\infty} \int_{0}^{2y} \left| \frac{e^{-p\tau(z,2y)}}{g(2y)} - \frac{e^{-p\tau(z,2y+2\delta)}}{g(2y+2\delta)} \right| \varphi(z) dz dy \\ \leq \sup_{x \in \Omega} \frac{1}{g(x)} \int_{0}^{\infty} \int_{z/2-\delta}^{z/2} e^{-p\tau(2y,2y+2\delta)} e^{-p\tau(z,2y)} dy \varphi(z) dz \\ + \left( \sup_{x \in \Omega} \frac{1}{g(x)} \right)^{2} \int_{0}^{\infty} \int_{z/2}^{\infty} \left| g(2y+2\delta) e^{-p\tau(z,2y)} - e^{-p\tau(z,2y+2\delta)} g(2y) \right| \varphi(z) dy dz \\ \leq \sup_{x \in \Omega} \frac{1}{g(x)} \hat{c} \delta \|\varphi\|_{1} + \left( \sup_{x \in \Omega} \frac{1}{g(x)} \right)^{2} c' \delta \|\varphi\|_{1} \\ \leq \sup_{x \in \Omega} \frac{1}{g(x)} \left[ \hat{c} \delta \|\varphi\|_{1} + c^{*} 2\delta \|\varphi\|_{1} \right]$$

where  $\hat{c}, c^*, c' > 0$  and where we have used the Lipschitz continuity of g and of  $\tau$  with respect to its second argument. We deduce that  $\mathbb{K}^+(p)$  is compact for every p > 0, hence by Lemma 6.11 we have that  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \mathbb{C}$  with  $\Re \lambda > z_0$ .

We now check that  $\mathbb{K}_{\lambda}$  is non-supporting for every  $\lambda \in \mathbb{R} \cap \Delta$ . For every  $\varphi \in X_+$ , there exists a set *S* of positive Lebesgue measure with  $\varphi(x) \neq 0$  for every  $x \in S$ . Therefore for every  $2x > x_1 := \inf S$ 

$$\mathbb{K}_{\lambda}\varphi(x) = 4\Lambda(2x) \int_0^{2x} e^{-\lambda\tau(z,2x)} \hat{\mathscr{F}}(z,2x) \frac{\varphi(z)}{g(2x)} dz > 0.$$

This implies that for every  $x > x_1/4$  we have that  $\mathbb{K}^2_{\lambda}\varphi(x) > 0$ , indeed

$$\mathbb{K}_{\lambda}^{2}\varphi(x) = 4 \int_{0}^{2x} e^{-\lambda\tau(z,2x)} \hat{\mathscr{F}}(z,2x) \frac{\mathbb{K}_{\lambda}\varphi(z)}{g(2x)} dz.$$

Iterating this argument we deduce that for every  $\varphi \in X_+$  there exists an  $x_1 > 0$  and an  $n \in \mathbb{N}$  such that  $\mathbb{K}^n_\lambda \varphi(x) > 0$  for every  $x > \frac{x_1}{2^n}$ . As a consequence, this implies that for every  $F \in L^{\infty}_+(\Omega_0)$  and every  $\varphi \in X_+$  there exists an *n* such that  $\langle F, \mathbb{K}^n_\lambda \varphi \rangle > 0$ .

**Proposition 6.13.** Let  $g, \mu, \Lambda, v$  be such that Assumptions 6.1 holds. Let  $r, \psi_r$  be respectively the Malthusian parameter and the stable distribution. The solution B of (2.1) satisfies

$$\|e^{-rt}B(t,\cdot) - c\Psi_r\| \le Me^{-vt}$$

where c, M, v > 0 and  $\Psi_r(dx) = \psi_r dx$  and  $\|\cdot\| = \|\cdot\|_{TV} = \|\cdot\|_{b}$ ,

$$sign(r) = sign(R_0 - 1),$$

and  $R_0$  is the spectral radius of  $\mathbb{K}_0$  defined by

$$\mathbb{K}_0\varphi(x) = \int_0^\infty \frac{g(X(-t,2x))}{g(2x)} \mathscr{F}(t,X(-t,2x))\Lambda(2x)\varphi(X(-t,2x))dt.$$

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# 6.2.3. Waning and boosting

In this section we make Assumption 6.4. In this case the operator kernel  $\tilde{K}$  is such that for every  $a \ge 0$  the operator  $\tilde{K}(a)$  belongs to  $\mathscr{L}(L^1_+(\Omega_0)) = \mathscr{L}(L^1_+([m, M]))$  and is equal to

$$(\tilde{K}(s)\varphi)(z) := \begin{cases} \gamma e^{-\gamma s} \left[ -\beta_1(z)\varphi(X(-s, f_1^{-1}(z)))g(X(-s, f_1^{-1}(z))) + \beta_2(z)\varphi(X(-s, f_2^{-1}(z)))g(X(-s, f_2^{-1}(z))) \right], & z < r \\ \gamma e^{-\gamma s}\beta_2(z)\varphi(X(-s, f_2^{-1}(z)))g(X(-s, f_2^{-1}(z)), & z > r \end{cases}$$

$$(6.20)$$

for  $z \in [m, M]$ , where

$$\beta_1(z) = \frac{1}{g(f_1^{-1}(z))f'(f_1^{-1}(z))} > 0$$
(6.21)

while

$$\beta_2(z) = \frac{1}{g(f_2^{-1}(z))f'(f_2^{-1}(z))} < 0.$$
(6.22)

Indeed the measure (3.6) is equal to

$$\begin{split} &\int_{\Omega} K(s, x, \omega)\varphi(x)dx = \gamma e^{-\gamma s} \int_{\Omega_0} \delta_{f(X(s,x))}(\omega)\varphi(x)dx \\ &= \gamma e^{-\gamma s} \int_{\Omega} \delta_{f(y)}(\omega) \frac{g(X(-s, y))}{g(y)} \varphi(X(-s, y))dy \\ &= \gamma e^{-\gamma s} \left[ \int_{\omega \cap [m,r]} \left( -\frac{\varphi(X(-s, f_1^{-1}(z)))g(X(-s, f_1^{-1}(z)))}{g(f_1^{-1}(z))f'(f_1^{-1}(z))} \right) \\ &+ \frac{\varphi(X(-s, f_2^{-1}(z)))g(X(-s, f_2^{-1}(z)))}{g(f_2^{-1}(z))f'(f_2^{-1}(z))} \right) dz \\ &+ \int_{\omega \cap [r,M]} \frac{\varphi(X(-s, f_2^{-1}(z)))g(X(-s, f_2^{-1}(z)))}{g(f_2^{-1}(z))f'(f_2^{-1}(z))} dz \\ \end{bmatrix}$$

Hence the density of the measure (3.6) is (6.20).

By the definition of  $\tilde{K}$  we deduce the following.

**Lemma 6.14.** The kernel  $\tilde{K}$  satisfies Assumption 4.23.

**Lemma 6.15.** The operator  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \Delta$  and non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ .

*Proof.* By the definition of  $\tilde{K}$  and by the change of variables

$$y = X(-s, f_1^{-1}(z))$$

we deduce that  $\mathbb{K}_{\lambda}$  is equal to

$$\frac{1}{\gamma} \mathbb{K}_{\lambda} \varphi(z) = \begin{cases} D_1(z) \int_{f_1^{-1}(z)}^M e^{-(\lambda+\gamma)\tau(x,f_1^{-1}(z))} \varphi(y) dy \\ + D_2(z) \int_{f_2^{-1}(z)}^M e^{-(\lambda+\gamma)\tau(x,f_2^{-1}(z))} \varphi(y) dy & m < z < r \\ D_2(z) \int_{f_2^{-1}(z)}^M e^{-(\lambda+\gamma)\tau(x,f_2^{-1}(z))} \varphi(y) dy & r < z < M \end{cases}$$

where

$$D_1(z) = \beta_1(z) > 0$$
 and  $D_2(z) = -\beta_2(z) > 0$ .

Hence  $\mathbb{K}_{\lambda}$  is the sum of the three operators  $\mathbb{K}^{i}_{\lambda}$  defined as

$$\mathbb{K}_{\lambda}^{1}\varphi(z) = \begin{cases} \gamma D_{1}(z) \int_{f_{1}^{-1}(z)}^{M} e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z))}\varphi(y)dy & m < z < r \\ 0 & r < z < M \end{cases}$$
$$\mathbb{K}_{\lambda}^{2}\varphi(z) = \begin{cases} \gamma D_{2}(z) \int_{f_{2}^{-1}(z)}^{M} e^{-(\lambda+\gamma)\tau(x,f_{2}^{-1}(z))}\varphi(y)dy & m < z < r \\ 0 & r < z < M \end{cases}$$

and

$$\mathbb{K}_{\lambda}^{3}\varphi(z) = \begin{cases} \gamma D_{2}(z) \int_{f_{2}^{-1}(z)}^{M} e^{-(\lambda+\gamma)\tau(x,f_{2}^{-1}(z))}\varphi(y)dy & r < z < M \\ 0 & z < r \end{cases}$$

Since  $\mathbb{K}_{\lambda} = \sum_{i=1}^{3} \mathbb{K}_{\lambda}^{i}$  if we prove that for i = 1, 2, 3 the operator  $\mathbb{K}_{\lambda}^{i}$  is compact, then we deduce that  $\mathbb{K}_{\lambda}$  is compact.

To prove that each  $\mathbb{K}^i_{\lambda}$  is compact we apply Lemma 6.7. We describe in detail how to prove that  $\mathbb{K}^1_{\lambda}$  is compact. Consider  $\delta < \min\{m, r - m\}$ . If  $z \in [m, r - \delta]$ , then since  $f_1^{-1}(z) > f_1^{-1}(z + \delta)$ 

$$\begin{split} &\frac{1}{\gamma} \left| \mathbb{K}_{\lambda}^{1} \varphi(z+\delta) - \mathbb{K}_{\lambda}^{1} \varphi(z) \right| \\ &= \left| D_{1}(z) \int_{f_{1}^{-1}(z)}^{M} e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z))} \varphi(x) dx \right| \\ &- D_{1}(z+\delta) \int_{f_{1}^{-1}(z+\delta)}^{M} e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z+\delta))} \varphi(x) dx \right| \\ &\leq \int_{f_{1}^{-1}(z)}^{M} \left| D_{1}(z) \ e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z))} - D_{1}(z+\delta) e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z+\delta))} \right| \varphi(x) dx \\ &+ \int_{f_{1}^{-1}(z+\delta)}^{f_{1}^{-1}(z)} D_{1}(z+\delta) e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z+\delta))} \varphi(x) dx. \end{split}$$

On the other hand if  $z \in [r - \delta, r]$  we have that

$$\frac{1}{\gamma} \left| \mathbb{K}^{1}_{\lambda} \varphi(z + \delta) - \mathbb{K}^{1}_{\lambda} \varphi(z) \right|$$

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$$= D_1(z) \int_{f_1^{-1}(z)}^M e^{-(\lambda+\gamma)\tau(x,f_1^{-1}(z))} \varphi(x) dx$$

Hence

$$\frac{1}{\gamma} \left\| \mathbb{K}_{\lambda}^{1} \varphi(\cdot + \delta) - \mathbb{K}_{\lambda}^{1} \varphi(\cdot) \right\|_{1} \\
\leq \int_{m}^{r-\delta} \int_{f_{1}^{-1}(z)}^{M} \left| D_{1}(z) \ e^{-(\lambda+\gamma)\tau(x, f_{1}^{-1}(z))} - D_{1}(z+\delta) e^{-(\lambda+\gamma)\tau(x, f_{1}^{-1}(z+\delta))} \right| \varphi(x) dx dz \\
+ \int_{m}^{r-\delta} \int_{f_{1}^{-1}(z+\delta)}^{f_{1}^{-1}(z)} D_{1}(z+\delta) e^{-(\lambda+\gamma)\tau(x, f_{1}^{-1}(z+\delta))} \varphi(x) dx dz \\
+ \int_{r-\delta}^{r} D_{1}(z) \int_{f_{1}^{-1}(z)}^{M} e^{-(\lambda+\gamma)\tau(x, f_{1}^{-1}(z))} \varphi(x) dx dz.$$
(6.23)

Since  $f_1^{-1}(z) \in [0, x_c]$ , and  $f_1^{-1}(z + \delta) \in [0, x_c]$  if  $z \in [m, r]$ , then

$$D_1(z) = -\frac{1}{\alpha_1} \frac{1}{g(f_1^{-1}(z))}$$
 and  $D_1(z+\delta) = -\frac{1}{\alpha_1} \frac{1}{g(f_1^{-1}(z+\delta))}$ 

Using similar arguments to the one used in the proof of Lemma 6.12 we estimate the first term of inequality (6.23) in the following way

$$\begin{split} &\int_{m}^{r-\delta} \int_{f_{1}^{-1}(z)}^{M} \left| D_{1}(z)e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z))} \right. \\ &\left. -D_{1}(z+\delta)e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z+\delta))} \right| \varphi(x)dxdz \\ &\leq \frac{1}{\alpha_{1}} \int_{m}^{r-\delta} \int_{f_{1}^{-1}(z)}^{M} e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z+\delta))} \left| \frac{1}{g(f_{1}^{-1}(z))}e^{-(\lambda+\gamma)\tau(f_{1}^{-1}(z),f_{1}^{-1}(z+\delta))} \right. \\ &\left. -\frac{1}{g(f_{1}^{-1}(z+\delta))} \right| \varphi(x)dxdz \leq c\delta \|\varphi\|_{1} \end{split}$$

where we have used the uniform continuity of g on compact intervals and the Lipschitz continuity of the function  $\tau$  in the second argument. On the other hand, using the expression for  $f_1$  we deduce that the second term in inequality (6.23) can be estimated in the following way

$$\int_{r}^{m-\delta} \int_{f_{1}^{-1}(z+\delta)}^{f_{1}^{-1}(z)} D_{1}(z+\delta) e^{-(\lambda+\gamma)\tau(x,f_{1}^{-1}(z+\delta))} \varphi(x) dx dz$$
$$\leq c \sup_{x \in [m,M]} \frac{1}{g(x)} \int_{m}^{r-\delta} \int_{-\frac{z}{\alpha_{1}}+\frac{q_{1}}{\alpha_{1}}}^{-\frac{z+\delta}{\alpha_{1}}+\frac{q_{1}}{\alpha_{1}}} \varphi(x) dx dz$$

$$\leq c \sup_{x \in [m,M]} \frac{1}{g(x)} \int_m^r \int_{q_1-\delta-\alpha_1 x}^{q_1-x\alpha_1} dz \varphi(x) dx \leq c \delta \|\varphi\|_1$$

for a suitable constant c > 0. Finally the third term in inequality (6.23) can be estimated in the following way

$$\int_{r-\delta}^{r} D_1(z) \int_{f_1^{-1}(z)}^{M} e^{-(\lambda+\gamma)\tau(x, f_1^{-1}(z))} \varphi(x) dx dz \le c' \delta \|\varphi\|_1$$

As a consequence, for every  $\varepsilon > 0$  there exists a  $\delta_{\varepsilon} > 0$  such that, for every  $\delta < \delta_{\varepsilon}$ 

$$\|\mathbb{K}^{1}_{\lambda}\varphi(\cdot+\delta) - \mathbb{K}^{1}_{\lambda}\varphi(\cdot)\|_{1} < \varepsilon \|\varphi\|_{1}$$

and, hence the operator  $\mathbb{K}^1_{\lambda}$  is compact. The same technique can be used to prove that the operators  $\mathbb{K}^2_{\lambda}$  and  $\mathbb{K}^3_{\lambda}$  are compact, hence the operator  $\mathbb{K}_{\lambda}$  is compact for every  $\lambda \in \mathbb{C}$  with  $\Re \lambda > -\gamma$ .

Now we have to prove that the operator  $\mathbb{K}_{\lambda}$  is non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$ . For every  $\varphi \in X_+ = L^1_+([m, M])$  there exists a  $x_0 \in (m, M)$  such that  $\varphi \neq 0$  for a subset *S* of  $[x_0, M]$  with positive measure. On the other hand for every  $F \in L^{\infty}_+(\Omega_0) = L^{\infty}_+([m, M])$  there exists a set  $S_F$  of positive Lebesgue measure on which *F* is strictly positive. If  $x < x_0$  we have that

$$(\mathbb{K}_{\lambda}\varphi)(x) \geq \frac{-1}{\alpha_{2}g(f_{2}^{-1}(x))} \int_{f_{2}^{-1}(x)}^{M} e^{-(\gamma+\lambda)\tau(z,f_{2}^{-1}(x))}\varphi(z)dz$$
$$\geq \frac{-1}{\alpha_{2}g(f_{2}^{-1}(x))} \int_{x}^{M} e^{-(\gamma+\lambda)\tau(z,f_{2}^{-1}(x))}\varphi(z)dz$$
$$\geq \frac{-1}{\alpha_{2}g(f_{2}^{-1}(x))} \int_{x_{0}}^{M} e^{-(\gamma+\lambda)\tau(z,f_{2}^{-1}(x))}\varphi(z)dz$$

then  $\mathbb{K}_{\lambda}\varphi(x) > 0$ .

Assume now that  $x > x_0$ . Also in this case we have that

$$(\mathbb{K}_{\lambda}\varphi)(x) \geq \frac{-1}{\alpha_2 g(f_2^{-1}(x))} \int_{f_2^{-1}(x)}^M e^{-(\gamma+\lambda)\tau(z,f_2^{-1}(x))}\varphi(z)dz.$$

Thanks to the fact that  $f_2$  is monotonically increasing we deduce that, if  $x < f_2(x_0)$  then  $f_2^{-1}(x) < x_0$  and hence  $\mathbb{K}_{\lambda}\varphi(x) > 0$  for every  $x < f_2(x_0)$ . Iterating this argument we deduce that  $\mathbb{K}_{\lambda}\varphi(x) > 0$  for every  $x < f_2^n(x_0)$ .

Since for every z < M there exists an  $\overline{n}$  such that  $f_2^{\overline{n}}(x_0) > z$ , we deduce that there exists an  $\overline{n}$  such that the set  $\{x < f^{\overline{n}}(x_0)\} \cap S_F$  has positive measure and therefore  $\mathbb{K}_{\lambda}$  is non-supporting.

**Proposition 6.16.** Let  $g, \mu, \Lambda, v$  be such that Assumptions 6.4 hold. Let  $\psi_0$  be the stable distribution. The Malthusian parameter is equal to 0 and  $R_0 = 1$ . The solution *B* of (2.1) satisfies

$$\|B(t,\cdot) - c\Psi_0\| \le Me^{-vt}$$

where c, v, M > 0 and  $\Psi_0(dx) = \psi_0(x) dx$  the norm  $\|\cdot\| = \|\cdot\|_{TV} = \|\cdot\|_{b}$ .

# 7. Relation between the PDE formulation and the RE

In this section we prove asynchronous exponential growth/decline for the population distribution for the model examples introduced in Sect. 6.

We assume that the kernel K is defined by (5.1) for parameters satisfying one among the three Assumptions 6.1, 6.2, 6.4; hence K is a  $z_0$ -bounded regularizing kernel and induces via formula (4.27) an operator kernel  $\tilde{K}$  that satisfies either Assumption 4.23 or Assumption 4.24. The operator kernel  $\tilde{K}$  in turn induces the discounted next generation operator  $\mathbb{K}_{\lambda}$  through the Laplace transform (4.7). We assume that  $\mathbb{K}_{\lambda}$  is non-supporting for every  $\lambda \in \Delta \cap \mathbb{R}$  and compact for every  $\lambda \in \Delta$ .

7.1. From the population birth rate to the population distribution

We start by making the connection between the renewal equations and the partial differential equations formalising the model examples presented in Sect. 5. Let  $M(t, \omega)$  be the number of individuals in the population with state in the set  $\omega$  at time t. Assume that at time t = 0 we have  $M(0, \cdot) = M_0$  with  $M_0 \in \mathcal{M}_{+,b}(\Omega)$ . Then the number of individuals, born before time zero, with state in the set  $\omega$  at time t is equal to

$$\int_{\Omega} \mathcal{F}(t,x) \delta_{X(t,x)}(\omega) M_0(dx).$$

On the other hand, the number of individuals, born after time zero, with state in the set  $\omega$  at time *t* equals

$$\int_0^t \int_{\Omega_0} B(t-a,d\xi) \mathscr{F}(a,\xi) \delta_{X(a,\xi)}(\omega) da$$

where *B* is the population birth rate. The two above observations lead to the following expression of *M* in terms of *B* and  $M_0$ 

$$M(t,\omega) = \int_0^t \int_{\Omega_0} B(t-a,d\xi) \mathscr{F}(a,\xi) \delta_{X(a,\xi)}(\omega) da + \int_{\Omega} \mathscr{F}(t,x) \delta_{X(t,x)}(\omega) M_0(dx).$$
(7.1)

Once *B* has been solved from the renewal equation (2.1), the formula (7.1) is an explicit formula for *M*.

An alternative way to define M, see for instance [8], is to define it by duality with the solution of the backward equation corresponding to (6.2), (6.1), (6.11), that reads, in its general form, as

$$\partial_t \varphi(t, x) = g(x) \partial_x \varphi(s, x) - \tilde{\mu}(x) \varphi(s, x) + \int_{\Omega_0} \varphi(s, \eta) \nu(x, d\eta) \Lambda(x).$$
(7.2)

If M is differentiable this amounts to define M as the function that satisfies

$$\int_{\Omega} \frac{d}{dt} M(t, dx) \varphi(x) = \int_{\Omega} \left( g(x) \partial_x \varphi(x) - \tilde{\mu}(x) \varphi(x) \right) M(t, dx) + \int_{\Omega} \left( \int_{\Omega_0} \varphi(\eta) \nu(x, d\eta) \right) \Lambda(x) M(t, dx)$$
(7.3)

for every  $\varphi \in C_c^1(\mathbb{R}_+)$ . We provide more details on how to interpret the term  $\int_{\Omega} \frac{d}{dt} M(t, dx)\varphi(x)$  in Appendix B (proof of Proposition B.2).

If *M* is not differentiable, as in the present case, this alternative way cannot be used. However, *M* can still be defined as the solution of an equation, namely equation (7.4) below, which can be seen as a weak version of the PDEs (6.2), (6.1), (6.11) when  $\nu$  is equal to (6.6), (6.10) or (6.15), respectively.

**Proposition 7.1.** Assume  $\mu$ , g,  $\Lambda$ ,  $\nu$  are either as in Assumptions 6.1, Assumption 6.2 or Assumption 6.4.

The function M, defined by equation (7.1), is the unique function mapping  $\mathbb{R}_+ \times \mathscr{B}(\Omega)$  into  $\mathbb{R}_+$ , that satisfies the following equation for every  $\varphi \in C^1(\mathbb{R}_+, C_c^1(\Omega))$ 

$$\int_{\Omega} \varphi(t, x) M(t, dx) - \int_{\Omega} \varphi(0, x) M_0(dx) - \int_0^t \int_{\Omega} \partial_s \varphi(s, x) M(s, dx) ds$$
$$= \int_0^t \int_{\Omega} (g(x) \partial_x \varphi(s, x) - \tilde{\mu}(x) \varphi(s, x)) M(s, dx) ds$$
$$+ \int_0^t \int_{\Omega} \left( \int_{\Omega_0} \varphi(s, x) \nu(\eta, dx) \right) \Lambda(\eta) M(s, d\eta) ds$$
(7.4)

and the initial condition  $M(0, \cdot) = M_0(\cdot)$ .

We refer to the appendix for the proof of this proposition.

Equation (7.4) is used in the literature, see for instance [10] and also [21] in a slightly different situation. It is not entirely intuitive because it relies on what one could call a double duality (both in the state variable and in the time variable). In our approach we use the interpretation to define M by (7.1). In the next section we shall deduce the large time behaviour of M from that of B in a simple natural way. So there is no need to formulate a PDE for M and to specify in which sense we solve it. Our motivation to, nevertheless, formulate and prove Proposition 7.1 is simply to show that our constructively defined M does indeed coincide with M as defined in other works.

By the interpretation of  $\mathscr{F}(t, x)$  as the survival probability we expect  $\mathscr{F}(t, x)$  to tend to zero as time tends to infinity. Indeed, it follows from the assumption on the model parameters that we have made in this section that there exists a constant C > 0 such that

$$\sup_{x \in \Omega_0} \mathscr{F}(t, x) \le C e^{z_0 t} \quad \text{for all } t > 0.$$
(7.5)

The exponential bound (7.5) is crucial in deducing the asymptotic behaviour of the solution *B* of the renewal equation (2.1) and subsequently of *M* defined in terms of *B* in (7.1). This will be done in the next subsection.

### 7.2. Asymptotic behaviour of the solution of the PDE

We now state and prove our result on asynchronous exponential growth/decline of the population distribution M.

**Theorem 7.2.** Assume that  $\mu$ , g,  $\Lambda$ ,  $\nu$  are either as in Assumptions 6.1, Assumption 6.2, or Assumption 6.4. Let M be given by (7.1) and let  $\psi_r$  and r be as in Corollary 4.30. Then there exist a constant C > 0 and a constant  $\ell > 0$  such that

$$\left\| e^{-rt} M(t, \cdot) - c M_{\psi_r}(\cdot) \right\| \le C e^{-\ell t} \quad t > 0.$$
(7.6)

where c > 0 and  $M_{\psi_r}$  is defined by

$$M_{\psi_r}(\omega) := \int_0^\infty \int_{\Omega_0} e^{-ar} \psi_r(\xi) \mathscr{F}(a,\xi) \delta_{X(a,\xi)}(\omega) d\xi da \quad \omega \in \mathscr{B}(\Omega)$$
(7.7)

and where  $\|\cdot\| = \|\cdot\|_{TV} = \|\cdot\|_{\flat}$ .

*Proof.* We start by introducing some useful notation. Let  $\tilde{M}^{AC}$  be the measure defined by

$$\tilde{M}^{AC}(t,\omega) := \int_0^t \int_{\Omega_0} b(t-a)(\xi) \mathscr{F}(a,\xi) \delta_{X(a,\xi)}(\omega) d\xi da$$

where b is the density of  $B^{AC}$ . In analogy we define  $\tilde{M}^s$  as follows

$$\tilde{M}^{s}(t,\omega) := \int_{0}^{t} \int_{\Omega_{0}} B^{s}(t-a,d\xi) \mathscr{F}(a,\xi) \delta_{X(a,\xi)}(\omega) da.$$

With  $\tilde{M}$  we denote the measure defined by

$$\tilde{M}(t,\omega) := \int_{\Omega} \mathscr{F}(t,x) \delta_{X(t,x)}(\omega) M_0(dx).$$

Notice that

$$\begin{split} \left\| M(t,\cdot) - ce^{rt} M_{\psi_r}(\cdot) \right\| &\leq \left\| M(t,\cdot) - \tilde{M}^{AC}(t,\cdot) \right\| + \left\| \tilde{M}^{AC}(t,\cdot) - ce^{rt} M_{\psi_r}(\cdot) \right\| \\ &\leq \left\| \tilde{M}(t,\cdot) \right\| + \left\| \tilde{M}^s(t,\cdot) \right\| + \left\| \tilde{M}^{AC}(t,\cdot) - ce^{rt} M_{\psi_r}(\cdot) \right\|. \end{split}$$

Now we estimate all these terms. In the estimates that follow we shall denote by C a suitably chosen positive constant the value of which may change from line to line. Thanks to (7.5) we have

$$\left\|\tilde{M}(t,\cdot)\right\| = \int_{\Omega_0} M_0(d\xi)\mathscr{F}(t,\xi)\delta_{X(t,\xi)}(\Omega) \le \int_{\Omega_0} M_0(d\xi)\mathscr{F}(t,\xi) \le C \|M_0\|e^{z_0t}$$

for every  $t \ge 0$ . It follows from (3.7) and (7.5) that

$$\begin{split} \left\|\tilde{M}_{s}(t,\cdot)\right\| &= \int_{0}^{t} \int_{\Omega_{0}} B^{s}(t-a,d\xi) \mathscr{F}(a,\xi) \delta_{X(a,\xi)}(\Omega) da \\ &\leq \int_{0}^{t} \left(c_{1}e^{z_{0}(t-a)} + c_{2}te^{z_{0}(t-a)}\right) \sup_{\xi \in \Omega} \mathscr{F}(a,\xi) da \\ &\leq \left(c_{1}e^{z_{0}t} + c_{2}te^{z_{0}t}\right) t. \end{split}$$

Let *m* be the density of  $\tilde{M}^{AC}$  and let  $m_{\psi_r}$  be the density of  $M_{\psi_r}$ . This means that

$$m_{\psi_r}(y) := \int_0^\infty e^{-ra} \psi_r(X(-a, y)) \mathscr{F}(a, X(-a, y)) \frac{g(y)}{g(X(-a, y))} da$$

and

$$m(t, y) := \int_0^t b(t-a)(X(-a, y))\mathscr{F}(a, X(-a, y)) \frac{g(y)}{g(X(-a, y))} da,$$

where b(t - a)(X(-a, y)) is the evaluation in X(-a, y) of the function b(t - a). By the definition of the total variation norm and of the flat norm, we then have

$$\left\|\tilde{M}^{AC}(t,\cdot) - ce^{rt}M_{\psi_r}(\cdot)\right\| = \left\|m(t,\cdot) - ce^{rt}m_{\psi_r}(\cdot)\right\|_1.$$

Notice that by the change of variable X(-a, y) = x we get

$$\begin{split} \left\| m(t,\cdot) - ce^{rt} m_{\psi_r}(t,\cdot) \right\|_1 &\leq e^{rt} \int_t^\infty \int_{\Omega_0} \psi_r(x) e^{-ra} \mathscr{F}(a,x) dx da \\ &+ \int_0^t \int_{\Omega_0} \left| b(a)(x) - ce^{ra} \psi_r(x) \right| \mathscr{F}(t-a,x) dx da \end{split}$$

The fact that  $\mathscr{F}$  satisfies (7.5) and the fact that  $r > z_0$  imply

$$e^{rt}\int_{t}^{\infty}\int_{\Omega_{0}}\psi_{r}(x)e^{-ra}\mathscr{F}(a,x)dxda\leq Ce^{z_{0}t}.$$

Recall that by Corollary 4.30 there exists a constants C > 0 and r > k > 0 such that

$$\|b(t) - ce^{rt}\psi_r\|_1 \le Ce^{-kt+rt}$$
 for every  $t > 0$ .

Therefore, using (7.5), as well as the fact that r-k > 0 and, hence,  $\max_{a \in [0,t]} e^{(r-k)a} = e^{(r-k)t}$  we deduce that

$$\int_0^t \int_{\Omega_0} \left| b(a)(x) - ce^{ra} \psi_r(x) \right| \mathscr{F}(t-a,x) \, dx \, da$$
  
$$\leq C \int_0^t e^{(r-k)a} \sup_{x \in \Omega} \mathscr{F}(t-a,x) \, da \leq C e^{(r-k)t} \int_0^\infty e^{z_0 a} \, da.$$

Combining all the bounds that we have for  $\|\tilde{M}(t,\cdot)\|$ ,  $\|m^s(t,\cdot)\|$  and  $\|\tilde{M}^s(t,\cdot) - e^{-rt}\psi_r(\cdot)\|$  we deduce that

$$\left\| M(t, \cdot) - c e^{rt} M_{\psi_r}(\cdot) \right\| \le C e^{(r-\ell)t}$$

fore some  $\ell > 0$ , that is, (7.6) holds.

# 8. Concluding remarks

Models of physiologically structured populations can be formulated from first principles as renewal equations for the population birth rate B, which takes on values in the space of measures on the set of admissible states-at-birth [11, 19]. In this paper we proved the asynchronous exponential growth of the measure-valued solution B of the renewal equation, (2.1) under a regularisation assumption on the kernel K. This assumption enabled us to derive the asymptotic behaviour of B from the behaviour of its absolutely continuous part  $B^{AC}$ . Moreover, using the regularisation assumption, we proved that also the density of  $B^{AC}$  satisfies a renewal equation. We studied the long term behaviour of this density by way of Laplace transform methods.

We applied our results to a model of cell growth and fission (either into equal or unequal parts) and to a model of waning and boosting of the level of immunity against a pathogen. For these examples we then used the interpretation to express in Equation (7.1) the population state M, that is, the distribution of individual states, in terms of the population birth rate B. If we assume that the values of  $B(t, \omega)$  for t < 0 are given, we can write (7.1) as follows:

$$M(t,\omega) = \int_0^\infty \int_{\Omega_0} B(t-a,d\xi) \mathscr{F}(a,\xi) \delta_{X(a,\xi)}(\omega) da.$$
(8.1)

Vice versa, we can express *B* in terms of of *M*:

$$B(t,\omega) = \int_{\Omega} \Lambda(\eta) \nu(\eta,\omega) M(t,d\eta).$$
(8.2)

Combining Equations (8.1) and (8.2) we deduce the translation invariant formulation

$$B(t,\omega) = \int_0^\infty \int_{\Omega_0} B(t-a,d\xi) K(a,\xi,\omega) da$$
(8.3)

of Equation (2.1).

When we solved (8.3) and then used (8.1) to define M, we actually solved a PDE, the weak version of which is (7.4) (see Section 6 of [19] for general remarks about the way RE arise when solving certain types of PDE). However, as noted above, there is no need to write down the PDE itself and to specify the notion of solution, nor to rigorously prove the existence of such a solution, since the interpretation justifies our conclusions. So guided by the interpretation we determined the asymptotic behaviour

of the population distribution efficiently using (8.1) and thus avoided demanding technicalities associated with PDEs.

When the measure  $M(t, \cdot)$  is absolutely continuous with respect to the Lebesgue measure, it is simpler to write down the PDE. For the model of cell growth and fission into equal parts it takes the form (6.1), for fission into unequal parts it becomes (6.2) and for the model of waning and boosting we have (6.11). These PDEs have been treated for instance in [14], [25] and [12], respectively.

The corresponding backward formulation of these equations is (7.2). When  $\Omega \subset \mathbb{R}$ , then the measure  $M(t, \cdot)$  can be represented by the NBV function N defined by

$$N(t,x) := \int_{[0,x]} M(t,d\eta).$$

The function N satisfies the following forward equation

$$\partial_t N(t, x) = -g(x)\partial_x N(t, x) - \int_{[0, x]} \tilde{\mu}(\xi) N(t, d\xi) + \int_{\Omega} \Lambda(\eta) \nu(\xi, [0, x]) N(t, d\xi).$$
(8.4)

The regularization assumption on the kernel K entails, of course, a restriction concerning the class of models that is covered. For the special example of fission into two equal parts, it is shown in Section II.12 of [34] that one can establish convergence to an absolutely continuous stable distribution under a relaxed regularity condition. So there is definitely room for deriving sharper results. On the other hand, it is known that a stable distribution may have a non-zero singular component. Indeed, this can happen in the context of the selection-mutation balance as analyzed in [1, 6]. We now briefly comment on the similarities and differences of the models considered here and those treated in [1,6]. In [6], the nonlinearity is of the 'replicator' type, meaning that it is due to dividing by the total population size, so due to working with relative magnitudes. In the context of our framework we can, if we wish, do the same. In [1] the per capita birth and death rates are allowed to depend on the total population size (see below for a more general setup). Neither [1] nor [6] considers a dynamical trait and both implicitly assume that the survival probability as a function of age is an exponential function. In these respects the model considered here is far more general. In [6] mutation is incorporated as a random change of trait, while in [1] it is incorporated as production of offspring with a different trait. If in our framework we put  $K = K_1 + K_2$ , with  $K_1(a,\xi,.)$  equal to a  $(a,\xi)$  dependent multiple of the Dirac measure concentrated in  $\xi$  (describing production of offspring with exactly the same trait) and  $K_2(a, \xi, .)$ equal to a  $(a, \xi)$  dependent multiple of a fixed absolutely continuous probability distribution, we obtain a 'house-of-cards' type model in the spirit of Section 4 of [6]. Perhaps one can do a lot of more or less explicit calculations for this special case of a one-dimensional range perturbation of a rather degenerate kernel  $K_1$ , but this has not been done so far.

It is a challenge to extend the analysis developed in this paper to the case of a structured population embedded in a non-constant environment which influences the evolution of the population and which in turn is influenced by feedback from the population. An example of an environment for cell growth and fission is the amount of nutrient resources, as it is known that the availability of nutrients affects both the growth and fission rates [35]. In the waning and boosting context, the force of infection  $\gamma$  is the most relevant environmental variable.

Let us denote the environment by *E*. The evolution in time of (B(t), E(t)) is given by the following system of equations

$$B(t,\omega) = \int_0^\infty \int_{\Omega_0} B(t-a,d\xi) K(a,\xi,E_t,E(t),\omega) da$$
(8.5)

$$\frac{d}{dt}E(t) = f(E(t)) - \int_0^\infty \int_{\Omega_0} B(t-a, d\xi)c(a, \xi, E_t, E(t))da \qquad (8.6)$$

where  $\frac{dE(t)}{dt} = f(E(t))$  describes the evolution in time of the environment in the absence of a consumer population and  $c(a, \xi, E_t, E(t))$  represents the influence on the environment of an individual born with state  $\xi$ , that at time *t* has age *a*. Both *c* and the kernel *K* in equation (8.5) depend on E(t) as well as on the *history*  $E_t$ , that is on all the values of *E* before time *t* and this dependence on *E* introduces, via (8.6), a non-linearity in equation (8.5).

It is an open problem to study the asymptotic behaviour of (B(t), E(t)) under an (adapted) regularisation assumption on the kernel *K* and to uncover the connection with the corresponding PDE formulation. The special case  $\Omega_0 = \{x_0\}$  is elaborated in [2].

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### A Notation

In this appendix we introduce the notation used in the paper. We denote by  $\mathbb{R}_+$  the set  $[0, \infty)$  and by  $\mathbb{R}^*_+$  the set  $(0, \infty)$ . Given a Borel measurable subset A of  $\mathbb{R}$  we denote by  $\mathscr{B}(A)$  the  $\sigma$ -algebra of all Borel subsets of A.  $\mathscr{M}(A)$  is the set of the signed Borel measures on A,  $\mathscr{M}_+(A)$  is the cone of the positive measures and  $\mathscr{M}_{+,b}(A)$  the set of the positive and bounded measures on A. Furthermore,  $\mathscr{M}_{+,AC}(A)$  is the subset of the measures which are absolutely continuous with respect to the Lebesgue measure. We denote by  $\mu^s$  the singular part of the measure  $\mu$  and by  $\mu^{AC}$  its absolutely continuous part, again with respect to the Lebesgue measure. We have  $\mu = \mu^s + \mu^{AC}$ . Finally, we denote by |A| the Lebesgue measure of the Borel set A.

The total variation norm  $\|\mu\|_{TV}$  of a measure  $\mu \in \mathcal{M}(A)$  is defined by

$$\|\mu\|_{TV} = \sup_{\Pi} \sum_{i=1}^{n} |\mu(A^i)|,$$

where the supremum is taken over all the finite measurable partitions  $\Pi := \{A^1, \ldots, A^n\}$  of the set *A*. We denote by BL(A) the space of the real valued bounded Lipschitz functions, endowed with the norm

$$||f||_{BL} := \sup_{x \in A} |f(x)| + \sup_{x, y \in A: x \neq y} \frac{|f(x) - f(y)|}{|x - y|}.$$

Finally, the flat norm  $\|\mu\|_{\flat}$  of a measure  $\mu \in M(A)$  is defined by

$$\|\mu\|_{\flat} = \sup\left\{ \left| \int_{A} f d\mu \right| : f \in BL(A) \text{ such that } \|f\|_{BL} \le 1 \right\}.$$

For positive measures  $\mu$  the equality  $\|\mu\|_{\flat} = \|\mu\|_{TV}$  holds, see [24].

We denote by  $L^1_+(A)$  the set of the positive functions belonging to  $L^1(A)$ . The set  $L^1_+(A)$  is a cone in  $L^1(A)$ . Similarly, we denote by  $L^\infty_+(A)$  the cone of the positive functions belonging to  $L^\infty(A)$ .

For real numbers  $\rho$ ,  $L^1_{\rho}(A)$  is the space of the measurable functions  $f : A \to \mathbb{R}$  such that

$$\int_A \left| f(a) e^{\rho a} \right| da < \infty.$$

 $\mathscr{L}(X)$  is the space of the bounded linear operators from the normed linear space X into itself equipped with the operator norm by  $\|\cdot\|_{op}$ . The spectral radius of the linear operator T is denoted by  $\rho(T)$ .

### **B** Proof of Proposition 7.1

Let the assumptions made in the beginning of Sect. 7 hold.

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To prove that *M* defined by (7.1) is the unique solution of equation (7.4), we use the Riesz–Markov–Kakutani representation theorem and (7.1) to identify  $M(t, \cdot)$  with the element

$$T_B(t) + T_{M_0}(t) \tag{2.87}$$

of  $(C_c(\Omega))^*$ , where the function  $T_B : \mathbb{R}_+ \to (C_c(\Omega))^*$  is defined by

$$T_B: t \mapsto \left(\varphi \mapsto \int_0^t \int_{\Omega_0} B(t-a, d\xi) \mathscr{F}(a, \xi) \varphi(X(a, \xi)) da\right) \quad t \ge 0 \quad (2.88)$$

while the function  $T_{M_0} : \mathbb{R}_+ \to (C_c(\Omega))^*$  is defined by

$$T_{M_0}: t \mapsto \left(\varphi \mapsto \int_{\Omega} M_0(d\xi) \mathscr{F}(t,\xi) \varphi(X(t,\xi))\right) \quad t \ge 0.$$
(2.89)

We use this representation to compute  $\frac{d}{dt}M(t, \cdot)$ . To this end we will identify  $T_B(t)$  and  $T_{M_0}(t)$  with their restrictions on  $C_c^1(\Omega)$ . We start with an auxiliary lemma that explain how to compute  $\frac{d}{dt}T_B(t)$  and  $\frac{d}{dt}T_{M_0}(t)$ .

**Lemma B.1.** The functions  $T_B : \mathbb{R}_+ \to (C_c^1(\Omega))^*$  and  $T_{M_0} : \mathbb{R}_+ \to (C_c^1(\Omega))^*$ defined by (2.88) and (2.89), respectively, are a.e. differentiable and differentiable. For the values of time  $t \ge 0$  for which  $T_B$  is differentiable, its derivative  $\frac{d}{dt}T_B(t) \in (C_c^1(\Omega))^*$  is given by

$$\frac{d}{dt}T_B(t)\varphi = F_B(t)\varphi \quad \text{for every } \varphi \in C_c^1(\Omega),$$

where

$$F_B(t)\varphi := \int_{\Omega_0} B(t, d\xi)\varphi(\xi) + \int_0^t \int_{\Omega_0} B(t-a, d\xi)\mathscr{F}(a, \xi)G(\varphi)(X(a, \xi))da$$

with

$$G(\varphi)(x) := -\tilde{\mu}(x)\varphi(x) + g(x)\varphi'(x).$$

The derivative  $\frac{d}{dt}T_{M_0}(t) \in (C_c^1(\Omega))^*$  of  $T_{M_0}$  is given by

$$\frac{d}{dt}T_{M_0}(t)\varphi = F_{M_0}(t)\varphi \quad \text{for every } \varphi \in C_c^1(\Omega),$$

where

$$F_{M_0}(t)\varphi := \int_{\Omega} \mathscr{F}(t,\xi) G(\varphi)(X(t,\xi)) M_0(d\xi)$$

The proof of this lemma is technical as it deals with function with values in  $(C_c^1(\Omega))^*$ , but the result is intuitively credible as it is formally obtained by simply applying Leibniz rule for differentiating under the integral sign.

*Proof.* We start by proving that  $T_B$  is differentiable. Notice that for every  $\varphi \in C_c^1(\Omega)$ ,

$$\left\|\frac{T_B(t) - T_B(t+h)}{h} - F_B(t)\right\|_{op} = \sup_{\|\varphi\|_{C_c^1(\Omega)} \le 1} \left|\frac{T_B(t)\varphi - T_B(t+h)\varphi}{h} - F_B(t)\varphi\right|.$$

By the Lebesgue point theorem we have that for almost every t > 0

$$\lim_{h \to 0} \frac{1}{h} \int_{t}^{t+h} \int_{\Omega} B(a, dy) \mathscr{F}(t-a, y) \varphi(X(t-a, y)) da = \int_{\Omega} B(t, dy) \varphi(y)$$

for every  $\varphi \in C_c^1(\Omega)$  with  $\|\varphi\|_{C_c^1(\Omega)} \leq 1$ . The fact that  $\varphi$  is Lipschitz continuous and that for every  $y \in \Omega_0$  the map  $X(\cdot, y)$  is continuous implies that the convergence is uniform in  $\varphi$ . Let us illustrate why. Notice that

$$\begin{split} &\frac{1}{h} \left| \int_{t}^{t+h} \int_{\Omega} B(a, dy) \mathscr{F}(t-a, y) \varphi(X(t-a, y)) da - \int_{\Omega} B(t, dy) \varphi(y) \right| \\ &\leq \frac{1}{h} \int_{t}^{t+h} \left| \int_{\Omega} B(a, dy) \mathscr{F}(t-a, y) \varphi(X(t-a, y)) \right| \\ &- \int_{\Omega} B(a, dy) \mathscr{F}(t-a, y) \varphi(y) \right| da \\ &+ \frac{1}{h} \left| \int_{t}^{t+h} \int_{\Omega} B(a, dy) \mathscr{F}(t-a, y) \varphi(y) da - \int_{\Omega} B(t, dy) \varphi(y) \right| da \\ &\leq \frac{1}{h} \int_{t}^{t+h} \int_{\Omega} B(a, dy) \left| \varphi(X(t-a, y)) - \varphi(y) \right| da \\ &+ \frac{1}{h} \int_{t}^{t+h} \left| \int_{\Omega} B(a, dy) \mathscr{F}(t-a, y) da - \int_{\Omega} B(t, dy) \right| da \end{split}$$

The second term goes to zero a.e., uniformly in  $\varphi$ . Since  $\varphi$  is compactly supported, and Lipschitz continuous, we have that for every  $\varepsilon > 0$  there exists a  $\delta > 0$  such that for every  $h < \delta$  we have  $|\varphi(X(h, y)) - \varphi(y)| \le ||\varphi'||_{\infty} |X(h, y) - y| < \varepsilon$ . It follows that

$$\frac{1}{h} \int_{t}^{t+h} \int_{\Omega} B(a, dy) \left| \varphi(X(t-a, y)) - \varphi(y) \right| da \to 0$$

uniformly in  $\varphi$  with  $\|\varphi\|_{C^1_c(\Omega)} \leq 1$  as  $h \to 0$ .

On the other hand, by the dominated convergence theorem we deduce that

$$\lim_{h \to 0} \int_0^t \int_{\Omega_0} \frac{\Delta_h \mathscr{F}\varphi(t, a, y)}{h} G(\varphi)(X(a, y)) B(a, dy) da$$
$$= \int_0^t \int_{\Omega_0} \mathscr{F}(a, y) G(\varphi)(X(a, y)) B(a, dy) da$$

where

$$\Delta_h \mathscr{F} \varphi(t, a, y)$$

$$=\mathscr{F}(t+h-a,y)\varphi(X(t+h-a,y))-\mathscr{F}(t-a,y)\varphi(X(t-a,y)).$$

Since for every  $y \in \Omega_0$  the map  $X(\cdot, y)$  is continuous and since  $\varphi \in C_c^1(\mathbb{R})$ , hence Lipschitz continuous function, the convergence is uniform in  $\varphi$ .

The proof of the fact that

$$\frac{dT_{M_0}(t)\varphi}{dt} = F_{M_0}(t)\varphi$$

is analogous and we omit it.

**Proposition B.2.** The function M, defined by equation (7.1) satisfies (7.4) for every  $\varphi \in C^1(\mathbb{R}_+, C_c^1(\Omega)).$ 

Proof. Integrating by parts we find that

$$\int_{\Omega} \varphi(t, x) M(t, dx) - \int_{\Omega} \varphi(0, x) M_0(dx) - \int_0^t \int_{\Omega} \partial_s \varphi(s, x) M(s, dx) ds$$
$$= \int_0^t \int_{\Omega} \varphi(s, x) \frac{d}{ds} M(s, dx) ds$$

where the term  $\int_{\Omega} \varphi(s, x) M(s, dx)$  is equal to  $F_B(s)\varphi(s, \cdot) + F_{M_0}(s)\varphi(s, \cdot)$ . Hence thanks to Lemma B.1

$$\int_0^t \int_{\Omega} \varphi(s, x) \frac{d}{ds} M(s, dx) ds = \int_0^t \int_{\Omega_0} B(t, d\xi) \varphi(s, \xi) ds$$
  
+ 
$$\int_0^t \int_0^s \int_{\Omega_0} B(s - a, d\xi) \mathscr{F}(a, \xi) G(\varphi(s, \cdot))(X(a, \xi)) dads$$
  
+ 
$$\int_0^t \int_{\Omega} \mathscr{F}(s, x) G(\varphi(s, \cdot))(x) M_0(dx) ds.$$

This implies that

$$\begin{split} &\int_{\Omega} \varphi(t,x) M(t,dx) - \int_{\Omega} \varphi(0,x) M_0(dx) - \int_0^t \int_{\Omega} \partial_s \varphi(s,x) M(s,dx) ds \\ &= \int_0^t \int_{\Omega_0} B(s,d\xi) \varphi(s,\xi) ds \\ &+ \int_0^t \int_0^s \int_{\Omega_0} B(s-a,d\xi) \mathscr{F}(a,\xi) G(\varphi(s,\cdot))(X(a,\xi)) dads \\ &+ \int_0^t \int_{\Omega} \mathscr{F}(s,x) G(\varphi(s,\cdot))(x) M_0(dx) ds. \end{split}$$

Hence, to deduce that M satisfies (7.4), we have to prove that

$$\int_0^t \int_{\Omega_0} B(s, d\xi) \varphi(s, \xi) ds$$

$$+\int_{0}^{t}\int_{\Omega}^{s}\int_{\Omega_{0}}B(s-a,d\xi)\mathscr{F}(a,\xi)G(\varphi(s,\cdot))(X(a,\xi))dads$$
  
+
$$\int_{0}^{t}\int_{\Omega}\mathscr{F}(s,x)G(\varphi(s,\cdot))(x)M_{0}(dx)ds$$
  
=
$$\int_{0}^{t}\int_{\Omega}G(\varphi(s,\cdot))M(s,dx)ds$$
  
+
$$\int_{0}^{t}\int_{\Omega}\left(\int_{\Omega}\varphi(s,x)v(\eta,dx)\right)\Lambda(\eta)M(s,d\eta)ds$$
 (2.90)

Using (7.1) to compute

$$\int_0^t \int_{\Omega} G(\varphi(s, \cdot))(x) M(s, dx) ds$$

we deduce that

$$\int_{0}^{t} \int_{0}^{s} \int_{\Omega_{0}} B(s-a, d\xi) \mathscr{F}(a, \xi) G(\varphi(a, \cdot))(X(a, \xi)) dads$$
  
= 
$$\int_{0}^{t} \int_{\Omega} G(\varphi(s, \cdot))(x) M(s, dx) ds$$
  
$$- \int_{0}^{t} \int_{\Omega} \mathscr{F}(s, x) G(\varphi(s, \cdot))(x) M_{0}(dx) ds$$
(2.91)

Let

$$L(s, x) := \Lambda(x) \int_{\Omega} \nu(x, dy) \varphi(s, y).$$

We integrate the function  $L(s, \eta)$  against the measure  $M(s, d\eta)ds$  on  $\mathbb{R}_+ \times \Omega$  and deduce that

$$\int_0^t \int_{\Omega} L(s,\eta) M(s,d\eta) ds = \int_0^t \int_{\Omega} \int_{\Omega} \varphi(s,x) \nu(\eta,dx) \Lambda(\eta) M(s,d\eta) ds$$

On the other hand, integrating  $L(s, \eta)$  against the following measure on  $\mathbb{R}_+ \times \Omega$ 

$$\int_0^s \int_{\Omega_0} B(s-a,d\xi) \mathscr{F}(a,\xi) \delta_{X(a,\xi)}(\cdot) dads + \int_{\Omega} \mathscr{F}(s,x) \delta_{X(s,x)}(\cdot) M_0(dx) ds,$$

and, additionally, using the fact that B satisfies (2.1), as well as the formula (7.1), we deduce that

$$\int_{0}^{t} \int_{\Omega_{0}} B(s, d\xi) \varphi(s, \xi) ds$$
  
=  $\int_{0}^{t} \int_{\Omega} L(s, \eta) M(s, d\eta) ds$   
=  $\int_{0}^{t} \int_{\Omega} \int_{\Omega} (\varphi(s, y) \nu(\eta, dy)) \Lambda(\eta) M(s, d\eta) ds$  (2.92)

Combining (2.90) with (2.91) and with (2.92) we find that M satisfies (7.4).

Finally we prove that there exists a unique solution for equation (7.4).

**Proposition B.3.** If both  $M_1$  and  $M_2$  solve (7.4) with the same initial condition  $M_1(0, \cdot) = M_2(0, \cdot) = M_0(\cdot)$ , then  $M_1(t, \cdot) = M_2(t, \cdot)$  for every t > 0.

*Proof.* Let  $M = M_1 - M_2$ . Since  $M_1$  and  $M_2$  satisfy equation (7.4), it follows that

$$\int_{\Omega} \varphi(t, x) M(t, dx) = \int_0^t \int_{\Omega} \mathscr{G} \varphi(s, x) M(s, dx) ds,$$

where

$$\mathscr{G}\varphi(s,x) := \partial_s \varphi(s,x) + g(x)\partial_x \varphi(s,x) - \tilde{\mu}(x)\varphi(s,x) + \int_{\Omega} \varphi(s,\eta)\Lambda(x)\nu(x,d\eta).$$
(2.93)

We prove that for every  $\psi \in C_c(\Omega_0)$  there exists a  $\varphi \in C^1([0, t], C_c^1(\Omega_0))$  such that  $\mathscr{G}\varphi = 0$  and  $\varphi(t, x) = \psi(x)$ . This implies that  $M(t, \operatorname{supp}\psi) = 0$ . Making the function  $\psi$  vary we deduce that M(t, A) = 0 for every  $A \in \mathscr{B}(\Omega_0)$ . From this we find that  $M_1 = M_2$ .

Let us prove that for every  $\psi$  there exists a solution to the equation  $\mathscr{G}\varphi = 0$  with final condition  $\varphi(t, x) = \psi(x)$ . Thanks to the definition of  $\mathscr{G}$ , this is equivalent to prove that there exists a unique solution to

$$\partial_s \varphi(s, x) = -g(x)\partial_x \varphi(s, x) + \tilde{\mu}(x)\varphi(s, x) - \int_{\Omega} \varphi(s, \eta)\Lambda(x)\nu(x, d\eta).$$
(2.94)

Integrating along the characteristic we can rewrite the equation in a fixed point form:

$$\varphi(s, X(s, x)) = \mathscr{T}\varphi(s, x)$$

with X(s, x) being the solution of the ODE  $\frac{dy}{ds} = g(y)$  with initial datum y(0) = xand with

$$\begin{aligned} \mathscr{T}\varphi(s,x) &:= \psi(X(t,x))e^{-\int_s^t \tilde{\mu}(X(v,x))dv} \\ &+ \int_s^t \int_{\Omega} \varphi(v,\eta)\Lambda(X(v,x))\nu(X(v,x),d\eta)e^{-\int_s^v \tilde{\mu}(X(v,x))dv}dv \end{aligned}$$

Since

$$\begin{split} \|\mathscr{T}\varphi_{2} - \mathscr{T}\varphi_{2}\|_{\infty} &\leq 2 \cdot \|\varphi_{1} - \varphi_{2}\|_{\infty} \cdot \sup_{x \in \Omega} \int_{s}^{t} \tilde{\mu}(X(v, x))e^{-\int_{v}^{s} \tilde{\mu}(X(a, x))da} dv \\ &\leq 2 \cdot \|\varphi_{1} - \varphi_{2}\|_{\infty} \cdot \sup_{x \in \Omega} \left(1 - e^{-\int_{0}^{t} \tilde{\mu}(X(a, x))da}\right), \end{split}$$

we deduce that for sufficiently small  $\bar{t} > 0$  the operator  $\mathscr{T}$ , that maps  $C^1([0, \bar{t}], C_c^1(\Omega_0))$ in itself, is a contraction. Hence there exists a unique solution of equation (2.94) as *s* varies between 0 and  $\bar{t}$ . A solution for every time *t* can be proven to exists by repeating the above reasoning for every interval of time of length  $\bar{t}$ .

*Proof of Proposition 7.1.* It is enough to combine the statement of Proposition B.3 and B.2.  $\Box$ 

#### REFERENCES

- Ackleh, A., Cleveland, J., Thieme, H.R.: Population dynamics under selection and mutation: Longtime behavior for differential equations in measure spaces. Journal of Differential Equations 261(2), 1472–1505 (2016)
- [2] Barril, C., Calsina, A., Diekmann, O., Farkas, J.: On the formulation of size-structured consumer resource models (with special attention for the principle of linearized stability). 2111.09678 (2021)
- [3] Bell, G., Anderson, E (1967) Cell growth and division: I. A mathematical model with applications to cell volume distributions in mammalian suspension cultures. Biophysical journal 7(4), 329–351
- [4] Bernard, E., Doumic, M., Gabriel, P.: Cyclic asymptotic behaviour of a population reproducing by fission into two equal parts. 1609.03846 (2016)
- [5] Bertoin, J.: On a Feynman-Kac approach to growth-fragmentation semigroups and their asymptotic behaviors. Journal of Functional Analysis 277(11), 108270–108299 (2019)
- [6] Bürger, R., Bomze, I.M.: Stationary distributions under mutation-selection balance: structure and properties. Advances in applied probability 28(1), 227–251 (1996)
- [7] Calsina, À., Diekmann, O., Farkas, J.: Structured populations with distributed recruitment: from PDE to delay formulation. Mathematical Methods in the Applied Sciences 39(18), 5175–5191 (2016)
- [8] Cañizo, J., Gabriel, P., Yoldas, H.: Spectral gap for the growth-fragmentation equation via harris's theorem. SIAM Journal on Mathematical Analysis 53(5), 5185–5214 (2021)
- [9] Caswell, H.: Matrix Population Models, vol. 1. Sinauer Sunderland, MA, USA (2000)
- [10] Debiec, T., Doumic, M., Gwiazda, P., Wiedemann, E.: Relative Entropy Method for Measure Solutions of the Growth-Fragmentation Equation. SIAM Journal on Mathematical Analysis 50(6), 5811–5824 (2018)
- [11] Diekmann, O., Getto, P., Gyllenberg, M.: Stability and bifurcation analysis of volterra functional equations in the light of suns and stars. SIAM Journal on Mathematical Analysis **39**, 1023–1069 (2007)
- [12] Diekmann, O., de Graaf, W., Kretzschmar, M., Teunis, P.: Waning and boosting: on the dynamics of immune status. Journal of mathematical biology 77(6), 2023–2048 (2018)
- [13] Diekmann, O., Gyllenberg, M., Thieme, H.: Semigroups and renewal equations on dual Banach spaces with applications to population dynamics. In: Delay Differential Equations and Dynamical Systems, pp. 116–129. Springer (1991)
- [14] Diekmann, O., Heijmans, H., Thieme, H.: On the stability of the cell size distribution. Journal of Mathematical Biology 19(2), 227–248 (1984)
- [15] Düll, C., Gwiazda, P., Marciniak-Czochra, A., Skrzeczkowski, J.: Spaces of measures and their applications to structured population models, vol. 36. Cambridge University Press, UK (2021)
- [16] Ellner, S., Childs, D., Rees, M.: Data-Driven Modelling of Structured Populations. A practical guide to the Integral Projection Model. Cham: Springer (2016)
- [17] Euler, L.: Recherches générales sur la mortalité et la multiplication du genre humain. Mémoires de l'académie des sciences de Berlin pp. 144–164 (1767)
- [18] Fan, G., Lou, Y., Thieme, H., Jianhong, W.: Stability and persistence in ODE models for populations with many stages. Mathematical Biosciences and Engineering 12(4), 661–686 (2015)
- [19] Franco, E., Gyllenberg, M., Diekmann, O.: One Dimensional Reduction of a Renewal Equation for a Measure-Valued Function of Time Describing Population Dynamics. Acta Applicandae Mathematicae 175(1), 1–67 (2021)
- [20] Friedman, A., Shinbrot, M.: Nonlinear eigenvalue problems. Acta Mathematica 121(1), 77–125 (1968)
- [21] Gabriel, P.: Measure solutions to the conservative renewal equation. ESAIM Proceedings and Surveys 62, 68–78 (2018)
- [22] Gripenberg, G.: Asymptotic behaviour of resolvents of abstract volterra equations. Journal of mathematical analysis and applications 122(2), 427–438 (1987)
- [23] Gripenberg, G., Londen, S.O., Staffans, O.: Volterra Integral and Functional Equations. Cambridge University Press, UK (1990)
- [24] Gwiazda, P., Marciniak-Czochra, A., Thieme, H.: Measures under the flat norm as ordered normed vector space. Positivity 22(1), 105–138 (2018)

- [25] Heijmans, H.: On the stable size distribution of populations reproducing by fission into two unequal parts. Mathematical biosciences 72(1), 19–50 (1984)
- [26] Heijmans, H.: The Dynamical Behaviour of the Age-Size-Distribution of a Cell Population. In: The dynamics of physiologically structured populations, pp. 185–202. Springer (1986)
- [27] Hille, E., Phillips, R.: Functional Analysis and Semi-groups. RI (1957)
- [28] Inaba, H.: Age-Structured Population Dynamics in Demography and Epidemiology. Springer, UK (2017)
- [29] Krasnoselskii, M., Zabreiko, P., Pustylnik, E., Sobolevskii, P.: Integral Operators in Spaces of Summable Functions, Noordhoff Int. Springer Netherlands (1976)
- [30] Kufner, A., John, O., Fucik, S.: Function Spaces, vol. 3. Springer Science & Business Media, UK (1977)
- [31] Lotka, A.: Relation Between Birth Rates and Death Rates. Science 26(653), 21–22 (1907)
- [32] Marek, I.: Frobenius Theory of Positive Operators: Comparison Theorems and Applications. SIAM Journal on Applied Mathematics 19(3), 607–628 (1970)
- [33] McKendrick, A.: Applications of Mathematics to Medical Problems. Proceedings of the Edinburgh Mathematical Society 44, 98–130 (1925)
- [34] Metz, J., Diekmann, O.: The Dynamics of Physiologically Structured Populations. Springer-Verlag, Berlin Heidelberg (1986)
- [35] Monahan, L., Hajduk, I., Blaber, S., Charles, I., Harry, E.: Coordinating bacterial cell division with nutrient availability: a role for glycolysis. MBIO 5(3), e00935–14 (2014)
- [36] Pichór, K., Rudnicki, R.: Dynamics of antibody levels: Asymptotic properties. Mathematical Methods in the Applied Sciences 43(18), 10490–10499 (2020)
- [37] Rudin, W.: Real and Complex Analysis, 3rd Ed., McGraw-Hill Series in Higher Mathematics. McGraw-Hill, UK (1987)
- [38] Sawashima, I.: On Spectal Properties of Some Positive Operators. Natural Science Report of the Ochanomizu University 15, 53–64 (1965)
- [39] Sharpe, F., Lotka, A.: A Problem in Age-Distribution. In: Mathematical Demography, pp. 97–100. Springer (1977)
- [40] Stadler, E., Müller, J.: Analyzing plasmid segregation: Existence and stability of the eigensolution in a non-compact case. Discrete & Continuous Dynamical Systems-B 25(11), 4127–4164 (2020)
- [41] Steinberg, R.: Endomorphisms of Linear Algebraic Groups. 80. American Mathematical Society, Rhode Island (1968)
- [42] Thieme, H.: Mathematics in Population Biology. Princeton University Press, UK (2018)
- [43] Thieme, H.: Discrete-time population dynamics on the state space of measures. Mathematical Bioscience Engineering 17(2), 1168–1217 (2020)
- [44] Tsuchiya, H., Fredrickson, A., Aris, R.: Dynamics of microbial cell populations. In: Advances in chemical engineering, vol. 6, pp. 125–206. Elsevier (1966)

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