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The Asymptotic Behavior of a Transport Equation in Cell Population Dynamics with a Null Maturation Velocity

Laboratoire de Modélisation Mécanique et de Mathématiques Appliquées, Université de Poitiers, Boulevard Marie et Pierre Curie, Teleport 2, BP 30179, 86962 FUTUROSCOPE Cedex, France
E-mail: boulanou@l3ma.univ-poitiers.fr; emamirad@l3ma.univ-poitiers.fr

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In this paper we complete the study of Rotenberg's model (M. Rotenberg, 1983, *J. Theoret. Biol.* **103,** 181–199) describing the growth of a cell population and treated partially by M. Boulanouar and H. Emamirad (*Differential Integral Equations*, **13** (2000), 125–144). In contrast to our previously cited treatment, here we impose the condition that the maturation velocity for any cell can become null. This consideration implies that the cell population never completely leaves its initial distribution, because at every time we can find some cells of initial cell population that are not divided. In this case, the generated semigroup is not compact. To surmount this difficulty, after studying the irreducibility of the generated semigroup, we calculate explicitly its essential type and we show the asymptotic convergence of the generated semigroup to a projection of rank 1.

1. INTRODUCTION

This paper is the continuation of [4] in which we distinguish any cell by its *degree of maturity* $\mu \in I = (0,1)$ and its *maturation velocity* $v \in J = (0,b)$. By taking the degree of maturity between 0 and 1, we mean that the cells are born at $\mu = 0$ and divide at $\mu = 1$. We denote by $r(\mu, v, v')$ the *transition rate* at which cells change their velocities from v to v'. If we denote by $f = f(\mu, v, t)$ the density of this cell population with respect to the degree of maturity μ and maturation velocity v, then this density

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satisfies the following partial differential equation:

$$\frac{\partial f}{\partial t} + v\frac{\partial f}{\partial \mu} = -\left[\int_0^b r(\mu, v', v)\, dv'\right] f + \int_0^b r(\mu, v, v') f(\mu, v', t)\, dv'. \tag{1.1}$$

This model is proposed by Rotenberg [10] and can be considered as one of the models of structured population dynamics with inherited properties. Inherited properties models do allow memory of generation time and among such models are the age–time and maturity–time models of proliferating cell populations with inherited cycle length of Lebowitz and Rubinow [7]. These models are based on the assumption that the duration of the cycle from cell birth to cell division is determined at birth. Lebowitz and Rubinow proposed that the birth law can be considered as a boundary condition and has the form of an integral equation on the trace space. The transition probability kernel of this equation is determined by the correlation between generation times of mother–daughter pairs in proliferating cell populations. Although it is controversial, many researchers have claimed that such correlations do exist. The recent analysis of Sennerstam and Strömberg [11] has even shown that it might be possible for a near-zero mother–daughter generation time correlation to accord with epigenetic and genetic inheritance transferred from mother to daughters. This remark justifies the main objective of this paper to put v near 0.

An important experimentally observed property of proliferating cell populations is their dispersion of various physical characteristics as time evolves. This property is known as *asynchronous exponential growth*. A rigorous mathematical treatment of the Lebowitz–Rubinow model can be found in [15, 16]. In these papers Webb proved that asynchronous exponential growth occurs provided that the transition kernel satisfies certain smoothness and positivity conditions.

Let $p \geq 0$ be the average number of viable daughters per mitosis and let $k(v, v')$ be the positive correlation between velocities of mother and daughter cells. In [10], Rotenberg proposed as in [7] that the reproduction rule is given by the boundary condition

$$vf(0, v, t) = p\int_0^b k(v, v')v'f(1, v', t)\, dv'. \tag{1.2}$$

To ensure the current continuity he imposed the normalization condition

$$\int_0^b k(v, v')\, dv = 1. \tag{1.3}$$

We show that the Cauchy problem (1.1) and (1.2) with initial condition

$$f(\mu, v, 0) = \varphi(\mu, v) \tag{1.4}$$

is generated by a C_0-semigroup $\{e^{tT_p}\}_{t \geq 0}$. To study the asymptotic behavior of this semigroup we will use an operator-theoretic formulation of asynchronous exponential growth of $\{e^{tT_p}\}_{t \geq 0}$ which is given in [17]. This formulation is based on three facts about this C_0-semigroup. The semigroup should be positive and irreducible and its essential type $\omega_{\text{ess}}(T_p)$ should be strictly less than its exponential growth bound $\omega_0(T_p)$, where

$$\omega_{\text{ess}}(A) = \lim_{t \to \infty} t^{-1} \ln \alpha[e^{tA}]$$

and $\alpha[\ ]$ is the measure of noncompactness (see [17]). To establish the main inequality

$$\omega_{\text{ess}}(T_p) < \omega_0(T_p)$$

we have imposed in [4] that the minimum maturation velocity of all cells is positive. That is, $J = (a, b)$ with $a > 0$. This implies that $\omega_{\text{ess}}(T_p) = -\infty$. Since this assertion is biologically unjustifiable (see [11]), our main aim in this paper is to remove this assertion and recover the asynchronous exponential growth of the generated semigroup with a new treatment. If we impose that the maturation velocity of every cell may vanish, then at any moment one can find some cells of the initial cell population that are not divided. So this cell population never goes out of the initial evolution phase and this may explain the noncompactness of the generated semigroup in this case.

In this paper we adopt the notation of [4] and we will show that, in spite of the noncompactness of the generated semigroup, the conclusion of [4] on asymptotic behavior holds. In the next section we give a new expression of the resolvent of the unperturbed operator (i.e., $r = 0$). This expression is used to prove that the consideration $a = 0$ does not spoil the generation theorem and positivity of the C_0-semigroup for this model. In Section 3 we recover the irreducibility of the generated semigroup either by using the irreducibility of the boundary operator or by imposing an appropriate assumption on the kernel r. In the last section, the boundedness of the kernel k permits us to calculate explicitly the essential type of the semigroup generated without perturbation (i.e., $r = 0$). The essential type of globally generated semigroup is also calculated explicitly under an assumption on the kernel r. Finally, we show that the generated semigroup converges asymptotically to a projection of rank 1 in the operator norm topology. Some of these results are announced in [1]. Here we complete [1] by stating some new results and outlining the proofs. The case $b = \infty$ is discussed partially in [2].

2. A NEW FORMULATION OF THE GENERATED SEMIGROUP

Let $\Omega = (0,1) \times (0,b) = I \times J$ with $0 < b < \infty$. We begin by introducing the Lebesgue space $L^1(\Omega)$ with its natural norm denoted by $\|\cdot\|_1$ and the partial Sobolev space $W^1(\Omega) = \{\varphi \in L^1(\Omega) | v(\partial\varphi/\partial\mu) \in L^1(\Omega)\}$ and correspondence trace space $L^1(J, v\,dv)$. $W^1(\Omega)$ and $L^1(J, v\,dv)$ are the Banach spaces endowed with the norms

$$\|\varphi\|_{W^1(\Omega)} = \|\varphi\|_1 + \left\| v \frac{\partial\varphi}{\partial\mu} \right\|_1 \qquad \text{and} \qquad \|g\|_{L^1(J, v\,dv)} = \int_0^b v|g(v)|\,dv.$$

In [4, Theorem 3.1], we have shown that the trace mappings

$$\gamma_0 \colon \varphi \mapsto \varphi(0,\cdot),$$
$$\gamma_1 \colon \varphi \mapsto \varphi(1,\cdot)$$

are linear continuous from $W^1(\Omega)$ on $L^1(J, v\,dv)$, and we have characterized the boundary condition (1.2) by introducing the multiplying boundary operator K_p defined by

$$K_p \psi(v) \equiv \frac{p}{v} \int_0^b k(v,v') v' \psi(v')\,dv'.$$

This operator is positive from the Banach lattice $L^1(J, v\,dv)$ into itself. Furthermore the relation (1.3) implies that

$$\int_0^b v K_p \psi(v)\,dv = p \int_0^b v\psi(v)\,dv \qquad \text{for any } \psi \in L^1(J, v\,dv).$$

Thus

$$\|K_p\|_{\mathscr{L}(L^1(J, v\,dv))} = p. \tag{2.1}$$

If, for any $p \geq 0$, one defines the operator $T_{p,0}$ by

$$T_{p,0}\varphi(\mu,v) \equiv -v\frac{\partial\varphi}{\partial\mu}(\mu,v),$$

with domain

$$D(T_{p,0}) = \left\{\varphi \in W^1(\Omega) \mid \gamma_0\varphi = K_p\gamma_1\varphi\right\},$$

the operator $T_{0,0}$ on $D(T_{0,0}) = \{\varphi \in W^1(\Omega) \mid \gamma_0\varphi = 0\}$ generates a strongly continuous positive contraction semigroup given by

$$e^{tT_{0,0}}\varphi(\mu,v) = \chi(\mu,v,t)\varphi(\mu - tv, v),$$

where

$$\chi(\mu, v, t) = \begin{cases} 1 & \text{if } \mu \geq tv, \\ 0 & \text{if } \mu < tv, \end{cases}$$

and, for $\lambda > 0$, we have

$$(\lambda - T_{0,0})^{-1}\varphi(\mu, v) = \int_0^{\mu/v} e^{-\lambda t}\varphi(\mu - tv, v)\, dt.$$

The operators $(\lambda - T_{0,0})^{-1}$ and $\gamma_1(\lambda - T_{0,0})^{-1}$ are obviously bounded and strictly positive. That is,

$$(\lambda - T_{0,0})^{-1}\big((L^1(\Omega))_+ \backslash \{0\}\big) \subset \big((L^1(\Omega))_+ \backslash \{0\}\big) \tag{2.2}$$

and

$$\gamma_1(\lambda - T_{0,0})^{-1}\big((L^1(\Omega))_+ \backslash \{0\}\big) \subset \big((L^1(J, v\,dv))_+ \backslash \{0\}\big). \tag{2.3}$$

Now, let us define the operator $\overline{K}_{p,\lambda}$ by

$$\overline{K}_{p,\lambda} = (\gamma_1 \epsilon_\lambda) K_p,$$

where

$$\epsilon_\lambda(\mu, v) = \exp\left(-\lambda \frac{\mu}{v}\right). \tag{2.4}$$

THEOREM 2.1. *For any* $\lambda > \max\{0, b \ln p\}$, *the resolvent operator of* $T_{p,0}$ *is a positive operator given by*

$$\left(\lambda - T_{p,0}\right)^{-1} = \epsilon_\lambda K_p\left(I - \overline{K}_{p,\lambda}\right)^{-1}\gamma_1(\lambda - T_{0,0})^{-1} + (\lambda - T_{0,0})^{-1}. \tag{2.5}$$

Proof. Let $\lambda > \max\{0, b \ln p\}$. We know from [4] that

$$\left(\lambda - T_{p,0}\right)^{-1} = \epsilon_\lambda\left(I - K_{p,\lambda}\right)^{-1} K_p \gamma_1(\lambda - T_{0,0})^{-1} + (\lambda - T_{0,0})^{-1}, \tag{2.6}$$

where the operator $K_{p,\lambda}$ is given by

$$K_{p,\lambda}\psi = K_p(\gamma_1 \epsilon_\lambda)\psi \tag{2.7}$$

for all $\psi \in L^1(J, v\,dv)$. To obtain the new expression (2.5) of $(\lambda - T_{0,0})^{-1}$ it suffices to show that

$$K_p\left(I - \overline{K}_{p,\lambda}\right)^{-1} = \left(I - K_{p,\lambda}\right)^{-1} K_p.$$

Since the operators $K_{p,\lambda}$ and $\overline{K}_{p,\lambda}$ are positive on $L^1(J, v\,dv)$, from (2.1) we have

$$\|K_{p,\lambda}\|_{\mathscr{L}(L^1(J,v\,dv))} < 1 \qquad \text{and} \qquad \|\overline{K}_{p,\lambda}\|_{\mathscr{L}(L^1(J,v\,dv))} < 1$$

for all $\lambda > \max\{0, b \ln p\}$. On the other hand, for any $n \in \mathbb{N}$ we have

$$K_p \overline{K}^n_{p,\lambda} = K^n_{p,\lambda} K_p,$$

which implies that

$$\begin{aligned} K_p\left(I - \overline{K}_{p,\lambda}\right)^{-1} &= \sum_{n \geq 0} K_p \overline{K}^n_{p,\lambda} \\ &= \sum_{n \geq 0} K^n_{p,\lambda} K_p \\ &= \left(I - K_{p,\lambda}\right)^{-1} K_p. \end{aligned}$$

The positivity of the operator $(\lambda - T_{p,\lambda})^{-1}$ follows from the positivity of the operators $(\lambda - T_{0,0})^{-1}$, $\gamma_1(\lambda - T_{0,0})^{-1}$, and K_p. ∎

The coincidence between (2.5) and (2.6) implies that Theorems 3.5 and 3.6 of [4] are valid, even if $a = 0$. As consequence we have

LEMMA 2.1 (see [4]). *The operator $T_{p,0}$ generates on $L^1(\Omega)$ a strongly continuous semigroup $\{e^{tT_{p,0}}\}_{t \geq 0}$ satisfying*

(1) $e^{tT_{0,0}} \leq e^{tT_{p,0}}$;

(2) $e^{tT_{p,0}} \leq q e^{tb \ln q} e^{tT_{p/q,0}}$ *if* $p \geq 1$ *and all* $q > p$;

(3) $\|e^{tT_{p,0}}\|_{1,1} \leq 1$ *if* $p < 1$;

(4) $\|e^{tT_{p,0}}\|_{1,1} = 1$ *if* $p = 1$;

(5) $\|e^{tT_{p,0}}\|_{1,1} \geq 1$ *if* $p > 1$;

(6) *when* $p < 1$, *this semigroup is expressed by*

$$e^{tT_{p,0}}\varphi(\mu, v) = e^{tT_{0,0}}\varphi(\mu, v) + A(t)\varphi(\mu, v), \qquad t \geq 0, \tag{2.8}$$

with

$$A(t)\varphi(\mu, v) = \overline{\chi}(\mu, v, t)\left[K_p \gamma_1 \exp\left[\left(t - \frac{\mu}{v}\right) t T_{p,0}\right]\varphi\right](v) \tag{2.9}$$

and

$$\overline{\chi} = 1 - \chi, \tag{2.10}$$

where $\|\cdot\|_{1,1} \equiv \|\cdot\|_{\mathscr{L}(L^1(\Omega))}$.

When $t \in (0, b^{-1})$, we give the following expression of the semigroup $\{e^{tT_{p,0}}\}_{t \geq 0}$ for all $p \geq 0$.

THEOREM 2.2. *If $t \in (0, b^{-1})$, then for all $p \geq 0$ we have*

$$\exp(tT_{p,0})\varphi(\mu, v) = \exp(tT_{0,0})\varphi(\mu, v) + \bar{\chi}(\mu, v, t)\left[K_p\gamma_1 \exp\left[\left(t - \frac{\mu}{v}\right)T_{0,0}\right]\varphi\right](v).$$

Proof. Let $t \in (0, b^{-1})$ and $\varphi \in L^1(\Omega)$. We define the following function

$$f(t)(x, y) = \exp(tT_{0,0})\varphi(\mu, v) + \bar{\chi}(\mu, v, t)\left[K_p\gamma_1 \exp\left[\left(t - \frac{\mu}{v}\right)T_{0,0}\right]\varphi\right](v).$$

If $t > 0$ is small then the same calculation of [4, Theorem 4.5] gives us

$$\lim_{t \to 0}\left\|\frac{f(t) - \varphi}{t} + v\frac{\partial\varphi}{\partial\mu}\right\|_1 = \lim_{t \to 0}\left\|\frac{e^{tT_{0,0}\varphi} - \varphi}{t} + v\frac{\partial\varphi}{\partial\mu}\right\|_1 = 0.$$

Furthermore, if $\varphi \in D(T_{p,0})$ then we have $\gamma_0 f(t) = K_p\gamma_1 e^{tT_{0,0}}$ and $\gamma_1 f(t) = \gamma_1 e^{tT_{0,0}}$, because $t \in (0, b^{-1})$. Thus $f(t) \in D(T_{p,0})$. Consequently, the function f is a strong solution of the Cauchy problem

$$\begin{cases} \dfrac{df}{dt} = T_{p,0} f, \\ f(0) = \varphi. \end{cases}$$

But $e^{tT_{p,0}}$ is another solution of the same Cauchy problem. By uniqueness we complete the proof. ∎

Next we define the absorption operator $T_{p,1}$ and the transport operator T_p by

$$T_{p,1} = T_{p,0} + S \qquad \text{and} \qquad T_p = T_{p,0} + S + R = T_{p,1} + R,$$

where the operators R and S are given by

$$R\varphi(\mu, v) = \int_0^b r(\mu, v, v')\varphi(\mu, v')\, dv'$$

and

$$S\varphi(\mu, v) = -\left[\int_0^b r(\mu, v', v)\, dv'\right]\varphi(\mu, v).$$

For the boundedness of these operators in $L^1(\Omega)$ we assume that

$$\text{(H1)} \qquad \begin{cases} r \text{ is a measurable positive function}, \\ M = \operatorname{ess} \sup_{(\mu, v) \in \Omega} \int_0^b r(\mu, v', v)\, dv' < \infty. \end{cases}$$

In the following lemma we announce some facts concerning the perturbed operator T_p, which is used later. This lemma is proved in [4] for $a > 0$, and the same proof is valid for $a = 0$.

LEMMA 2.2. *Under hypothesis* (H1), $-S$ *and* R *are positive linear bounded operators on* $L^1(\Omega)$. *Furthermore, the operators* T_p *and* $T_{p,1}$ *with the domain* $D(T_p) = D(T_{p,1}) \equiv D(T_{p,0})$ *generate on* $L^1(\Omega)$ *the positive* C_0*-semigroups* $\{e^{tT_p}\}_{t \geq 0}$ *and* $\{e^{tT_{p,1}}\}_{t \geq 0}$ *satisfying for all* $p \geq 0$ *the following assertions*:

(1) $e^{tT_{0,1}} \leq e^{tT_{p,1}}$, $t \geq 0$;

(2) $e^{-Mt} e^{tT_{p,0}} \leq e^{tT_{p,1}} \leq e^{tT_{p,0}}$, $t \geq 0$;

(3) $e^{tT_{p,1}} \leq e^{tT_p}$, $t \geq 0$;

(4) *if* $p < 1$, *then* $\|e^{tT_p}\|_{1,1} \leq 1$, $t \geq 0$;

(5) *if* $p \geq 1$, *then* $1 \leq \|e^{tT_p}\|_{1,1} \leq p e^{tb \ln p}$, $t \geq 0$.

3. IRREDUCIBILITY

The main result of this section is to show that the semigroup $\{e^{tT_p}\}_{t \geq 0}$ is irreducible. The proof of irreducibility given in [4, Lemma 6.1] is not valid here, because we cannot find a constant $c > 0$ such that the function ϵ_λ given by (2.4) satisfies $\gamma_1 \epsilon_\lambda(v) \geq c > 0$ for all $v \in J$. Consequently, the inequality $K_{p,\lambda} \geq cK_p$ is no longer valid in the present context and this forces us to choose a new treatment. For the irreducibility of e^{tT_p}, we have two alternatives: either we can impose the appropriate conditions on the boundary operator K_p or we can endow the function r with some conditions as it is defined in the sequel. First assume that the kernel of the operator K_p satisfies the following condition

$$\text{(H2)} \qquad \int_0 \int_{J \setminus A} k(v, v')\, dv'\, dv > 0,$$

where A is a measurable subset of J such that $\operatorname{meas}(A) > 0$ and $\operatorname{meas}(J \setminus A) > 0$.

By the standard argument assumption (H2) implies the irreducibility of the operator K_p on $L^1(J, v\, dv)$ (see [18]).

LEMMA 3.1. *Under assumption* (H2), *the operator* $\overline{K}_{p,\lambda}$ *is irreducible for all* $\lambda > \max\{0, b \ln p\}$.

Proof. Let $\lambda > \max\{0, b \ln p\}$ and let M be a closed ideal of the trace space $L^1(J, v\,dv)$ such that

$$\overline{K}_{p,\lambda}(M) \subset M. \tag{3.1}$$

By the characterization of the closed ideal in $L^1(J, v\,dv)$ (see [9]), there exists a measurable subset $\omega \subset J$ such that

$$M = \{\psi \in L^1(J, v\,dv) \mid \psi(v) = 0 \text{ for a.e. } v \in \omega\}. \tag{3.2}$$

If $g \in K_p(M)$, then there exists $\psi \in M$ such that $g = K_p\psi$ and $(\gamma_1 \epsilon_\lambda)g = (\gamma_1 \epsilon_\lambda)K_p\psi = \overline{K}_{p,\lambda}\psi$. Thus by (3.1) we obtain $(\gamma_1 \epsilon_\lambda)g \in M$ and (3.2) implies that $K_p(M) \subset M$. Finally, the irreducibility of the operator K_p implies that $M = \emptyset$ or $M = L^1(J, v\,dv)$ and this completes the proof. ∎

THEOREM 3.1. *Under assumption* (H2), *the semigroup* $\{e^{tT_{p,0}}\}_{t \geq 0}$ *is irreducible*.

Proof. Let $\lambda > \max\{0, b \ln p\}$ and let g be a strictly positive function in $L^1(\Omega)$. According to (2.3) the function $\gamma_1(\lambda - T_{0,0})^{-1}g \in L^1(J, v\,dv)$ is also strictly positive and from the irreducibility of the operator $\overline{K}_{p,\lambda}$, it follows that there exists an integer $m > 0$ such that

$$\overline{K}^m_{p,\lambda}\gamma_1(\lambda - T_{0,0})^{-1}g > 0 \qquad \text{a.e. in } J.$$

The positivity of the operator $(\lambda - T_{0,0})^{-1}$ and the inequality $K_p \geq \overline{K}_{p,\lambda}$ imply that

$$\begin{aligned}(\lambda - T_{p,0})^{-1}g &\geq \epsilon_\lambda K_p\left(I - \overline{K}_{p,\lambda}\right)^{-1}\gamma_1(\lambda - T_{0,0})^{-1}g \\ &= \epsilon_\lambda K_p \sum_{n \geq 0} \overline{K}^n_{p,\lambda}\gamma_1(\lambda - T_{0,0})^{-1}g \\ &\geq \epsilon_\lambda \overline{K}_{p,\lambda}\overline{K}^{m-1}_{p,\lambda}\gamma_1(\lambda - T_{0,0})^{-1}g \\ &= \epsilon_\lambda \overline{K}^m_{p,\lambda}\gamma_1(\lambda - T_{0,0})^{-1}g.\end{aligned} \tag{3.3}$$

Thus the resolvent operator of $T_{p,0}$ is irreducible, which is equivalent to irreducibility of the semigroup $\{e^{tT_{p,0}}\}_{t \geq 0}$ (see [5] or [4, Lemma 2.1]). ∎

THEOREM 3.2. *Suppose that hypotheses* (H1) *and* (H2) *hold. Then the semigroup* $\{e^{tT_p}\}_{t \geq 0}$ *is irreducible*.

Proof. By using assertions (2) and (3) of Lemma 2.2, we obtain

$$e^{tT_p} \geq e^{-Mt} e^{tT_{p,0}}, \qquad t \geq 0.$$

Now the irreducibility of the semigroup $\{e^{tT_p}\}_{t \geq 0}$ follows immediately from the previous theorem. ∎

When K_p is not irreducible, we impose the following hypothesis:

$$\text{(H3)} \quad \begin{cases} \text{There exists } a' \text{ and } b' \ (0 \leq a' < b' \leq b) \text{ such that} \\ r(\mu, v, v') > 0 \text{ a.e. on } ((0,1) \times J \times (a', b')) \\ \quad \cup ((0,1) \times (a', b') \times J). \end{cases}$$

The proof of [4, Theorem 6.4] is valid and establishes the following lemma.

LEMMA 3.2. *Under hypotheses* (H1) *and* (H3), *the C_0-semigroup $\{e^{tT_p}\}_{t \geq 0}$ is irreducible.*

4. ASYMPTOTIC BEHAVIOR OF THE SEMIGROUP $\{e^{tT_p}\}_{t \geq 0}$

In this section we describe the asymptotic behavior of the semigroup $\{e^{tT_p}\}_{t \geq 0}$ under some hypotheses on the functions k and r. We note that from points (2) and (3) of Lemma 2.2 and point (1) of Lemma 2.1 we get

$$e^{-Mt} e^{tT_{0,0}} \leq e^{-Mt} e^{tT_{p,0}} \leq e^{tT_{p,1}} \leq e^{tT_p}, \qquad t \geq 0.$$

Since the semigroup $\{e^{tT_{0,0}}\}_{t \geq 0}$ is not compact, the semigroup $\{e^{tT_p}\}_{t \geq 0}$ is neither (see [6, Prop. 2.1]). Consequently, we cannot use the method in [4] that $\omega_{\text{ess}}(T_p) = -\infty$. To obtain this result we apply a new treatment, assuming that

$$\text{(H4)} \qquad k \in L^{\infty}(J \times J).$$

This assumption permits us to calculate explicitly the essential type of the semigroup $\{e^{tT_{p,1}}\}_{t \geq 0}$.

LEMMA 4.1. *Suppose that assumption* (H4) *holds. Then, for all $0 < t < b^{-1}$ and $s \geq 0$, the operator*

$$L(t,s) \equiv [e^{tT_{p,0}} - e^{tT_{0,0}}] e^{sT_{0,0}} [e^{tT_{p,0}} - e^{tT_{0,0}}]$$

is weakly compact on $L^1(\Omega)$.

Proof. Let $\varphi \in (L^1(\Omega))_+$. If $0 < t < b^{-1}$, it follows from Theorem 2.2 and hypothesis (H4) that

$$\begin{aligned}
&\left[\exp\left(tT_{p,0}\right) - \exp\left(tT_{0,0}\right)\right]\varphi(\mu, v) \\
&\quad \le p\|k\|_\infty \frac{\bar{\chi}(\mu, v, t)}{v} \int_0^b v'\gamma_1\left[\exp\left[\left(t - \frac{\mu}{v}\right)T_{0,0}\right]\varphi\right](v')\,dv' \\
&\quad = p\|k\|_\infty \frac{\bar{\chi}(\mu, v, t)}{v} \int_0^b v'\chi\left(1, v', t - \frac{\mu}{v}\right)\varphi\left(1 - \left(t - \frac{\mu}{v}\right)v', v'\right)dv'.
\end{aligned}$$

Let $s \ge 0$. Then

$$\begin{aligned}
&L(t,s)\varphi(\mu, v) \\
&\quad \le p\|k\|_\infty \frac{\bar{\chi}(\mu, v, t)}{v} \int_0^b v'\gamma_1\Bigg[\exp\left[\left(t + s - \frac{\mu}{v}\right)T_{0,0}\right] \\
&\qquad\qquad \times\left\{\exp\left(tT_{p,0}\right) - \exp\left(tT_{0,0}\right)\right\}\varphi\Bigg](v')\,dv' \\
&\quad = p\|k\|_\infty \frac{\bar{\chi}(\mu, v, t)}{v} \int_0^b v'\chi\left(1, v', t + s - \frac{\mu}{v}\right) \\
&\qquad \times\left[\exp\left(tT_{p,0}\right) - \exp\left(tT_{0,0}\right)\right]\varphi\left(1 - \left(t + s - \frac{\mu}{v}\right)v', v'\right)dv' \\
&\quad \le p^2\|k\|_\infty^2 \frac{\bar{\chi}(\mu, v, t)}{v} \int_0^b\int_0^b v''\chi\left(1, v', t + s - \frac{\mu}{v}\right) \\
&\qquad \times\bar{\chi}\left(1 - \left(t + s - \frac{\mu}{v}\right)v', v', t\right) \\
&\qquad \times\chi\left(1, v'', 2t + s - \frac{\mu}{v} - \frac{1}{v'}\right) \\
&\qquad \times\varphi\left(1 - \left(2t + s - \frac{\mu}{v} - \frac{1}{v'}\right)v'', v''\right)dv''\,dv'.
\end{aligned}$$

The following change of variables

$$\begin{cases}
\mu' = 1 - \left(2t + s - \dfrac{\mu}{v} - \dfrac{1}{v'}\right)v'', \\[2ex]
dv' = -\dfrac{u^2}{v''}\,d\mu', \\[2ex]
\quad\text{where } u = u(t, s, \mu, v, \mu', v'') = \left[2t + s - \mu v^{-1} + (\mu' - 1)\dfrac{1}{v''}\right]^{-1}
\end{cases}$$

implies that

$$L(t,s)\varphi(\mu,v) \leq p^2\|k\|_\infty^2 \frac{\overline{\chi}(\mu,v,t)}{v}$$
$$\times \int_0^b \int_{1-(2t+s-\mu/v-1/b)v''}^{\infty} \chi\left(1, v'', 2t+s-\frac{\mu}{v}-\frac{1}{u}\right)$$
$$\times u^2 \chi(1,u,t+s-\mu v^{-1})$$
$$\times \overline{\chi}\left(1-\left(t+s-\frac{\mu}{v}\right)u, u, t\right)\varphi(\mu', v'')\, d\mu'\, dv''. \tag{4.1}$$

Replacing u by its value, a simple calculation gives

$$\chi(1,u,t+s-\mu v^{-1})\overline{\chi}\left(1-(t+s-\mu v^{-1})u, u, t\right) = \begin{cases} 1 & \text{if } 1-tv'' < \mu' \leq 1, \\ 0 & \text{elsewhere}, \end{cases}$$

and $0 \leq u \leq b$ and in any case $\chi(1, v', 2t+s-\mu v^{-1}-u^{-1}) = 1$. Thus relation (4.1) becomes

$$L(t,s)\varphi(\mu,v) \leq p^2 b^2 \|k\|_\infty^2 \frac{\overline{\chi}(\mu,v,t)}{v} \int_0^b \int_0^1 \varphi(\mu', v')\, d\mu'\, dv'$$
$$\equiv H_t \varphi(\mu, v).$$

Since $\int_\Omega(\overline{\chi}(\mu,v,t)/v)\, d\mu\, dv < \infty$, the operator H_t is of rank 1 and, consequently, weakly compact on $L^1(\Omega)$. Further, so is the operator $L(t,s)$ which is dominated by H_t (see [6, Prop. 2.1]). ∎

LEMMA 4.2. *Suppose that assumption* (H4) *holds. Then the operator*

$$[e^{tT_{p,1}} - e^{tT_{0,1}}]e^{sT_{0,1}}[e^{tT_{p,1}} - e^{tT_{0,1}}]$$

is weakly compact on $L^1(\Omega)$ *for all* $0 < t < b^{-1}$ *and* $s \geq 0$.

Proof. To show this lemma, it suffices to note that the operator $T_{p,1}$ (resp. $T_{0,1}$) is a perturbation of the operator $T_{p,0}$ (resp. $T_{0,0}$) by the bounded operator S. Duhamel's formula gives us

$$e^{tT_{p,1}} = e^{tT_{p,0}} + \int_0^t e^{(t-s)T_{p,0}} S e^{sT_{p,1}}\, ds$$

and

$$e^{tT_{0,1}} = e^{tT_{0,0}} + \int_0^t e^{(t-s)T_{0,0}} S e^{sT_{0,1}}\, ds.$$

The positivity of the operator $-S$ and (1) of Lemma 2.1 implies that

$$\begin{aligned} e^{tT_{p,1}} - e^{tT_{0,1}} &= e^{tT_{p,0}} - e^{tT_{0,0}} + \int_0^t e^{(t-s)T_{p,0}} S e^{sT_{p,1}}\,ds - \int_0^t e^{(t-s)T_{0,0}} S e^{eT_{0,1}}\,ds \\ &\le e^{tT_{p,0}} - e^{tT_{0,0}} + \int_0^t e^{(t-s)T_{0,0}} S\big[e^{sT_{p,1}} - e^{sT_{0,1}}\big]\,ds \\ &\le e^{tT_{p,0}} - e^{tT_{0,0}}. \end{aligned}$$

Consequently,

$$[e^{tT_{p,1}} - e^{tT_{0,1}}]e^{sT_{0,1}}[e^{tT_{p,1}} - e^{tT_{0,1}}] \le [e^{tT_{p,0}} - e^{tT_{0,0}}]e^{sT_{0,0}}[e^{tT_{p,0}} - e^{tT_{0,0}}].$$

Once more, the fact that the operator $[e^{tT_{p,1}} - e^{tT_{0,1}}]e^{sT_{0,1}}[e^{tT_{p,1}} - e^{tT_{0,1}}]$ is dominated by a weakly compact operator in $L^1(\Omega)$ implies that it is weakly compact. ∎

LEMMA 4.3. *If assumption* (H4) *holds, then* $\omega_{\text{ess}}(T_{p,1}) = \omega_{\text{ess}}(T_{0,1})$.

Proof. Let $0 < t < b^{-1}$. Then by the previous lemma the operator

$$2^{-n}[e^{tT_{p,1}} - e^{tT_{0,1}}]e^{ntT_{0,1}}[e^{tT_{p,1}} - e^{tT_{0,1}}]$$

is weakly compact for all $n \in N$. Consequently, the following operator

$$2^{-1}[e^{tT_{p,1}} - e^{tT_{0,1}}]\left[\sum_{n=0}^{m} 2^{-n} e^{ntT_{0,1}}\right][e^{tT_{p,1}} - e^{tT_{0,1}}]$$

is also weakly compact for any $m \in N$. Since $\{e^{tT_{0,1}}\}_{t \ge 0}$ is a contraction semigroup, the last sum converges in $\mathscr{L}(L^1(\Omega))$ to the operator

$$[e^{tT_{p,1}} - e^{tT_{0,1}}](2 - e^{tT_{0,1}})^{-1}[e^{tT_{p,1}} - e^{tT_{0,1}}],$$

which becomes weakly compact. The Dunford–Pettis property of $L^1(\Omega)$ (see [8]) implies the compactness of

$$\left[(e^{tT_{p,1}} - e^{tT_{0,1}})(2 - e^{tT_{0,1}})^{-1}\right]^4.$$

According to [12, Corollary 1.4], this implies that the spectral radius $r_{\text{ess}}(e^{tT_{0,1}})$ of $e^{tT_{0,1}}$ and $r_{\text{ess}}(e^{tT_{p,1}})$ are the same. We complete the proof of the lemma by recalling that for all $t \ge 0$ we have $r_{\text{ess}}(e^{tT_{p,1}}) = e^{t\omega_{\text{ess}}(T_{p,1})}$ and $r_{\text{ess}}(e^{tT_{0,1}}) = e^{t\omega_{\text{ess}}(T_{0,1})}$ (see [5]). ∎

To calculate the essential type of the semigroup $\{e^{tT_p}\}_{t \ge 0}$, we have to assume that

$$\text{(H5)} \qquad r_1 = r_1(\mu, v, v') = \frac{r(\mu, v, v')}{\mu} \in L^\infty(I \times J^2).$$

LEMMA 4.4. *If* (H1), (H4), *and* (H5) *hold, then* $\omega_{\text{ess}}(T_p) = \omega_{\text{ess}}(T_{p,1})$.

Proof. Let $t > 0$. If $p < 1$, then for any function $\varphi \in (L^1(\Omega))_+$ relation (2.8) gives us

$$Re^{tT_{p,0}}R\varphi = Re^{tT_{0,0}}R\varphi + RA(t)R\varphi,$$

where the operator $A(t)$ is defined in (2.9). If hypothesis (H5) holds, then the kernel r is bounded and by a simple calculation we obtain

$$Re^{tT_{0,0}}R\varphi \leq \frac{\|r\|_\infty^2}{t}\int_\Omega \varphi(\mu', v')\,d\mu'\,dv'\mathbf{1}, \tag{4.2}$$

where $\mathbf{1} \in L^1(\Omega)$ is the function equal to 1 on Ω. By using assumptions (H4) and (H5) we obtain

$$RA(t)R\varphi(\mu, v) \leq \|k\|_\infty \|r_1\|_\infty \int_0^b \int_0^b \mu\bar{\chi}(\mu, v', t) \times \exp\left[(t - \mu v'^{-1})T_{p,0}\right] R\varphi(1, v'')v''\,dv'\,dv''.$$

The change of variables $s = t - \mu v'^{-1}$ implies that

$$RA(t)R\varphi(\mu, v) \leq \|k\|_\infty \|r_1\|_\infty \int_0^b \int_{-\infty}^{t-\mu/b} \bar{\chi}\left(\mu, \frac{\mu}{t-s}, t\right) \times e^{sT_{p,0}}R\varphi(1, v'')v''\left[\frac{\mu}{t-s}\right]^2 ds\,dv''.$$

Since $\bar{\chi}(\mu, \mu/(t-s), t) = 0$ for $s < 0$,

$$RA(t)R\varphi(\mu, v) \leq b^2\|k\|_\infty \|r_1\|_\infty \int_0^b \int_0^t e^{sT_{p,0}}R\varphi(1, v'')v''\,ds\,dv''.$$

As there exists an integer n such that $n \leq bt < n + 1$, we have

$$\begin{aligned} &RA(t)R\varphi(\mu, v) \\ &\quad \leq b^2\|k\|_\infty \|r_1\|_\infty \sum_{i=0}^{n} \int_0^b \int_{i/b}^{(i+1)/b} \exp(sT_{p,0})R\varphi(1, v'')\,ds\,dv'' \\ &\quad = b^2\|k\|_\infty \|r_1\|_\infty \sum_{i=0}^{n} \int_0^b \int_0^{1/b} \exp\left[\left(s + \frac{i}{b}\right)T_{p,0}\right]R\varphi(1, v'')\,ds\,dv'' \\ &\quad = b^2\|k\|_\infty \|r_1\|_\infty \sum_{i=0}^{n} \int_0^b \int_0^{1/b} \exp(sT_{p,0})\exp\left(\frac{i}{b}T_{p,0}\right)R\varphi(1, v'')\,ds\,dv''. \end{aligned}$$

When $0 \le s \le b^{-1}$, by Theorem 2.2 we obtain $e^{sT_{p,0}}\varphi(1,\cdot) = e^{sT_{0,0}}\varphi(1,\cdot)$ and

$$\begin{aligned} &RA(t)R\varphi(\mu,v) \\ &\quad \le b^2\|k\|_\infty\|r_1\|_\infty \sum_{i=0}^{n} \int_0^b \int_0^{1/b} \exp(sT_{0,0}) \exp\left(\frac{i}{b}T_{p,0}\right) R\varphi(1,v'')\, ds\, dv''. \end{aligned}$$

Using the definition of semigroup $\{e^{tT_{0,0}}\}_{t\ge 0}$ we get

$$\begin{aligned} &RA(t)R\varphi(\mu,v) \\ &\quad \le b^2\|k\|_\infty\|r_1\|_\infty \sum_{i=0}^{n} \int_0^b \int_0^{1/b} \chi(1,v'',s) \exp\left(\frac{i}{b}T_{p,0}\right) \\ &\qquad \times R\varphi(1-sv'',v'')\, ds\, dv'' \\ &\quad \le b^2\|k\|_\infty\|r_1\|_\infty \sum_{i=0}^{n} \int_0^b \int_0^{1} \exp\left(\frac{i}{b}T_{p,0}\right) R\varphi(\mu',v'')\, d\mu'\, dv''. \end{aligned}$$

The contraction of the linear operator $\exp((i/b)T_{p,0})$, $i = 0,\dots,n-1$ (see Lemma 2.1), and the boundedness of the positive operator R yield that

$$RA(t)R\varphi(\mu,v) \le (n+1)b^2\|k\|_\infty\|r_1\|_\infty\|R\|_{1,1} \int_\Omega \varphi(\mu',v'')\, d\mu'\, dv''.$$

Thus

$$RA(t)R\varphi(\mu,v) \le (bt+1)b^2\|k\|_\infty\|r_1\|_\infty\|R\|_{1,1} \int_\Omega \varphi(\mu',v')\, d\mu'\, dv'\, \mathbf{1}. \tag{4.3}$$

Now relations (4.2) and (4.3) give us

$$\begin{aligned} Re^{tT_{p,0}}R\varphi &\le \left[\frac{\|r\|_\infty^2}{t} + (bt+1)b^2\|k\|_\infty\|r_1\|_\infty\|R\|_{1,1}\right] \\ &\qquad \times \int_\Omega \varphi(\mu',v')\, d\mu'\, dv'\, \mathbf{1}. \end{aligned}$$

As the operator $\varphi \in L^1(\Omega) \mapsto \int_\Omega \varphi(\mu',v'')\, d\mu'\, dv''\, \mathbf{1} \in L^1(\Omega)$ is rank 1, then by [6, Prop. 2.1], we obtain the weak compactness of $Re^{tT_{p,0}}R$ for all $t > 0$. Finally, the same result holds for $p \ge 1$ (see Lemma 2.1). We achieve this proof by applying the main result of [14] (see also [4]). ∎

To describe the asymptotic behavior of the semigroup $\{e^{tT_p}\}_{t \geq 0}$ we introduce the following assumption

$$\text{(H6)} \qquad m = \operatorname{ess} \inf_{(\mu, v) \in \Omega} \int_\Omega r(\mu, v', v)\, dv' > 0.$$

The following theorem is a simple application of Lemma 2.3 in [4] and describes the asymptotic behavior of the semigroup $\{e^{tT_p}\}_{t \geq 0}$ for $p > 1$. In fact, only in this case does the density of cells increase (see Lemma 2.2), which is the biologically meaningful case.

THEOREM 4.1. *Suppose that hypotheses* (H1), (H4), (H5), (H6), *and* (H2) *or* (H1), (H4), (H5), (H6), *and* (H3) *hold. Then there exists* $\epsilon > 0$ *such that, for all* $\eta \in (0, \epsilon)$, *there exists* $M(\eta) \geq 1$ *such that, for all* $\varphi \in L^1(\Omega)$ *and* $t \geq 0$, *we have*

$$\|e^{-\omega(T_p)t} e^{tT_p} \varphi - \langle \varphi, \varphi_0^* \rangle \varphi_0\|_1 \leq M(\eta) e^{-\eta t} \|\varphi\|_1.$$

Proof. By using hypotheses (H1), (H4), (H5), and (H6) and Lemmas 4.3 and 4.4 we get

$$\omega_{\text{ess}}(T_p) = \omega_{\text{ess}}(T_{p,1}) = \omega_{\text{ess}}(T_{0,1}) \leq \omega_0(T_{0,1}).$$

Following the arguments given in [13] hypothesis (H6) yields

$$\omega_0(T_{0,1}) \leq -m < 0.$$

Thus

$$\omega_{\text{ess}}(T_{0,1}) \leq -m < 0.$$

Claim (5) of Lemma 2.2 gives us

$$\omega_0(T_p) \geq 0,$$

and thus from previous relations we infer that

$$\omega_{\text{ess}}(T_p) < \omega_0(T_p).$$

Now either one of the hypotheses (H2) or (H3) implies the irreducibility of the semigroup generated by T_p and the proof is completed by using the main theorem of [17]. ∎

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