# An Eigenvalue Problem Related to Cell Growth

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In this paper, the eigenvalues of the operator corresponding to the partial differential equation which describes the evolution of a population reproducing by simple fission are investigated. This is done by transforming the eigenvalue problem to an integral equation. The theory concerning positive operators on a Banach space appears to be very useful. © 1985 Academic Press. Inc.

#### Introduction

Let us consider a cell population whose members can be distinguished from one another according to their size, which we denote by the parameter x. Instead of size one may also read volume, mass, amount of protein, or any other quantity which obeys a physical conservation law. The individuals (cells) are subject to growth, death, and division and it is assumed that the rates of these physiological processes only depend on the individual's size. For a cell having size x the change in cell size dx in time dt is given by dx = g(x) dt, and g(x) is called the (deterministic) individual growth rate. In other words x = x(t) obeys the ordinary differential equation

$$\frac{dx}{dt} = g(x) \tag{0.1}$$

as long as no fission occurs.

We assume that a mother always divides into two equal daughters. In a forthcoming paper [4] we study the case that division into two unequal parts may occur.

The mathematical model, which is the subject of our investigation, was originally formulated by Bell and Anderson [1]. As a matter of fact, they formulated a more general model incorporating both size and age dependence. A similar model was applied by Sinko and Streifer [14] to populations of the planarian worm *Dugesia tigrina*.

In the present paper we will be concerned with the eigenvalue problem associated with the size-dependent model, which is a special case of the Bell and Anderson model. Our main question is whether there exists a strictly dominant eigenvalue (i.e., an eigenvalue having a real part which is strictly larger than the real parts of the remaining eigenvalues). In [2] it is proved that this strictly dominant eigenvalue (if it exists) determines the large-time behaviour of solutions of the time-dependent equation. Our main conclusion will be that the existence of a strictly dominant eigenvalue heavily depends on the growth rate g(x). More precisely, if g(2x) < 2g(x) for all x (or g(2x) > 2g(x)) then such an eigenvalue exists, and if g(2x) = 2g(x) for all x, then it does not exist.

The organization of this paper is as follows. In Section 1 we will present the Bell and Anderson model, and by means of some elementary transformation we will put it in a more tractable form. In Section 2 the associated eigenvalue problem is reduced to an integral equation.

In Section 3 some results from the theory of positive operators are presented, and in Sections 4 and 5 these results will be used to prove the existence of a dominant eigenvalue (i.e., an eigenvalue with largest real part). The eigenvector corresponding to this dominant eigenvalue will appear to be positive. In Section 6 we shall derive the characteristic equation.

In Section 7 we shall handle the case g(2x) < 2g(x) for all x, and we shall prove among others, that in this case the dominant eigenvalue is strictly dominant. The case g(2x) = 2g(x) is investigated in Section 8. At that place we shall also give a biological interpretation of this relation. In Section 9, finally, some remarks on the adjoint eigenvalue problem are made.

#### 1. THE MODEL AND ITS INTERPRETATION

The eigenvalue problem, which is the subject of our investigation, comes from the partial differential equation

$$\frac{\partial n}{\partial t}(t,x) + \frac{\partial}{\partial x}(g(x) n(t,x))$$

$$= -\mu(x) n(t,x) - b(x) n(t,x) + 4b(2x) n(t,2x)$$
(1.1)

which describes the dynamics of a population reproducing by fission into two equal parts (for instance, algae, cells, or bacteria). Here t is the time, x stands for the size of an individual, n is the population density function, i.e.,  $\int_{x_1}^{x_2} n(t, x) dx$  is the number of individuals with size between  $x_1$  and  $x_2$  at time t,  $\mu$  is the death rate, b is the division rate (i.e.,  $\mu(x)$  dt respectively b(x) dt is the probability that an individual having size x at time t dies resp.

divides in the time interval (t, t+dt), and g is the individual growth rate, which has been discussed in the introduction.

In this paper we assume that an individual cannot divide before reaching a minimal size  $a \ge 0$ . Consequently cells with size less than  $\frac{1}{2}a$  cannot exist, which is expressed by the boundary condition

$$n(t, \frac{1}{2}a) = 0. {(1.2)}$$

Moreover, we assume that cells have to divide before reaching a maximal size which is normalized to be 1. In order that this is satisfied we have to impose the following condition on b:

$$\int_a^1 b(x) \ dx = \infty.$$

It is explained below why this condition is sufficient.

Throughout this paper we make the following assumptions on g,  $\mu$ , and b:

 $[H_g]$  g is a continuous, strictly positive function on  $[\frac{1}{2}a, 1]$ .

 $[H_{\mu}]$   $\mu$  is a non-negative, integrable function on  $[\frac{1}{2}a, 1]$ .

[H<sub>b</sub>] 1° b(x) = 0 on  $\left[\frac{1}{2}a, a\right]$  and b(x) > 0 on (a, 1), 2° b is integrable on  $[a, 1 - \varepsilon]$  for all  $\varepsilon > 0$ , 3°  $\lim_{\varepsilon \downarrow 0} \int_a^{1-\varepsilon} b(x) dx = \infty$ .

Let

$$E(x) = \exp\left(-\int_{a/2}^{x} \frac{b(\xi) + \mu(\xi)}{g(\xi)} d\xi\right). \tag{1.3}$$

E(x) has a clear biological interpretation. It is the probability that an individual with size  $\frac{1}{2}a$  will reach x without having died or divided. It is clear that E(1) = 0, which means that cells with size larger than 1 cannot exist. Consequently, the last term at the right-hand side of (1.1) must be interpreted as zero for  $x \ge \frac{1}{2}$ . Substitution of

$$g(x) n(t, x) = E(x) m(t, x)$$
 (1.4)

into Eq. (1.1) leads to

$$\frac{\partial m}{\partial t} + g(x)\frac{\partial m}{\partial x} = k(x) m(t, 2x), \tag{1.5}$$

(one should read k(x) m(t, 2x) = 0 if  $x \ge \frac{1}{2}$ ) where

$$k(x) = 4 \frac{g(x)}{E(x)} \frac{b(2x)}{g(2x)} E(2x). \tag{1.6}$$

Notice that k is only defined on  $\left[\frac{1}{2}a, \frac{1}{2}\right]$ , and k is integrable, because the possible singularity of k in  $x = \frac{1}{2}$  is determined by the expression

$$\frac{b(2x)}{g(2x)}\exp\bigg[-\int_a^{2x}\frac{b(\xi)}{g(\xi)}\,d\xi\bigg].$$

Equation (1.5) is to be supplemented with the boundary condition

$$m(t, \frac{1}{2}a) = 0. (1.7)$$

From a mathematical point of view, the time-dependent equation (1.5) is more tractable than (1.1) because of the integrability of k, and from now on we will restrict our attention to Eq. (1.5).

## 2. REDUCTION OF THE EIGENVALUE PROBLEM TO AN INTEGRAL EQUATION

The inhomogeneous eigenvalue problem associated with (1.5), (1.7) is given by

$$\lambda \psi(x) + g(x) \frac{d\psi}{dx} - k(x) \psi(2x) = f(x)$$
 (2.1)

$$\psi(\frac{1}{2}a) = 0 \tag{2.2}$$

where  $f \in L_1[\frac{1}{2}a, 1]$ , and we are looking for  $L_1$ -solutions  $\psi$  of (2.1)–(2.2).

Remark. The eigenvalue problem (2.1)–(2.2) can also be studied in the space of continuous functions. As a matter of fact, all results obtained in this paper remain valid if one works with continuous functions instead of  $L_1$ -functions. Moreover for both cases one finds the same set of eigenvalues and eigenvectors. These eigenvectors are continuous functions.

An abstract way of writing (2.1)–(2.2) is

$$\lambda \psi - A\psi = f \tag{2.3}$$

where A is the unbounded, linear operator given by

$$(A\psi)(x) = -g(x)\frac{d\psi}{dx} + k(x)\psi(2x)$$
 (2.4)

having a domain

$$D(A) = \{ \psi \in L_1[\frac{1}{2}a, 1] | \psi \text{ is absolutely continuous and }$$
 (2.5) 
$$\psi(\frac{1}{2}a) = 0 \}.$$

THEOREM 2.1. A is a closed operator with dense domain.

*Proof.* It is clear that A has a dense domain. Without loss of generality we may assume that  $g(x) \equiv 1$ . Let  $\psi_n \in D(A)$ ,  $\psi_n \to \psi$ ,  $n \to \infty$  and  $A\psi_n \to f$ ,  $n \to \infty$ . We must prove that  $\psi \in D(A)$  and  $A\psi = f$ . Let  $r \in \mathbb{R}$  be such that  $\int_{a/2}^{1/2} k(\xi) e^{-r\xi} d\xi < 1$ . Obviously

$$-\frac{d\psi_n}{dx} - r\psi_n(x) + k(x)\psi_n(2x) \to f(x) - r\psi(x) \qquad \text{in } L_1\text{-sense.}$$

Let  $\phi_n$  be given by  $\phi_n(x) = e^{rx} \psi_n(x)$ . Substitution yields

$$-\frac{d\phi_n}{dx} + k(x) e^{-rx}\phi_n(2x) \to \{f(x) - r\psi(x)\} e^{rx} \quad \text{in } L_1\text{-sense.}$$

If we integrate from  $\frac{1}{2}a$  to x we obtain  $-\phi_n + L\phi_n \to F$ ,  $n \to \infty$  in the supnorm, where L defines a bounded linear operator on the space of continuous functions (notice that  $\phi_n$  is continuous because  $\psi_n \in D(A)$ ), given by

$$(L\phi)(x) = \int_{a/2}^{x} k(\xi) e^{-r\xi} \phi(2\xi) d\xi,$$

and

$$F(x) = \int_{a/2}^{x} \left\{ f(\xi) - r\psi(\xi) \right\} e^{r\xi} d\xi$$

is a continuous function.

 $\|L\| < 1$  because  $\int_{a/2}^{1/2} k(x) \, e^{-rx} \, dx < 1$ , and therefore L-I is invertible. Consequently  $\phi_n \to (L-I)^{-1} F$  in the sup-norm. We also have  $\phi_n(x) \to e^{rx} \psi(x)$  in the  $L_1$ -norm, and we conclude that  $e^{rx} \psi(x) = ((L-I)^{-1} F)(x)$ . Let  $\phi(x) = e^{rx} \psi(x)$ , then  $L\phi - \phi = F$ , and this yields that  $\phi$  is absolutely continuous and  $\phi(\frac{1}{2}a) = 0$ . The same result holds for  $\psi$ . If we differentiate again we obtain  $A\psi = f$ , and the result is proved.

Let

$$G(x) := \int_{a/2}^{x} \frac{d\xi}{g(\xi)}.$$
 (2.6)

G(x) can be interpreted as the time which it takes for a cell to grow from  $\frac{1}{2}a$  to x.

If we substitute in (2.1)

$$\psi(x) = e^{-\lambda G(x)} \phi(x), \tag{2.7}$$

we obtain

$$\frac{d\phi}{dx} - k_{\lambda}(x) \ \phi(2x) = \frac{f(x)}{g(x)} e^{\lambda G(x)},$$

where

$$k_{\lambda}(x) = \frac{k(x)}{g(x)} e^{-\lambda(G(2x) - G(x))}.$$
 (2.8)

Integration of this expression from  $\frac{1}{2}a$  to x yields

$$\phi(x) - \int_{a/2}^{\min(1/2, x)} k_{\lambda}(\xi) \, \phi(2\xi) \, d\xi = \int_{a/2}^{x} \frac{f(\xi)}{g(\xi)} e^{\lambda G(\xi)} \, d\xi. \tag{2.9}$$

In order that  $\psi$  can be a solution of (2.1)–(2.2) we must have  $\psi \in D(A)$  which implies that  $\psi$  is continuous and  $\psi(\frac{1}{2}a) = 0$ . This should also be true for  $\phi$ . Let  $X_0$  be the Banach space

$$X_0 = \{ \phi \in C[\frac{1}{2}a, \frac{1}{2}] | \phi(\frac{1}{2}a) = 0 \}$$
 (2.10)

supplied with the sup-norm. Let for  $\lambda \in \mathbb{C}$  the operators  $T_{\lambda}: X_0 \to X_0$  and  $U_{\lambda}: L_1[\frac{1}{2}a, 1] \to L_1[\frac{1}{2}a, 1]$  be given by

$$(T_{\lambda}\phi)(x) = \int_{a/2}^{\min(1/2, x)} k_{\lambda}(\xi) \,\phi(2\xi) \,d\xi, \qquad \phi \in X_0, \tag{2.11}$$

$$(U_{\lambda}f)(x) = \int_{a/2}^{x} \frac{f(\xi)}{g(\xi)} e^{\lambda G(\xi)} d\xi, \qquad f \in L_{1}\left[\frac{1}{2}a, 1\right]. \tag{2.12}$$

THEOREM 2.2. For all  $\lambda \in \mathbb{C}$ , the linear operators  $T_{\lambda}: X_0 \to X_0$  and  $U_{\lambda}: L_1[\frac{1}{2}a, 1] \to L_1[\frac{1}{2}a, 1]$  are compact.

The proof uses Arzèla-Ascoli-like arguments. See, e.g., [16]. For an operator L we denote by  $\sigma(L)$  resp.  $P\sigma(L)$  the spectrum of L resp. the point spectrum of L. The spectral radius is denoted by r(L). Let

$$\Sigma := \{ \lambda \in \mathbb{C} \mid 1 \in P\sigma(T_{\lambda}) \}. \tag{2.13}$$

We can prove the following result.

THEOREM 2.3.  $\sigma(A) = P\sigma(A) = \Sigma$ . For all  $\lambda \in \mathbb{C} \setminus \sigma(A)$  the resolvent  $(\lambda I - A)^{-1}$  is compact.

*Proof.* Putting f = 0 in (2.1) it follows that  $A\psi = \lambda \psi$  if and only if  $T_{\lambda}\phi = \phi$ , where  $\phi$  is given by (2.7). This yields that  $P\sigma(A) = \Sigma$ . Now suppose that  $\lambda \notin P\sigma(A)$ . Then we have that  $1 - T_{\lambda}$  is invertible.

Let  $f \in L_1[\frac{1}{2}a, 1]$  and let  $\phi$  be the solution of  $\phi - T_\lambda \phi = U_\lambda f$ . Then  $\phi$  is well defined because  $U_\lambda f$  is (absolutely) continuous and can be regarded as an element of  $X_0$  (more precisely: as an element of the embedding of  $X_0$  in  $L_1[\frac{1}{2}a, 1]$ ). It follows immediately that  $\phi$  is absolutely continuous. (This is yielded by the fact that  $U_\lambda f$  and  $T_\lambda \phi$  are absolutely continuous.). Now  $\psi$ , given by  $\psi(x) = e^{-\lambda G(x)}\phi(x)$ , is a solution of  $\lambda \psi - A\psi = f$ . Therefore  $\lambda \notin \sigma(A)$ . Moreover,  $\psi$  is absolutely continuous. Hence, for all  $f \in L_1[\frac{1}{2}a, 1]$  we have that  $(\lambda I - A)^{-1} f$  exists and is absolutely continuous. This yields the compactness of  $(\lambda I - A)^{-1}$ .

Thus the spectrum of A consists entirely of eigenvalues, and these can be found by means of the equation  $T_{\lambda}\phi = \phi$ ,  $\phi \in X_0$ .

We shall end this section by showing that all elements of  $\sigma(A)$  are isolated. To do this we need a theorem, proved by S. Steinberg [15].

Theorem 2.4. Let E be a Banach space and  $K(\lambda)$  an analytic family of compact operators, defined on a domain  $\Omega$ . Let  $S(\lambda) = I - K(\lambda)$ . If  $S(\lambda)$  is invertible for some  $\lambda_0 \in \Omega$ , then  $S^{-1}(\lambda)$  exists for all  $\lambda \in \Omega \setminus \Lambda$  where  $\Lambda$  is a discrete subset of  $\Omega$ .

In our case, one sees immediately that  $T_{\lambda}$  is an analytic family of compact operators defined on the whole complex space  $\mathbb{C}$ . Furthermore, in Section 7, we shall prove that  $S_{\lambda} = I - T_{\lambda}$  is invertible for all  $\lambda$  in a right-half-plane. Consequently, a combination of Theorem 2.3 and Theorem 2.4 yields:

Theorem 2.5.  $\sigma(A)$  consists of isolated points which are eigenvalues.

It will turn out that the dominant eigenvalue of A, i.e., the eigenvalue with largest real part, is algebraically simple, and that the corresponding eigenvector is positive. In terms of the integral operator  $T_{\lambda}$ , this means that we must investigate the following "positive eigenvalue problem":

$$T_{\lambda}\phi = \phi, \qquad \phi \in X_0$$
  

$$\phi(x) \ge 0, \qquad \frac{1}{2}a \le x \le 1.$$
(2.14)

For doing this, we need some theory concerning positive operators.

#### 3. Positive Operators

In this section we shall present some results concerning positive operators, emphasizing the existence and uniqueness of positive eigenvectors.

With X we denote an arbitrary Banach space, while  $X^*$  stands for the dual space. Let  $T: X \to X$  be a bounded linear operator. With  $T^*: X^* \to X^*$  we denote the adjoint operator.

DEFINITION. A subset  $K \subset X$  is called a cone if

- (a) K is closed;
- (b)  $\alpha \phi + \beta \psi \in K \text{ if } \phi, \psi \in K \text{ and } \alpha, \beta \geqslant 0;$
- (c)  $K \cap (-K) = \{0\}.$

For the basic theory concerning cones and positive operators we refer to the monographs of Krasnosel'skii [7] and Schaefer [13].

The cone K is called reproducing if K - K = X.  $K^*$  is by definition the subset of  $X^*$  consisting of all positive functionals on K, i.e.,  $F \in K^*$  if and only if  $F \in X^*$  and  $F(\phi) \ge 0$ , for all  $\phi \in K$ . An element  $\phi \in K$  is called nonsupport if  $F \in K^*$ ,  $F \ne 0$  implies that  $F(\phi) > 0$ . (See Lemma 5.2 for an example.) The subset of K consisting of non-support elements is denoted by  $Q_K$ . The positive functional  $F \in K^*$  is said to be strictly positive if  $F(\phi) > 0$ , for all  $\phi \in K$  satisfying  $\phi \ne 0$ .

DEFINITION. Let  $T: X \to X$  be a bounded, linear operator, then T is called positive (with respect to the cone K; also K-positive) if  $T\phi \in K$  for all  $\phi \in K$ . Notation  $T \geqslant 0$ .

The first instigation for generalizing the Frobenius theory (of non-negative matrices) to the case of positive operators on a Banach space was given in 1948 by Krein and Rutman in their famous paper [8]. That paper gives a.o (partial) answers to two fundamental questions.

- (1) Does the positive eigenvalue problem  $T\phi = \lambda \phi$  have a solution  $\phi \in K, \ \phi \neq 0$ ?
  - (2) If so, is this solution unique?

The theorem that we need for answering these two questions are just generalizations of their results.

DEFINITION. Let  $T: X \to X$  be a positive operator with respect to the cone K and let  $u_0$  be some fixed non-zero element of K. Then the operator T is called  $u_0$ -positive if for every non-zero  $\phi \in K$  some positive numbers  $\alpha$ ,  $\beta$  and a positive integer n can be found such that  $\alpha u_0 \leqslant T^n \phi \leqslant \beta u_0$ .

THEOREM 3.1. Let the cone K be reproducing and let  $T: X \to X$  be positive and compact; suppose further that T is  $u_0$ -positive for some  $u_0 \in K$ : then:

- (a) There exists a  $\phi_0 \in K \setminus \{0\}$  such that  $T\phi_0 = \lambda_0 \phi_0$ , where  $\lambda_0 = r(T)$  is an algebraically simple eigenvalue.  $\phi_0$  is the only positive eigenvector of T.
- (b) There exists a strictly positive eigenfunctional  $F_0 \in K^* \setminus \{0\}$  such that  $T^*F_0 = \lambda_0 F_0$ .

Proof. (a) See Krasnosel'skii [7, Sect. 2.3].

(b) In [8], Krein and Rutman have proved the existence of a positive eigenfunctional  $F_0 \in K^* \setminus \{0\}$ , such that  $T^*F_0 = \lambda_0 F_0$ . We only have to prove that  $F_0$  is strictly positive. Suppose  $F_0(\phi) = 0$ , for some  $\phi \in K \setminus \{0\}$ ;  $\alpha u_0 \leq T^n \phi \leq \beta u_0$  for some  $n \in \mathbb{N}$  and  $\alpha, \beta > 0$ . Therefore  $\alpha F_0(u_0) \leq F_0(T^n \phi) = \lambda_0^n F_0(\phi) \leq \beta F_0(u_0)$ . Consequently  $F_0(u_0) = 0$ , which implies that  $F_0(\psi) = 0$ , for all  $\psi \in K$ . Here we have used:  $\alpha' u_0 \leq T^m \psi \leq \beta' u_0$ . Using the fact that K is reproducing, we find that  $F_0 = 0$ , which is a contradiction.

Theorem 3.1 in this form will appear not to be suitable for our purposes, since the requirement that the cone K has to be reproducing happens to be too strong. Therefore we shall weaken this condition.

DEFINITION. Let the operator T be positive with respect to the cone K. We say that K is T-reproducing if for all  $\phi \in X$  there exist  $\phi_1, \phi_2 \in K$  such that  $T\phi = \phi_1 - \phi_2$ .

Theorem 3.2. If in Theorem 3.1 the condition "K is reproducing" is replaced by "K is T-reproducing," then the conclusions remain valid.

*Proof.* Follows immediately from the proof of Theorem 3.1(a) which can be found in [7, Sect. 2.3].

We need another result, due to Sawashima [12]. She introduced the notion of a non-support operator which is in fact a generalization of the notion of an indecomposable, positive matrix.

DEFINITION. A bounded, positive operator  $T: X \to X$  is called non-support with respect to K, if for all  $\phi \in K$ ,  $\phi \neq 0$  and  $F \in K^*$ ,  $F \neq 0$ , there exists an integer p such that for all  $n \geq p$  we have  $F(T^n \phi) > 0$ .

THEOREM 3.3. Let the cone K be total and let T be non-support with respect to K; suppose that  $\lambda_0 = r(T)$  is a pole of the resolvent  $R(\lambda, T)$ , then:

- (a)  $\lambda_0$  is an algebraically simple eigenvalue of T.
- (b) There exists an eigenvector  $\phi_0 \in K$  such that  $T\phi_0 = \lambda_0 \phi_0$ . Furthermore  $\phi_0 \in Q_K$ , i.e.,  $\phi_0$  is non-support.
- (c) There exists a strictly positive eigenfunctional  $F_0 \in K^*$  such that  $T^*F_0 = \lambda_0 F_0$ .
  - (d)  $\phi_0$  is the only positive eigenvector of T.

*Proof.* (a), (b), and (c) were proved by Sawashima in [12]. To prove (d) we assume that there exists a  $\lambda_1 \neq \lambda_0$  and  $\phi \in K \setminus \{0\}$  such that  $T\phi = \lambda_1 \phi$ . Using the non-supportness of T, we have  $F_0(T^p\phi) > 0$  for some integer p. Clearly

$$0 < F_0(T^p \phi) = F_0(\lambda_1^p \phi) = \lambda_1^p F_0(\phi) = T^{*p} F_0(\phi) = \lambda_0^p F_0(\phi).$$

Hence  $\lambda_0^p = \lambda_1^p$ . Since  $\lambda_0 \neq \lambda_1$  and both values are positive, this is a contradiction.

Remark. Theorem 3.3 can also be found in the paper of Marek [9].

# 4. The Case a > 0

In Section 2 we have introduced a family of compact operators  $T_{\lambda}$ , where  $\lambda \in \mathbb{C}$ . Here we shall make clear that for all real  $\lambda$  the operator  $T_{\lambda}$  is positive with respect to some suitable cone. We assume during this and the following section that  $\lambda$  is real unless otherwise stated.

DEFINITION. Let the cones  $K_0$ ,  $K_m \subseteq X_0$  be defined by

$$K_0 = \{ \phi \in X_0 \mid \phi(x) \ge 0, \frac{1}{2}a \le x \le 1 \}, \tag{4.1}$$

$$K_m = \{ \phi \in X_0 | \phi(x) \ge 0, \frac{1}{2}a \le x \le 1 \text{ and } \phi \text{ is non-decreasing} \}. \tag{4.2}$$

Immediately it follows that  $K_m \subseteq K_0$ .

THEOREM 4.1. (a)  $K_0$  is reproducing.

- (b)  $T_{\lambda}K_0 \subseteq K_m$ .
- (c)  $K_m$  is  $T_{\lambda}$ -reproducing.
- (d)  $T_{\lambda}$  is positive with respect to both cones  $K_0$  and  $K_m$ .

*Proof.* (a), (b), and (d) are straightforward. We shall only prove (c). Suppose  $\phi \in X_0$ ; because of (a) we have  $\phi = \phi_1 - \phi_2$ , where  $\phi_1$ ,  $\phi_2 \in K_0$ . Hence  $T_{\lambda}\phi = T_{\lambda}\phi_1 - T_{\lambda}\phi_2$ . Using (b) we have  $T_{\lambda}\phi_1$ ,  $T_{\lambda}\phi_2 \in K_m$ .

Remark.  $T_{\lambda}K_0 \subset K_m$  implies among others that, if  $T_{\lambda}$  has an eigenvector  $\phi \in K_0$ , then also  $\phi \in K_m$ .

The Riesz-representation theorem tells us what the dual cone  $K_0^*$  looks like.

THEOREM 4.2. (a)  $F \in K_0^*$  if and only if F is given by  $F(\phi) = F_{\mu}(\phi) = \int_{\lceil a/2,1 \rceil} \phi \ d\mu, \ \phi \in X_0$ , for some positive Borel-measure  $\mu$  on  $\lceil \frac{1}{2}a, 1 \rceil$ .

(b)  $F = F_{\mu} \in K_0^*$  is not identically zero iff  $\mu$  is not identically zero, i.e.,  $\int_{(a/2,1)} d\mu \neq 0$ .

*Proof.* (a) See Rudin [11, Theorem 2.14].

(b) In order that F is not identically zero, it is not sufficient that  $\int_{[a/2,1]} d\mu \neq 0$ , because  $\phi(\frac{1}{2}a) = 0$ , for all  $\phi \in X_0$ .

As we have already mentioned, we shall make a distinction between two cases, namely, a > 0 and a = 0. In the rest of this section, we shall deal with the case a > 0. Let  $\lambda \in \mathbb{R}$  be fixed. Let  $u_0 \in K_m$  be defined by

$$u_0(x) := \int_{a/2}^{\min(1/2, x)} k_{\lambda}(\xi) d\xi, \qquad x \in [a/2, 1].$$
 (4.3)

Theorem 4.3.  $T_{\lambda}$  is  $u_0$ -positive with respect to the cone  $K_m$ .

*Proof.* Let  $\phi \in K_m$ ,  $\phi \neq 0$ .

A straightforward computation shows that  $T_{\lambda}^n \phi \in K_m$  and  $(T_{\lambda}^n \phi)(x) > 0$ , for all  $2^{-n} \le x \le 1$ . If n is such that  $2^{-n} \le \frac{1}{2}a$ , then we have  $T_{\lambda}^n \phi \in K_m$  and  $(T_{\lambda}^n \phi)(x) > 0$ ,  $\frac{1}{2}a \le x \le 1$ . Therefore

$$\begin{split} (T_{\lambda}^{n+1}\phi)(x) - (T_{\lambda}^{n}\phi)(a) \cdot u_0(x) \\ = \int_{a/2}^{\min(1/2,x)} k_{\lambda}(\xi) \cdot \left\{ (T_{\lambda}^{n}\phi)(2\xi) - (T_{\lambda}^{n}\phi)(a) \right\} d\xi \in K_m, \end{split}$$

because  $(T_{\lambda}^n \phi)(2\xi) - (T_{\lambda}^n \phi)(a) \geqslant 0$ , for  $\frac{1}{2}a \leqslant \xi \leqslant \frac{1}{2}$ . Therefore  $T_{\lambda}^{n+1} \phi - (T_{\lambda}^n \phi)(a) \cdot u_0 \in K_m$ .

For all  $\psi \in K_m \setminus \{0\}$  we have

$$\psi(1) u_0(x) - (T_{\lambda}\psi)(x) = \int_{-\pi/2}^{\min(1/2,x)} k_{\lambda}(\xi) \{ \psi(1) - \psi(2\xi) \} d\xi,$$

which implies that  $\psi(1) \cdot u_0 - T_{\lambda} \psi \in K_m$ , because  $\psi(1) - \psi(2\xi) \ge 0$  for all  $\frac{1}{2}a \le \xi \le \frac{1}{2}$ . As a consequence  $T_{\lambda} \psi \le \psi(1) \cdot u_0$ . If we substitute  $\psi = T_{\lambda}^n \phi$  we find

$$T_{\lambda}^{n+1}\phi \leqslant (T_{\lambda}^{n}\phi)(1) \cdot u_{0},$$

and this completes the proof.

Using the fact that the cone  $K_m$  is  $T_{\lambda}$ -reproducing (Theorem 4.1(c)) and Theorem 3.2, we have the following. There exists a  $\phi_{\lambda} \in K_m$  and a strictly positive eigenfunctional  $F_{\lambda} \in K_m^*$  such that

$$T_{\lambda}\phi_{\lambda} = r_{\lambda}\phi_{\lambda},\tag{4.4}$$

$$T_{i}^{*}F_{i} = r_{i}F_{i},$$
 (4.5)

where  $r_{\lambda} = r(T_{\lambda})$  is an algebraically simple eigenvalue. Furthermore  $\phi_{\lambda}$  is the only positive eigenvector of  $T_{\lambda}$  with respect to  $K_m$ .

As we have seen in Section 2, we are only interested in positive eigenvectors of  $T_{\lambda}$  corresponding to the eigenvalue 1. Therefore we have to look for those values  $\lambda \in \mathbb{R}$  satisfying  $r(T_{\lambda}) = 1$ .

THEOREM 4.4.  $\lambda \in \mathbb{R}$  is uniquely determined by the condition  $r(T_{\lambda}) = 1$ .

*Proof.* Suppose  $\lambda$ ,  $\mu \in \mathbb{R}$ ,  $\mu > \lambda$ . Let  $\phi \in K_0$ .

$$(T_{\lambda}\phi)(x) = \int_{a/2}^{\min(1/2,x)} k_{\lambda}(\xi) \ \phi(2\xi) \ d\xi = \int_{a/2}^{\min(1/2,x)} k(\xi) \ e^{-\lambda r(\xi)}\phi(2\xi) \ d\xi,$$

where  $r(\xi) := G(2\xi) - G(\xi)$ . Let  $m := \min_{a/2 \le \xi \le 1/2} r(\xi)$ ,  $M := \max_{a/2 \le \xi \le 1/2} r(\xi)$ . Then  $0 < m \le M < \infty$ . (Here we have explicitly used that a > 0.)

$$(T_{\lambda}\phi)(x) = \int_{a/2}^{\min(1/2,x)} e^{(\mu-\lambda)r(\xi)} k(\xi) e^{-\mu r(\xi)} \phi(2\xi) d\xi$$

from which we deduce the following estimates:

$$e^{(\mu-\lambda)m}T_{\mu}\phi \leq T_{\lambda}\phi \leq e^{(\mu-\lambda)M}T_{\mu}\phi.$$

Substituting  $\phi = \phi_{\mu}$ , where  $\phi_{\mu}$  is given by (4.4), yields

$$e^{(\mu-\lambda)m}r_{\mu}\phi_{\mu}\leqslant T_{\lambda}\phi_{\mu}\leqslant e^{(\mu-\lambda)M}r_{\mu}\phi_{\mu}.$$

If we apply  $F_{\lambda}$ , determined by (4.5), on the three separate terms, we obtain

$$e^{(\mu-\lambda)m}r_{\mu}F_{\lambda}(\phi_{\mu}) \leqslant r_{\lambda}F_{\lambda}(\phi_{\mu}) \leqslant e^{(\mu-\lambda)M}r_{\mu}F_{\lambda}(\phi_{\mu}).$$

Because  $F_{\lambda}(\phi_{\mu}) > 0$ , this is equivalent to

$$e^{(\mu-\lambda)m}r_{\mu} \leqslant r_{\lambda} \leqslant e^{(\mu-\lambda)M}r_{\mu}. \tag{*}$$

From these inequalities we may conclude that  $\lambda \to r_{\lambda}$  defines a continuous and strictly monotone decreasing function on  $\mathbb{R}$ . Moreover,  $\lim_{\lambda \to \infty} r_{\lambda} = 0$ ,  $\lim_{\lambda \to -\infty} r_{\lambda} = \infty$ . This proves the result.

Remark. This proof is standard. For example, similar arguments have been used by Nussbaum [10, Lemma 6].

Now we have proved that there exists a unique  $\lambda_0 \in \mathbb{R}$ , a unique  $\phi_0 \in K_m$ , and a unique, strictly positive functional  $F_0$  such that

$$T_{\lambda_0}\phi_0 = \phi_0,$$
  
$$T_{\lambda_0}^* F_0 = F_0,$$

and the eigenvalue 1 of  $T_i$  is algebraically simple.

Remark. There is a more elegant and transparent way to obtain the results of this section. The basic idea is to study the integal equation (2.9) on the subinterval [a, 1]:

$$(\tilde{T}_{\lambda}\tilde{\phi})(x) = \int_{a/2}^{\min(1/2, x)} k_{\lambda}(\xi) \,\tilde{\phi}(2\xi) \,d\xi, \qquad \tilde{\phi} \in C[a, 1]. \tag{*}$$

The values of  $T_{\lambda}\phi$ , for  $\phi \in X_0$ , on the interval  $\left[\frac{1}{2}a, a\right]$  are completely determined by the values of

$$\widetilde{\phi} := \phi |_{[a,1]} \in C[a,1],$$
 i.e., the restriction of  $\phi$  to  $[a,1]$ .

Suppose  $\widetilde{\phi} \in C[a, 1]$  is a solution of  $\widetilde{T}_{\lambda}\widetilde{\phi} = \widetilde{\phi}$ , where  $\widetilde{T}_{\lambda}$  is given by (\*), and let the extension  $\phi$  of  $\widetilde{\phi}$  on  $\left[\frac{1}{2}a, 1\right]$  be defined by

$$\phi(x) = \widetilde{\phi}(x), \qquad a \le x \le 1$$

$$\phi(x) = \int_{a/2}^{x} k_{\lambda}(\xi) \, \widetilde{\phi}(2\xi) \, d\xi, \qquad \frac{1}{2} a \le x \le a.$$

Then  $\phi \in X_0$  and  $\phi$  is a solution of the original integral equation (2.12). The advantage of this method is that it permits us to work in the cone  $\widetilde{K} = \{ \widetilde{\phi} \in C[a, 1] | \widetilde{\phi}(x) \ge 0 \}$ , which has non-empty interior  $\widetilde{K}$ . The operator  $\widetilde{T}_{\lambda}$  is strongly-positive with respect to  $\widetilde{K}$ , i.e., for all  $\phi \in \widetilde{K}$  there exists an integer  $n = n(\phi)$  such that  $\widetilde{T}_{\lambda}^n \phi \in \widetilde{K}$ . Now the unicity of the positive eigenvector is given by Theorem 6.3 of Krein and Rutman. However, this approach fails in the case that a = 0, and for that reason, we have chosen a different road.

5. The Case 
$$a = 0$$

In this section we are going to deal with the case that a=0. There is an important distinction between this case and the former one. If a is non-zero, then the problem can be solved in a finite number of steps; this cannot be done if a=0. As a consequence the methods used in Section 4 have to be adapted.

Let  $\lambda \in \mathbb{R}$  be fixed.

Theorem 5.1. The operator  $T_{\lambda}$  is non-support with respect to the cone  $K_0$ .

*Proof.* Let  $\phi \in K_0$ ,  $\phi \neq 0$ , and  $F \in K_0^*$ ,  $F \neq 0$ . Following Theorem 4.2 there exists a positive Borel measure  $\mu$  on [0, 1] such that

$$\int_{\{0,1\}} d\mu \neq 0, \quad \text{and} \quad F(\psi) = F_{\mu}(\psi) = \int_{\{0,1\}} \psi \ d\mu, \quad \text{for all } \psi \in X_0.$$

Hence there exists an  $\alpha > 0$  such that for all  $\epsilon$  satisfying  $0 < \epsilon < \alpha$  one has:

$$\int_{(\alpha-\varepsilon,\alpha+\varepsilon)} d\mu > 0.$$

Let p be an integer such that  $2^{-p} < \alpha$ . Then for all  $n \ge p$  we have

$$(T_{\downarrow}^n \phi)(\alpha) > 0.$$

Hence

$$F(T_{\lambda}^{n}\phi) = F_{\mu}(T_{\lambda}^{n}\phi) = \int_{[0,1]} (T_{\lambda}^{n}\phi) d\mu \geqslant \int_{\alpha-\varepsilon}^{\alpha+\varepsilon} (T_{\lambda}^{n}\phi) d\mu > 0 \quad \text{if } n \geqslant p. \quad \blacksquare$$

Since  $T_{\lambda}$  is compact, all non-zero eigenvalues are poles of the resolvent. From estimate (\*) in the proof of Theorem 5.3 we conclude that  $r(T_{\lambda}) > 0$ . Furthermore  $K_0$  is reproducing (and hence total) as we have seen in Theorem 4.1. Therefore we can apply Theorem 3.3. There exist an eigenvector  $\phi_{\lambda} \in K_0$  (and hence  $\phi_{\lambda} \in K_m$ ) and a positive eigenfunctional  $F_{\lambda} \in K_0^*$  such that

$$T_{\lambda}\phi_{\lambda} = r_{\lambda}\phi_{\lambda},$$
$$T^*F_{\lambda} = r_{\lambda}F_{\lambda}.$$

where  $r_{\lambda} = r(T_{\lambda})$  is an algebraically simple eigenvalue,  $\phi_{\lambda} \in Q_{K_0}$ ,  $\phi_{\lambda}$  is the only positive eigenvector belonging to  $T_{\lambda}$ , and  $F_{\lambda}$  is strictly positive.

As in Section 4 it remains to prove that  $\lambda \in \mathbb{R}$  is uniquely determined by the condition  $r(T_{\lambda}) = 1$ . Note that we cannot apply Theorem 4.4, because the proof of that theorem explicitly makes use of the fact that a is non-zero. We need the following lemma.

LEMMA 5.2. Suppose  $\phi \in K_0$ . Then  $\phi \in Q_{K_0}$  iff  $\phi(x) > 0$  for all  $x \in (0, 1]$ .

*Proof.* (i) Let  $\phi \in Q_{K_0}$  and suppose  $\phi(\alpha) = 0$ , for some  $\alpha \in (0, 1]$ . Let the positive non-zero Borel measure  $\mu$  on (0, 1] be given by:

for every Borel set 
$$V \subset [0, 1]$$
:  $\mu(V) = 0$ , if  $\alpha \notin V$ ,  $\mu(V) = 1$ , if  $\alpha \in V$ .

Then

$$F_{\mu}(\phi) = \int_{[0,1]} \phi \ d\mu = \phi(\alpha) = 0$$
 and  $F_{\mu} \neq 0$ .

This is a contradiction.

(ii) Let  $\phi \in K_0$  and  $\phi(x) > 0$ , for all  $x \in (0, 1]$ . Suppose  $F = F_{\mu} \in K_0^* \setminus \{0\}$ ; then the positive Borel measure  $\mu$  is not identically zero, i.e.,  $\int_{(0,1]} d\mu > 0$  which means that for some  $\alpha > 0$ , and for  $\varepsilon > 0$  sufficiently small, we have  $\int_{(\alpha - \varepsilon, \alpha + \varepsilon)} d\mu > 0$ . Using  $\phi(\alpha) > 0$  we find

$$\int_{(0,1]} \phi \ d\mu = F_{\mu}(\phi) \geqslant \int_{(\alpha - \varepsilon, \alpha + \varepsilon)} \phi \ d\mu > 0. \quad \blacksquare$$

THEOREM 5.3. The number  $\lambda \in \mathbb{R}$  is uniquely determined by the condition  $r(T_{\lambda}) = 1$ .

*Proof.* Let  $\lambda_1 < \lambda_2$  and let  $\phi_{\lambda_i}$ ,  $F_{\lambda_i}$ , i = 1, 2, be the positive eigenvector and eigenfunctional of  $T_{\lambda_i}$  and  $T_{\lambda_i}^*$ :

$$T_{\lambda_i}\phi_{\lambda_i} = r_{\lambda_i}\phi_{\lambda_i}, \qquad i = 1, 2,$$
  

$$T_{\lambda_i}^*F_{\lambda_i} = r_{\lambda_i}F_{\lambda_i}, \qquad i = 1, 2.$$

Then

$$\begin{split} r_{\lambda_2} &= \frac{(T_{\lambda_2}^* F_{\lambda_2})(\phi_{\lambda_1})}{F_{\lambda_2}(\phi_{\lambda_1})} = \frac{F_{\lambda_2}(T_{\lambda_2}\phi_{\lambda_1})}{F_{\lambda_2}(\phi_{\lambda_1})} \\ &= \frac{F_{\lambda_2}(T_{\lambda_1}\phi_{\lambda_1})}{F_{\lambda_2}(\phi_{\lambda_1})} - \frac{F_{\lambda_2}((T_{\lambda_1} - T_{\lambda_2})\phi_{\lambda_1})}{F_{\lambda_2}(\phi_{\lambda_1})} = : r_{\lambda_1} - \Delta. \\ ((T_{\lambda_1^-} T_{\lambda_2})\phi_{\lambda_1})(x) &= \int_0^{\min(1/2,x)} \left\{ k_{\lambda_1}(\xi) - k_{\lambda_2}(\xi) \right\} \phi_{\lambda_1}(2\xi) \, d\xi > 0, \end{split}$$

for all x>0, which means that  $(T_{\lambda_1}-T_{\lambda_2})\,\phi_{\lambda_1}\in Q_{K_0}$ . Here we have used Lemma 5.2. This and the strict positivity of  $F_{\lambda_2}$  imply that  $\Delta>0$ . Hence  $r_{\lambda_1}>r_{\lambda_2}$  which implies that  $r(T_{\lambda})$  is strictly monotone decreasing in  $\lambda$ . Moreover,  $\lim_{\lambda_2\to\lambda_1}\Delta=0$ , which yields the continuity of  $r_{\lambda}$ . Now let  $\lambda\in\mathbb{R}$ : there exists a  $\phi_{\lambda}\in K_m$  such that  $T_{\lambda}\phi_{\lambda}=r_{\lambda}\phi_{\lambda}$  and  $\|\phi_{\lambda}\|=1$ . Clearly  $(T_{\lambda}\phi_{\lambda})(1)=\|T_{\lambda}\phi_{\lambda}\|=r_{\lambda}\phi_{\lambda}(1)=r_{\lambda}\|\phi_{\lambda}\|=r_{\lambda}=\int_0^{1/2}k_{\lambda}(\xi)\,\phi(2\xi)\,d\xi$ , where we have used that for any vector  $\Psi\in K_m$  we have  $\|\Psi\|=\Psi(1)$ . One sees immediately that  $\phi_{\lambda}(x)$  is constant for all  $x\in[\frac{1}{2},1]$ . It follows that

$$\int_{1/4}^{1/2} k_{\lambda}(\xi) d\xi \leqslant r_{\lambda} \leqslant \int_{0}^{1/2} k_{\lambda}(\xi) d\xi, \tag{*}$$

from which we conclude

$$\lim_{\lambda \to -\infty} r(T_{\lambda}) = \infty,$$

$$\lim_{\lambda \to +\infty} r(T_{\lambda}) = 0.$$

This completes the proof.

Now we have proved the existence and uniqueness of  $\lambda_0 \in \mathbb{R}$ ,  $\phi_0 \in K_m$ , and a strictly positive functional  $F_0$  such that

$$T_{\lambda_0}\phi_0 = \phi_0,$$
  
$$T_{\lambda_0}^*F_0 = F_0,$$

and the eigenvalue 1 of  $T_{\lambda_0}$  is algebraically simple.

The remaining part of this section is valid both for the cases a > 0 and a = 0.

Let  $\psi_0$  be defined by

$$\psi_0(x) = e^{-\lambda_0 G(x)} \phi_0(x), \tag{5.1}$$

then the following results hold:

$$\psi_0(x) \geqslant 0,$$
  $\frac{1}{2}a \leqslant x \leqslant 1$   $\psi_0$  is continuous  $A\psi_0 = \lambda_0 \psi_0$   $\psi_0$  is the only positive eigenvector of  $A$ .

Theorem 5.4. The eigenvalue  $\lambda_0 \in P\sigma(A)$  is algebraically simple.

Proof. The geometric simplicity of the eigenvalue  $\lambda_0 \in P\sigma(A)$  follows directly from the geometric simplicity of the eigenvalue  $1 \in P\sigma(T_{\lambda_0})$ . Now suppose that  $(\lambda_0 - A)^2 \psi = 0$ ,  $(\lambda_0 - A) \psi \neq 0$ , for some  $\psi \in D(A^2)$ . Let  $\psi := (\lambda_0 - A) \psi$ , then  $A\psi = \lambda_0 \psi$  and  $\psi \neq 0$ , from which we conclude that  $\psi = \alpha \cdot \psi_0$  for some constant  $\alpha \in \mathbb{C} \setminus \{0\}$ , which we may assume to be 1. In Section 2 we have seen that the equation  $\lambda_0 \psi - A\psi = \psi_0$  is equivalent to  $\psi - T_{\lambda_0} \psi = U_{\lambda_0} \psi_0$  where  $\psi(x) = e^{\lambda_0 G(x)} \psi(x)$ . Applying  $F_0$  (i.e., the strictly positive eigenfunctional satisfying  $T_{\lambda_0} *F_0 = F_0$ ) on both sides, we obtain:  $F_0(U_{\lambda_0} \psi_0) = 0$ , which is a contradiction because  $U_{\lambda_0} \psi_0 \in K_0 \setminus \{0\}$ . This proves the result.

## 6. THE CHARACTERISTIC EQUATION

Let the Banach space X be the space of all continuous functions on  $\left[\frac{1}{2}a,1\right]$  with the sup-norm. Clearly  $X_0$  is a closed subspace of X. For every  $\lambda \in \mathbb{C}$  the operator  $T_{\lambda}: X_0 \to X_0$  can be extended to the larger space X. This extension is also denoted by the symbol  $T_{\lambda}$ :

$$(T_{\lambda}\phi)(x) = \int_{a/2}^{\min(1/2, x)} k_{\lambda}(\xi) \,\phi(2\xi) \,d\xi, \qquad \phi \in X. \tag{6.1}$$

One sees immediately:  $T_{\lambda}X \subset X_0$ . As a consequence  $T_{\lambda}\phi = \phi$ ,  $\phi \in X$ , implies that  $\phi \in X_0$ . Using Theorem 2.2, we have

$$\lambda \in \sigma(A) \Leftrightarrow 1 \in P\sigma(T_{\lambda}|_{X_0}) \Leftrightarrow 1 \in P\sigma(T_{\lambda}) \tag{6.2}$$

where  $T_{\lambda}|_{X_0}$  denotes the restriction of  $T_{\lambda}: X \to X$  to the subspace  $X_0$ . Let  $e_1 \in X$  be defined by

$$e_1(x) = 1, \qquad \frac{1}{2}a \le x \le 1.$$
 (6.3)

 $T_{\lambda}: X \to X$  can be decomposed in the following way. Let  $\phi \in X$ :

$$(T_{\lambda}\phi)(x) = \int_{a/2}^{1/2} k_{\lambda}(\xi) \,\phi(2\xi) \,d\xi - \int_{\min(1/2,x)}^{1/2} k_{\lambda}(\xi) \,\phi(2\xi) \,d\xi = H_{\lambda}(\phi) \,e_1 + N_{\lambda}\phi,$$
(6.4)

where  $H_{\lambda}$  is a bounded linear functional,

$$H_{\lambda}(\phi) := \int_{a/2}^{1/2} k_{\lambda}(\xi) \,\phi(2\xi) \,d\xi,\tag{6.5}$$

and  $N_{\lambda}$  is a bounded linear operator on X,

$$(N_{\lambda}\phi)(x) := -\int_{\min(1/2,x)}^{1/2} k_{\lambda}(\xi) \,\phi(2\xi) \,d\xi. \tag{6.6}$$

The reason that we have embedded  $X_0$  in the larger space X might be clear now: X is invariant under  $N_{\lambda}$ , but  $X_0$  isn't. Again we make a distinction between the cases a > 0 and a = 0.

I. a > 0

LEMMA 6.1. The operator  $N_{\lambda}$  is compact and nilpotent, for all  $\lambda \in \mathbb{C}$ , i.e.,  $N_{\gamma}^{p} = 0$  for some  $p \in \mathbb{N}$ , where p does not depend on  $\lambda$ .

*Proof.* Compactness is trivial. Let  $p \in \mathbb{N}$  be such that  $2^{-p+1} \le a < 2^{-p+2}$ . Then we have  $N_{\lambda}^{p-1} \ne 0$  and  $N_{\lambda}^{p} = 0$ . To see this, we observe that for all  $\phi \in X$ 

$$(N_{\lambda}\phi)(x) = 0, \qquad x \geqslant \frac{1}{2}$$

$$(N_{\lambda}^{2}\phi)(x) = 0, \qquad x \geqslant \frac{1}{4}$$

$$\vdots \qquad \vdots$$

$$(N_{\lambda}^{p})(x) = 0, \qquad x \geqslant \frac{1}{2}a.$$

Substitution of  $T_{\lambda}\phi$  in (6.4) gives us

$$T_{\lambda}^{2}\phi = H_{\lambda}(T_{\lambda}\phi) e_{1} + N_{\lambda}(T_{\lambda}\phi) = H_{\lambda}(T_{\lambda}\phi) e_{1} + H_{\lambda}(\phi) N_{\lambda}e_{1} + N_{\lambda}^{2}\phi. \tag{6.7}$$

We define

$$e_j := N_{\lambda} e_{j-1}, \qquad j = 2, ..., p.$$
 (6.8)

Notice that

$$N_{\lambda}e_{p} = N_{\lambda}^{p}e_{1} = 0. \tag{6.9}$$

Lemma 6.2.  $e_1,...,e_p$  are linearly independent in X. Furthermore  $\operatorname{Ran}(T^p_\lambda) \subset \operatorname{span} \langle e_1,...,e_p \rangle$ , where  $\operatorname{span} \langle e_1,...,e_p \rangle$  is the subspace of X spanned by the functions  $e_1,...,e_p$ .

Proof.

$$e_2(x) = (N, e_1)(x) \neq 0,$$
 if  $x < \frac{1}{2}$ .

A straightforward computation shows that for all i, with  $1 \le i \le p$ , we have

$$e_i(x) \neq 0$$
 if  $x < 2^{-i+1}$ .

Now suppose that for certain  $\alpha_i \in \mathbb{C}$ , i = 1,..., p,

$$\alpha_1 e_1 + \cdots + \alpha_p e_p = 0.$$

Then

$$N_{\lambda}^{p-1}(\alpha_1 e_1 + \cdots + \alpha_p e_p) = \alpha_1 e_p = 0,$$

which implies that  $\alpha_1 = 0$ . Likewise we find that  $\alpha_i = 0$  for all i = 2,..., p. This proves the linear independence of  $e_1,..., e_p$ . A computation similar to (6.7) yields

$$T_{\lambda}^{p} \phi = H_{\lambda}(T_{\lambda}^{p-1} \phi) e_{1} + H_{\lambda}(T_{\lambda}^{p-2} \phi) e_{2} + \dots + H_{\lambda}(\phi) e_{n}$$
 (6.10)

for all  $\phi \in X$ , where we have used that  $N_i^p = 0$ . This completes the proof.

Defining

$$f_j := H_{\lambda}(e_j), \qquad j = 1, ..., p,$$
 (6.11)

we have

$$T_{\lambda}e_{j} = H_{\lambda}(e_{j}) e_{1} + N_{\lambda}e_{j} = f_{j}e_{1} + e_{j+1}, \quad j = 1,..., p, \text{ where } e_{p+1} := 0.$$
 (6.12)

Remark. One should keep in mind that  $e_j$  and  $f_j$  both depend on  $\lambda$ . Now suppose that  $\lambda \in \sigma(A)$ . This implies that  $1 \in P\sigma(T_\lambda)$ . Therefore  $T_\lambda \phi = \phi$  for some  $\phi \in X$ ,  $\phi \neq 0$ . Consequently  $T_\lambda^p \phi = \phi$ . In other words  $\phi \in \text{Ran}(T_\lambda^p) \subset \text{span } \langle e_1, ..., e_p \rangle$ . Hence we can write  $\phi = \phi_1 e_1 + \cdots + \phi_p e_p$ . Using (6.12) we find

$$\sum_{i=1}^{p} \phi_{i} e_{i} = \phi = T_{\lambda} \phi = \sum_{i=1}^{p} \phi_{i} T_{\lambda} e_{i} = \sum_{i=1}^{p} \phi_{i} (f_{i} e_{1} + e_{i+1}).$$

Using the linear independence of the functions  $e_i$  we conclude

$$\phi_1 = \phi_1 f_1 + \dots + \phi_p f_p,$$
  
$$\phi_1 = \phi_2 = \dots = \phi_p.$$

 $\phi \neq 0$  implies  $\phi_1 \neq 0$  and therefore  $f_1 + \cdots + f_p = 1$ . Furthermore  $f_p = H_{\lambda}(e_p) = 0$ . Now we have proved:

THEOREM 6.3.  $\lambda \in \sigma(A)$  if and only if  $H_{\lambda}(e_1 + \cdots + e_{p-1}) = 1$ .

II. a = 0

Let  $H_1$  and  $N_2$  be defined by (6.5) and (6.6) where  $\frac{1}{2}a$  is replaced by 0.

$$T_{i}\phi = H_{1}(\phi) e_{1} + N_{i}\phi, \qquad \phi \in X.$$
 (6.13)

Let  $e_j$  be defined by (6.8) for all  $j \ge 1$ .

LEMMA 6.4.  $N_{\lambda}$  is compact and quasinilpotent.

*Proof.* The proof that  $N_{\lambda}$  is compact is trivial. Now suppose that  $\mu \in P\sigma(N_{\lambda})$ ; hence there exists a  $\psi \in X \setminus \{0\}$  such that  $N_{\lambda}\psi = \mu\psi$ . Consequently  $N_{\lambda}^{k}\psi = \mu^{k}\psi$ , for all  $k \ge 1$ . Observing that  $(N_{\lambda}^{k}\psi)(x) = 0$ , for  $x \ge 2^{-k}$ , we conclude that  $\mu = 0$ . As a consequence  $\sigma(N_{\lambda}) = \{0\}$ , which proves the theorem.

LEMMA 6.5.  $\eta_{\lambda} := \sum_{k=1}^{\infty} e_k \in X$ , and  $\|\eta_{\lambda}\|$  is uniformly bounded in every vertical strip  $s \leq \text{Re } \lambda \leq t$ .

*Proof.* It suffices to prove that  $\sum_{j=1}^{\infty} ||e_j|| < \infty$ . We have  $||e_1|| = 1$ . Suppose  $s \le \text{Re } \lambda \le t$ .

$$|e_2(x)| \le \int_{\min(1/2,x)}^{1/2} |k_{\lambda}(\xi)| d\xi < \int_0^{1/2} |k_{\lambda}(\xi)| d\xi < \infty.$$

This yields

$$e_2(x) = 0, x \ge \frac{1}{2},$$
$$|e_2(x)| \le M, x \le \frac{1}{2},$$

where

$$M := \max_{s \leqslant \operatorname{Re} \lambda \leqslant t} \left( \int_0^{1/2} |k_{\lambda}(\xi)| d\xi \right),$$
$$|e_3(x)| \leqslant \int_0^{1/4} |k_{\lambda}(\xi)| M d\xi \leqslant \frac{1}{4} LM,$$

where

$$L := \max\{|k_{\lambda}(\xi)| \mid 0 \leqslant \xi \leqslant \frac{1}{4}, s \leqslant \operatorname{Re} \lambda \leqslant t\}. \tag{6.14}$$

By induction we find that

$$||e_k|| \leq \frac{1}{4} \cdot \frac{1}{8} \cdot \cdot \cdot \frac{1}{2^{k-1}} L^{k-2} \cdot M,$$

which completes the proof.

THEOREM 6.6.  $T_{\lambda}\phi = \phi$  is solvable if and only if  $H_{\lambda}(\eta_{\lambda}) = 1$ . In that case  $\phi = H_{\lambda}(\phi) \eta_{\lambda}$ .

*Proof.* (i) Suppose  $T_{\lambda}\phi = \phi$ . Inserting (6.13) we obtain  $N_{\lambda}\phi = \phi - H_{\lambda}(\phi) e_1$ . If we put  $\hat{\phi} := H_{\lambda}(\phi) \eta_{\lambda}$  then  $N_{\lambda}(\phi - \hat{\phi}) = \phi - H_{\lambda}(\phi) e_1 - H_{\lambda}(\phi) N_{\lambda} \eta_{\lambda} = \phi - H_{\lambda}(\phi) e_1 - H_{\lambda}(\phi) (e_2 + e_3 + \cdots) = \phi - \hat{\phi}$ . Now the quasi-nilpotence of  $N_{\lambda}$  implies that  $\phi - \hat{\phi} = 0$  and therefore  $\phi = H_{\lambda}(\phi) \eta_{\lambda}$ . Consequently  $H_{\lambda}(\phi) = H_{\lambda}(\phi) H_{\lambda}(\eta_{\lambda})$ . Moreover  $H_{\lambda}(\phi) \neq 0$  because  $\phi \neq 0$  and thus  $H_{\lambda}(\eta_{\lambda}) = 1$ .

(ii) Suppose  $H_{\lambda}(\eta_{\lambda}) = 1$ . Putting  $\phi := \alpha \eta_{\lambda}$  (where  $\alpha$  is to be determined), we obtain  $T_{\lambda}\phi = \alpha T_{\lambda}\eta_{\lambda} = \alpha H_{\lambda}(\eta_{\lambda}) e_{1} + \alpha N_{\lambda}\eta_{\lambda} = \alpha \eta_{\lambda} = \phi$ . As a consequence  $H_{\lambda}(\phi) = \alpha H_{\lambda}(\eta_{\lambda}) = \alpha$ . From this we conclude that  $\phi = H_{\lambda}(\phi) \eta_{\lambda}$ .

Now, both for the cases a > 0 (see Theorem 6.3) and a = 0 (see

Theorem 6.6) we have computed the characteristic equation from which all the eigenvalues of A can be computed numerically.

If  $a \ge \frac{1}{2}$  then this equation takes the following simple form:

$$\int_{a/2}^{1/2} k_{\lambda}(\xi) d\xi = 1.$$

# 7. Position of the Eigenvalues for the Case g(2x) < 2g(x)

In this and the next section we shall investigate the position of the eigenvalues of A. We are especially interested in the position of the eigenvalue  $\lambda_0$ . It appears that the outcome depends heavily on the individual growth rate g(x). This becomes clear by the following arguments.

The kernel  $k_{\lambda}(x)$  of the integral operator  $T_{\lambda}$  (see Section 2) can be written as

$$k_{\lambda}(x) = k(x) e^{-\lambda r(x)}, \qquad \frac{1}{2}a \leqslant x \leqslant \frac{1}{2}$$
 (7.1)

where

$$r(x) = G(2x) - G(x). (7.2)$$

Obviously

$$\frac{dr}{dx} = \frac{2g(x) - g(2x)}{g(x)g(2x)}.$$

Hence, if 2g(x) = g(2x) for all  $x \in \left[\frac{1}{2}a, \frac{1}{2}\right]$ , then r(x) does not depend on x, and in the next section it will be made clear that this has far-reaching consequences for the eigenvalues of A. In this section we shall restrict ourselves to the case

$$g(2x) < 2g(x), \qquad \frac{1}{2}a \le x \le \frac{1}{2}$$
 (7.3)

and from now on we assume that this relation is satisfied.

We have seen that the operator A has exactly one positive eigenvector corresponding to an eigenvalue  $\lambda_0 \in \mathbb{R}$ . (See Section 5.) Now we shall prove that  $\lambda_0$  is the strictly dominant value of A. We need the following elementary lemma.

LEMMA 7.1. Suppose a < b, and let  $f \in L_1[a, b]$  be a complex-valued function. Then we have:  $|\int_a^b f(x) dx| = \int_a^b |f(x)| dx$  if and only if there exists a constant  $\alpha \in \mathbb{C}$ , with  $|\alpha| = 1$ , such that  $|f(x)| = \alpha f(x)$  a.e. on [a, b].

*Proof.* Let  $z:=\int_a^b f(x)\,dx$  and define  $\alpha\in\mathbb{C}$  such that  $\alpha z=|z|$ . Clearly  $|\alpha|=1$ . Putting  $u(x):=\operatorname{Re}\{\alpha f(x)\}$  we have  $u(x)\leqslant |\alpha f(x)|=|f(x)|$  and the inequality is strict for all  $x\in V$ , where the subset  $V\subset [a,b]$  is defined by:  $x\in V$  iff  $\operatorname{Im}\{\alpha f(x)\}\neq 0$ . Hence  $u(x)<|\alpha f(x)|=|f(x)|$ , for  $x\in V$  and  $\int_a^b u(x)\,dx<\int_a^b |f(x)|\,dx$  iff  $\mu(V)>0$ , where  $\mu(V)$  is the measure of the set V.

$$\left| \int_{a}^{b} f(x) \, dx \right| = |z| = \alpha z = \int_{a}^{b} \alpha f(x) \, dx = \operatorname{Re} \left\{ \int_{a}^{b} \alpha f(x) \, dx \right\}$$
$$= \int_{a}^{b} \operatorname{Re} \left\{ \alpha f(x) \right\} \, dx = \int_{a}^{b} u(x) \, dx.$$

Consequently  $|\int_a^b f(x) dx| < \int_a^b |f(x)| dx$  iff  $\mu(V) > 0$ . In other words:  $|\int_a^b f(x) dx| = \int_a^b |f(x)| dx$  iff  $u(x) = \alpha f(x)$  a.e., which is the same as  $|f(x)| = \alpha f(x)$  a.e.

THEOREM 7.2. If  $\lambda \in P\sigma(A)$  and  $\lambda \neq \lambda_0$  then Re  $\lambda < \lambda_0$ .

*Proof.* (i) Suppose Re  $\lambda > \lambda_0$  and  $\lambda \in \sigma(A)$ . Then  $1 \in P\sigma(T_\lambda)$  which implies that  $T_\lambda \phi = \phi$  for some  $\phi \in X_0$ .

In other words

$$\int_{a/2}^{\min(1/2,x)} k_{\lambda}(\xi) \,\phi(2\xi) \,d\xi = \phi(x).$$

Using (7.1) we arrive at

$$\int_{a/2}^{\min(1/2,x)} k(\xi) e^{-\lambda r(\xi)} \phi(2\xi) d\xi = \phi(x).$$

Taking absolute values on both sides, we find  $\int_{a/2}^{\min(1/2,x)} k(\xi) e^{-\operatorname{Re}\lambda\cdot r(\xi)} |\phi(2\xi)| d\xi \geqslant |\phi(x)|$ , which can be written as:  $T_{\operatorname{Re}\lambda} |\phi| \geqslant |\phi|$  (with respect to  $K_0$ ) where  $|\phi| \in X_0$  is defined by  $|\phi|(x) := |\phi(x)|$ . Using Theorem 6.2 of Krein and Rutman (see [8]) we obtain  $T_{\operatorname{Re}\lambda} \psi = \rho \psi$  for some  $\psi \in K_0/\{0\}$  and  $\rho \geqslant 1$ . Consequently  $r(T_{\operatorname{Re}\lambda}) \geqslant 1$ . On the other hand, Theorem 4.4 and Theorem 5.3 state that  $r(T_{\operatorname{Re}\lambda}) < 1$  both for the cases a > 0 and a = 0. Now we have proved that  $\lambda \in \sigma(A)$  implies that  $\operatorname{Re}\lambda \leqslant \lambda_0$ .

(ii) Now suppose that  $\lambda = \lambda_0 + i\eta$  and  $\lambda \in \sigma(A)$ . This implies that  $T_{\lambda}\psi = \psi$  for some  $\psi \in X_0$  and as in (a) we deduce  $T_{\text{Re}\lambda} \mid \psi \mid \geqslant \mid \psi \mid$ , i.e.,  $T_{\lambda_0} \mid \psi \mid \geqslant \mid \psi \mid$ . Suppose that  $T_{\lambda_0} \mid \psi \mid \neq \mid \psi \mid$ . This yields  $T_{\lambda_0} \mid \psi \mid - \mid \psi \mid \in K_0 \setminus \{0\}$ . Let  $F_0$  be the strictly positive eigenfunctional satisfying  $T_{\lambda_0}^* F_0 = F_0$ . Then  $0 < F_0(T_{\lambda_0} \mid \psi \mid - \mid \psi \mid) = (T_{\lambda_0}^* F_0)(\mid \psi \mid) - F_0(\mid \psi \mid) = 0$ , which is a contradiction. Consequently  $T_{\lambda_0} \mid \psi \mid = \mid \psi \mid$ , which means, by the simplicity of

the eigenvalue 1 of  $T_{\lambda_0}$  that  $|\psi| = \gamma \phi_0$ , for some constant  $\gamma \in \mathbb{C}$ , which we may assume to be one, without loss of generality. As a consequence  $|\psi(x)| = \phi_0(x) e^{i\alpha(x)}$ , where  $\alpha(x) \in \mathbb{R}$ ,  $x \in [\frac{1}{2}a, 1]$ . Using  $|T_{\lambda}\psi| = |\psi| = T_{Re\lambda} |\psi| = T_{\lambda_0} \phi_0$ , we find

$$\begin{split} \int_{a/2}^{\min(1/2,x)} k_{\lambda_0}(\xi) \, \phi_0(2\xi) \, d\xi &= \left| \int_{a/2}^{\min(1/2,x)} k_{\lambda}(\xi) \, \psi(2\xi) \, d\xi \right| \\ &= \left| \int_{a/2}^{\min(1/2,x)} e^{-i\eta r(\xi)} k_{\lambda_0}(\xi) \, \phi_0(2\xi) \, e^{i\alpha(2\xi)} \, d\xi \right|. \end{split}$$

Using Lemma 7.1 we obtain  $\alpha(2\xi) - \eta r(\xi) = C$  where C is a constant. Hence  $\alpha(x) = C + \eta r(\frac{1}{2}x)$ . Inserting this in

$$\int_{a/2}^{\min(1/2,x)} k_{\lambda}(\xi) \, \psi(2\xi) \, d\xi = \psi(x)$$

$$= \int_{a/2}^{\min(1/2,x)} e^{-i\eta r(\xi)} k_{\lambda_0}(\xi) \, \phi_0(2\xi) \, e^{i\alpha(2\xi)} \, d\xi = \phi_0(x) \, e^{i\alpha(x)},$$

we obtain

$$e^{iC} \int_{a/2}^{\min(1/2,x)} k_{\lambda_0}(\xi) \,\phi_0(2\xi) \,d\xi = \phi_0(x) \,e^{iC + i\eta r(x/2)},$$

which implies

$$\phi_0(x) = \phi_0(x) e^{i\eta r(x/2)}$$
 a.e.

Because r is a continuous non-constant function on  $\left[\frac{1}{2}a, \frac{1}{2}\right]$  we obtain  $\eta = 0$ , which implies that  $\lambda = \lambda_0$ .

Remark. In [5, proof of Theorem 1], Hess and Kato use the same sort of argument.

In Section 2 we noticed that all elements of  $\sigma(A)$  are isolated. Now we are going to show that in every vertical strip  $s \le \text{Re } \lambda \le t$ , there are only finitely many of them.

Theorem 7.3. Suppose s < t. In the vertical strip  $s \le \text{Re } \lambda \le t$ , there are only finitely many points of  $\sigma(A)$ .

*Proof.* (i) Let a > 0. Suppose  $\lambda \in \sigma(A)$ . From Theorem 6.3 we conclude that  $H_1(e_1 + \cdots + e_{n-1}) = 1$ .

$$H_{\lambda}(e_1) = \int_{a/2}^{1/2} k_{\lambda}(\xi) d\xi = \int_{a/2}^{1/2} k(\xi) e^{-\lambda r(\xi)} d\xi,$$

where we have used (7.1). Because  $r'(\xi) \neq 0$  the well-known Riemann-Lebesgue lemma states that

$$\lim_{\mathrm{Im}\lambda\to\pm\infty}H_{\lambda}(e_1)=0,\qquad \text{uniformly in }s\leqslant\mathrm{Re}\ \lambda\leqslant t.$$

Using the same arguments for i > 1, we find

$$\lim_{\text{Im}\lambda \to \pm \infty} H_{\lambda}(e_1 + \dots + e_{p-1}) = 0, \quad \text{uniformly in } s \leq \text{Re } \lambda \leq t.$$

This together with the fact that all elements of  $\sigma(A)$  are isolated (see Theorem 2.5) proves the result for a > 0.

(ii) Let a = 0. Let  $\lambda \in \sigma(A)$  and  $s \le \text{Re } \lambda \le t$ . According to Lemma 6.5 there exists a constant  $M_1 > 0$  such that  $\|\eta_{\lambda}\| \le M_1$ . Theorem 6.6 yields that  $H_{\lambda}(\eta_{\lambda}) = 1$ . We have

$$H_{\lambda}(\eta_{\lambda}) = \int_{0}^{1} k_{\lambda}(\xi) \, \eta_{\lambda}(2\xi) \, d\xi$$
$$= \int_{0}^{\varepsilon} k_{\lambda}(\xi) \, \eta_{\lambda}(2\xi) \, d\xi + \int_{\varepsilon}^{1} k_{\lambda}(\xi) \, \eta_{\lambda}(2\xi) \, d\xi.$$

Now

$$\left| \int_0^\varepsilon k_{\lambda}(\xi) \, \eta_{\lambda}(2\xi) \, d\xi \right| \leq M_1 \int_0^\varepsilon |k_{\lambda}(\xi)| \, d\xi \leq L M_1 \varepsilon,$$

where L is defined by (6.14). We choose  $\varepsilon < \frac{1}{4}$  such that  $\varepsilon L M_1 \leqslant \frac{1}{2}$ . Hence

$$|H_{\lambda}(\eta_{\lambda})| \leq \frac{1}{2} + \left| \int_{\varepsilon}^{1/2} k_{\lambda}(\xi) \, \eta_{\lambda}(2\xi) \, d\xi \right|$$

for all  $\lambda$  satisfying  $s \le \text{Re } \lambda \le t$ . There exists a  $j_0 \in \mathbb{N}$  such that  $j > j_0$  implies  $e_j(x) = 0$  if  $x \ge \varepsilon$ . This yields

$$|H_{\lambda}(\eta_{\lambda})| \leq \frac{1}{2} + \sum_{j=1}^{j_0} |\int_{\varepsilon}^{1/2} k_{\lambda}(\xi) e_j(2\xi) d\xi|.$$

In (i) we have seen that  $\lim_{\mathrm{Im}\lambda\to\pm\infty}H_{\lambda}(e_1+\cdots e_p)=0$  uniformly in the vertical strip  $s\leqslant\mathrm{Re}\;\lambda\leqslant t$ . Similarly we have

$$\lim_{\mathrm{Im}\lambda \to \pm \infty} \left( \sum_{j=1}^{j_0} \left| \int_{\varepsilon}^{1/2} k_{\lambda}(\xi) e_j(2\xi) d\xi \right| \right) = 0$$

uniformly is the vertical strip  $s \le \text{Re } \lambda \le t$ . As a consequence, there exists a  $\Lambda > 0$  such that for all  $\lambda$  satisfying  $s \le \text{Re } \lambda \le t$  and  $|\text{Im } \lambda| \ge \Lambda$  we have

$$\left| \sum_{j=1}^{j_0} \left| \int_{\varepsilon}^{1/2} k_{\lambda}(\xi) e_j(2\xi) d\xi \right| \leq \frac{1}{4}.$$

For these values of  $\lambda$  we obtain  $|H_{\lambda}(\eta_{\lambda})| \leq \frac{3}{4}$  and we conclude from Theorem 6.6 that  $\lambda \notin \sigma(A)$ . Again, the fact that all elements of  $\sigma(A)$  are isolated proves the result for a=0.

*Remark.* The case g(2x) > 2g(x),  $\frac{1}{2}a \le x \le \frac{1}{2}$ , yields similar results. However, this situation seems rather unrealistic from a biological point of view.

# 8. Position of the Eigenvalues for the Case g(2x) = 2g(x)

In this section we shall investigate what happens if

$$g(2x) = 2g(x), \qquad \frac{1}{2}a \le x \le \frac{1}{2}.$$
 (8.1)

Then we have

$$r(x) = G(2x) - G(x) = r, \qquad \frac{1}{2}a \le x \le \frac{1}{2}$$
 (8.2)

where r does not depend on x. As a consequence  $k_{\lambda}(x) = k_0(x) e^{-\lambda r}$ , from which we conclude that

$$T_{\lambda} = e^{-\lambda r} T_0. \tag{8.3}$$

Because  $T_0$  defines a compact operator, it's spectrum is the union of  $\{0\}$  and a set containing at most countably many non-zero eigenvalues  $\sigma_1, ..., \sigma_a$ , where q is allowed to be  $\infty$ .

*Remark.* If a > 0 it can be shown that  $q \le p - 1$  where p is the integer determined by Lemma 6.1, i.e.,  $2^{-p+1} \le a < 2^{-p+2}$ .

Using (8.3) it follows immediately that  $\lambda \in \Sigma$  if and only if  $e^{-\lambda r}\sigma_j = 1$  for some  $1 \le j \le q$ . Let  $\lambda_j^0$  be a solution of  $e^{-\lambda r}\sigma_j = 1$ , then

$$\Sigma = \{ \lambda_i^0 + i \cdot (2k\pi/r) | 1 \le j \le q, k \in \mathbb{Z} \}.$$
 (8.4)

As a consequence we have that there does not exist a strictly dominant eigenvalue.

Remark. The above results can also be found if one determines the characteristic equation. If a>0 it can be proved in a straightforward way that  $H_{\lambda}(e_1+\cdots+e_{p-1})=C_1\cdot e^{-\lambda r}+C_2\cdot (e^{-\lambda r})^2+\cdots+C_{p-1}\cdot (e^{-\lambda r})^{p-1}$  (see Theorem 6.3) where  $C_i$ , i=1,...,p-1, are real coefficients. If a=0 we find  $H_{\lambda}(\eta_{\lambda})=\Phi$  ( $e^{-\lambda r}$ ) (see Theorem 6.6) where  $\Phi$  is an entire function on the complex domain.

The relation g(2x) = 2g(x) has a clear biological interpretation. A daughter cell having half the size of the mother will grow at just half the rate of the mother. So, if one starts with a cohort of cells of size x at time

t=0, then any daughter cell of this group will have a size which equals exactly half the size of an undivided member of this group, no matter when this daughter was born. This means that there is no dispersion of cell sizes if time increases. Of course, this argument becomes untrue if a mother cell does not necessarily divide into two equal daughters. In [4] we study the situation that division occurs into unequal parts, more precisely, the ratio (birth size of daughter)/(division size of the mother) is a random variable satisfying a smooth probability density function, and for that case we find that there indeed always exists a strictly dominant eigenvalue, no matter what g(x) looks like,

From a biological point of view, the most relevant solution of the functional equation g(2x) = 2g(x) is  $g(x) = \gamma x$ , where  $\gamma$  is some constant. In the literature, this is called the case of "exponential individual growth." (See, e.g., [1].) This nomenclature becomes clear if one observes that the solution of (0.1) is  $x(t) = x(0) e^{\gamma t}$ , if  $g(x) = \gamma x$ .

Remark. If the relation g(2x) = 2g(x) is satisfied on a nontrivial subset of  $\left[\frac{1}{2}a, \frac{1}{2}\right]$ , then the question concerning the existence of a strictly dominant eigenvalue may be very difficult to answer. However, in some simple cases the answer is straightforward. For instance, in [2, Sect. 8] it has been proved that for the case  $a \ge \frac{1}{2}$ ,

$$g(x) = x,$$
  $\frac{1}{2}a \le x \le \beta,$   
 $g(x) < x,$   $\beta \le x \le 1,$ 

where  $\beta$  is some value between a and 1, there does exist a strictly dominant eigenvalue, and it is our belief that this result can be extended to more general cases.

## 9. THE ADJOINT EIGENVALUE PROBLEM

In this section we shall state some results concerning the adjoint eigenvalue problem. The proofs of these results are straightforward and we shall omit them.

The adjoint operator  $A^*$  is given by

$$(A*f)(x) = \frac{d}{dx} (g(x) f(x)) + \frac{1}{2} k \left(\frac{1}{2} x\right) f\left(\frac{1}{2} x\right)$$
(9.1)

(one should read  $\frac{1}{2}k(\frac{1}{2}x) f(\frac{1}{2}x) = 0$ , if x < a) having a domain

$$D(A^*) = \{ f \in L_{\infty}[\frac{1}{2}a, 1] | gf \text{ is locally absolutely continuous, the function } x \to (d/dx)(g(x)f(x)) + \frac{1}{2}k(\frac{1}{2}x)f(\frac{1}{2}x)$$
 is an element of  $L_{\infty}[\frac{1}{2}a, 1]$  and  $f(1) = 0 \}.$  (9.2)

Here  $L_{\infty}[\frac{1}{2}a, 1]$  denotes the Banach space of essentially bounded, measurable functions. The eigenvalue problem  $A^*f = \lambda f$  can be rewritten as

$$h(x) = \int_{\max(x/2, a/2)}^{1} k_{\lambda}(\xi) h(\xi) d\xi$$
 (9.3)

where h is given by

$$h(x) = e^{-\lambda G(x)} g(x) f(x). \tag{9.4}$$

Notice that every solution h of (9.3) is a continuous function. Let  $h_0$  be the solution of (9.3) for  $\lambda = \lambda_0$ . Then  $h_0(x) > 0$  for  $\frac{1}{2}a \le x < 1$ . Let  $f_0$  be given by

$$f_0(x) = \frac{h_0(x)}{g(x)} \cdot e^{-\lambda_0 G(x)}$$
 (9.5)

then we have

$$A*f_0 = \lambda_0 f_0$$

$$f_0 \text{ is continuous on } \left[\frac{1}{2}a, 1\right]$$

$$f_0(x) > 0, \qquad \frac{1}{2}a \le x < 1; \qquad f_0(1) = 0.$$

Because of the algebraic simplicity of the eigenvalue  $\lambda_0$ , and the compactness of the resolvent of A (see Theorem 2.2), we can give the following decomposition of the space  $L_1[\frac{1}{2}a, 1]$ :

$$L_1\left[\frac{1}{2}a, 1\right] = \operatorname{Ker}(\lambda_0 I - A) \oplus \operatorname{Ran}(\lambda_0 I - A) \tag{9.6}$$

where  $\operatorname{Ker}(\lambda_0 I - A)$  is the null space of  $\lambda_0 I - A$  and  $\operatorname{Ran}(\lambda_0 I - A)$  denotes the range.

Let P be the projection on Ker  $(\lambda_0 I - A)$  with respect to this decomposition, then we have

$$P\phi = \int_{a/2}^{1} f_0(x) \,\phi(x) \,dx \cdot \psi_0,$$

where the pair  $f_0$ ,  $\psi_0$  is normalized by the condition

$$\int_{a/2}^{1} f_0(x) \, \psi_0(x) \, dx = 1.$$

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