DYNAMICS OF STRUCTURED POPULATIONS

Cover illustration: If in the Bell-Anderson model for cell growth (see section I.9 and chapters II - IV) the growth rate g of individual cells satisfies $g(2x) < 2g(x)$ for all x, then the size of a daughter cell depends among others on the moment of fission of her mother. In the figure a cell is represented by a square and its size x by the amount of black. A horizontal arrow denotes growth and an oblique arrow denotes growth followed by equal fission. The growth rate is given by $\dot{g}(x)=c$, where c is a constant.

DYNAMICS OF STRUCTURED POPULATIONS

ACADEMISCH PROEFSCHRIFT

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door

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aan mijn ouders
aan Marianne

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SAMENVATTING 175

DYNAMICS OF STRUCTURED POPULATIONS

H.J.A.M. Heijmans

Chapter II is a condensed version of the paper *An eigenvalue problem related to cell growth*, which will appear in Journal of Mathematical Analysis and Applications.

Chapter III has appeared in Journal of Mathematical Biology 19, 227-248, (1984).

Chapter IV will appear in *Dynamics of Physiologically Structured Populations*, J.A.J. Metz & O. Diekmann (eds), Springer Lecture Notes in Biomathematics.

Chapter V has appeared in Journal of Mathematical Biology 21, 115-143, (1984).

Introduction: History, Model-building and Mathematical Techniques

1. About the history of structured population dynamics[1].

As early as 1202 the Italian mathematician Fibonacci formulated a (discrete) model for the growth of a biological population (in fact of rabbits). His assumptions lead to the sequence 1, 1, 2, 3, 5, 8, ... which is called the *Fibonacci sequence* (see e.g. Cole (1954) for more information). Almost six hundred years later it was Thomas Malthus who shocked the scientific world (in particular the economic part of it) with his publication. *An essay on the principle of population as it affects the future improvement of society* which appeared in 1798. The (originally discrete) model of Malthus concerns the growth of the human race and can be described by the ordinary differential equation

$$\frac{dN}{dt}(t) = \gamma . N(t) \ , t \geqslant 0 \ , \tag{1.1}$$

where $N(t)$ denotes the total number of individuals at time t and γ is the population growth rate: $\gamma N = \beta N - \mu N$, where βN is the number of births and μN the number of deaths per unit of time. γ is sometimes called the *Malthusian parameter* or the *intrinsic growth constant*. The sensational message of Malthus was that, if no famines, plagues, wars or other catastrophes would occur, then the human population would increase exponentially (geometrically) whereas food supply increases at best only linearly (arithmetically). From this

1. We do certainly not pretend that this section gives a complete overview. It is only meant as a rough sketch of the lines along which population dynamics has developed, and it is very likely that we have overlooked a number of important and interesting references. For those who are interested in the history of population dynamics and demography we refer to Hutchinson (1978) and Smith and Keyfitz (1977).

he concluded that it would be impossible to banish the hunger from the world since this would automatically result in a new increase of the human population. (A reprint of Malthus' paper can be found in Malthus (1970).)

An obvious imperfection of Malthus' model is the implicit assumption that all individuals are equal, and therefore behave in the same way. (Most models concerning sexual populations only consider the female part, and contain the implicit assumption that the males are sufficiently numerous to fertilize the females. See e.g. Frederickson (1971).) A possible improvement of the model of Malthus is obtained if one distinguishes individuals according to their age. Already in 1760 (which is even before Malthus) Leonard Euler did some work in the field of age-structured population dynamics (for the original reference and an English translation of his work we refer to section 11 of Smith and Keyfitz (1977)). It was Alfred Lotka (1907) and four years later Sharpe and Lotka (1911) who gave an important new impulse to mathematical demography. They assumed that the birth and death process can be described as a linear function of the population density and they posed themselves the question:

Given the age-distribution in an isolated population at any instant of time, the 'life-curve' (life table), the rate of procreation at every age in life, and the ratio of male to female births, to find the age-distribution at any subsequent instant.

They formulated an *integral equation* (sometimes called *renewal equation)* for the function describing the number of births per unit of time which they used to make plausible that the age-distribution $n(t,a)$ at time t (i.e. $\int_{a_1}^{a_2} n(t,a)da$ is the number of individuals with age between a_1 and a_2) behaved, under reasonable assumptions, for $t \to \infty$ as

$$n(t,a) \sim C.\ e^{\gamma t} \psi(a),\ t \to \infty\ , \qquad \text{(SDT)}$$

where C is a constant and $\psi(a)$ is called the *stable age-distribution.* Usually one normalizes ψ such that

$$\int_0^\infty \psi(a)da = 1\ .$$

The letters *SDT* stand for *stable distribution theorem.* Later on in this chapter we formulate a version of (*SDT*), which applies to more general situations (see theorem 5.3). Note that the total population number $N(t)$ behaves like

$$N(t) = \int_0^\infty n(t,a)da \sim Ce^{\gamma t},\ t \to \infty\ ,$$

and this agrees with the behaviour of solutions of (1.1). The work of Lotka (1907) and Sharpe and Lotka (1911), initially subject to criticism from the mathematical community, gained universal appreciation after Feller (1941) provided a rigorous proof of (SDT).

It was probably McKendrick (1926) who formulated the age-dependent population problem as a *partial differential equation* for the age-distribution $n(t,a)$. About thirty years later Von Foerster (1959), seemingly unaware of McKendrick's work did something similar. Here we summarize some of their ideas. Let $\mu(a)$ be the probability per unit of time that an individual with age a dies, let $\beta(a)$ be the expected number of offspring per unit of time of an individual with age a, and let $\phi(a)$ be the age-distribution at time zero, then $n(t,a)$ can be computed from

$$\frac{\partial n}{\partial t}(t,a) + \frac{\partial n}{\partial a}(t,a) = -\mu(a)n(t,a), \quad t,\ a>0\ , \tag{1.2a}$$

$$n(t,0) = \int_0^\infty \beta(a)n(t,a)da \quad , \quad t>0\ , \tag{1.2b}$$

$$n(0,a) = \phi(a) \quad , \quad a>0\ . \tag{1.2c}$$

In the boundary condition (1.2b) the implicit but obvious assumption that all newborns have age zero is hidden. In the following section we shall discuss some model-building aspects in a more general context. Under some reasonable assumptions (which among others have to do with the choice of the underlying function space) one can show that (1.2) has a unique solution whose asymptotic behaviour is given by (SDT), where C depends linearly on the initial function ϕ (see for instance Webb (1984)).

One of the main applications of population dynamics is demography. But the same ideas apply to biological populations other than mankind, for instance insects, plants and micro-organisms and for such populations age often does not give a satisfactory description of an individual. These ideas must have been in the air around 1967, because at that time there appeared more or less independently a number of publications concerning population models, in which it is argued that variables different from age such as size or maturity (sometimes in combination with age) should play a role in the considerations: see Oldfield (1966), Bell and Anderson (1967), Sinko and Streifer (1967), Frederickson, Ramkrishna and Tsuchiya (1967), Rubinow (1968). In addition to the argument that age structure alone is inadequate to explain the population dynamics of certain species it is to be noted that for many species age is difficult to measure. John Van Sickle (1977) writes:

There are many ways to classify individuals other than age. Such individual physiological features as body size, dietary requirements, or chemical composition might strongly influence how individual birth and death phenomena "sum up" to give population birth and death rates.

Alternate methods of differentiating among individuals become especially important when describing non-human populations. Chronological age is difficult to assess in a great variety of plants and animals, and it is usually more *convenient to keep track of other physiological characteristics of individuals.*

Even if chronological age can be determined, it is often an unreliable indicator of an organism's sexual maturity, fertility, or its chances for future survival.

Metz and van Batenburg (1984a, 1984b, 1984c) formulated a model describing the predatory behaviour of invertebrate predators. In their model the structuring variables are *satiation* and *handling time of a prey*. In chapter V of this thesis we consider the variant of their model in which 'handling time' is omitted. Hadeler and Dietz (1984) study a host-parasite model in which age and *parasite-load* structure the host population. Edelstein (1983) has formulated a mathematical model for the dynamics of some plant-herbivore systems in which she assumes that each plant is characterized by a one-dimensional variable called *quality*. In a model for the growth of the waterflea *Daphnia magna* Kooijman (to appear) assumes that *weight* combined with *storage* gives a good description of the individual state. In the Lecture Notes by Metz and Diekmann (to appear) a lot of other interesting examples can be found.

Besides the implicit assumption of Malthus that all individuals are identical a second deficiency of his model is that it doesn't take *negative feedback-effects*, such as the exhaustion of food resources, into account. In most practical cases such environmental interactions have the effect that the population growth rate decreases if the population number increases. The Italian scientist Umberto d'Ancona writes in his book *The struggle for existence* (1954).

Since the reproductive capacity of animals and plants is normally greater than the possibilities of survival offered by the environment, the organisms in the majority of species, if they did not encounter obstacles and limitations of others kinds, would multiply with such rapidity as to overrun the earth in a short time.

Any population will therefore tend to saturate the area in which it can live, increasing the number of its individuals to the maximum which is compatible with the food available in the area. It will also tend to diffuse throughout the area until the conditions of the environment reach the limit beyond which existence is impossible, or until it encounters the opposition of competing organisms, whose competition it does not succeed in overcoming.

The Belgian scientist Pierre-Francois Verhulst (1838) recognized the deficiency in Malthus' work and he formulated a mathematical model of a growing population with an upper limit. His considerations led to the nonlinear ordinary differential equation:

$$\frac{dN}{dt}(t) = \gamma N(t).(1-N(t)/K),\ t>0\ , \tag{1.3}$$

the solutions of which are called the logistic growth curves. The solution $N(t)$ increases towards K if $0<N(0)\leqslant K$. If $N(0)>k$ then the solution $N(t)$ decreases towards K.

Gurtin and MacCamy (1974) combined the ideas contained in (1.2) and (1.3) by assuming that the functions β and μ in (1.2) depend on the total population number $N(t)$, which makes that the resulting problem is nonlinear. They proved existence and uniqueness of solutions and obtained local stability results for equilibrium distributions. Their pioneering work caused an outburst of publications in which several variants of their model are considered. We mention Haimovici (1979), Cushing (1980), Gyllenberg (1982), Prüss (1981, 1983a, 1983b) and the book of Webb (1985).

Although nonlinear age-structured models certainly play a role as an intermediate mathematical step from linear to nonlinear models, the main objection to be made against them is that the modelling assumptions describing the interaction between the population and its environment are usually rather arbitrary. A way to meet this objection is to look for one or more variables (distinguishing between individuals) which suffice to describe the interaction between the population and its environment properly (see also section 2). In chapter VI of this thesis we consider some relatively easy examples of such nonlinear models.

We end this section with a citation of William Streifer (1974) who says in his Concluding Remarks:

Realistic population models, based on the physiological, ecological and social behavior of individuals in the population, provide insight and have predictive validity. They are useful in determining optimal strategies for pest control, harvesting, preservation of species etc. Often the situations are of such complexity that their mathematical models can only be solved with the aid of large digital computers. Indeed, in such cases, the only way to gain insight into the combined effects of many interacting factors is to employ models and computers. One should, however, be careful to distinguish the real world and the mathematical model. Only those aspects of the real world which are accurately represented in the model are reflected therein and, as we are well aware, nature is exceedingly complex and rich in phenomena.

To date, realistic models have been employed with some measure of success. The objectives of workers in this field remain quite far in advance of present achievements; however, I believe the current state of understanding and mathematical capability are adequate to press forward vigorously in this very important area. The problems which remain are very interesting and difficult; the gains accruing from solving these problems could be great.

2. Some remarks on model-building

The treatise on the several aspects of model-building in this section is based on chapter III of Metz & Diekmann (to appear) where a very extensive and inspiring discussion can be found.

By a structured population we mean a population whose individuals can be distinguished from one another according to one or more physiological characteristics. Here we shall restrict ourselves to characteristic vectors which are finite dimensional (the dimension being denoted by k), although there exist situations for which an infinite dimensional vector is more appropriate. In this context 'individual' is a rather broad notion: it is not necessarily an individual in the proper sense of the word. Below we shall discuss an example in which an individual is a community and a population is a collection of communities. The incorporation of an internal structure makes it possible to relate the development of the population to the physiological processes within the individual and to describe the interaction between a population and its environment in a way which is biologically justified. In general the incorporation of such interactions gives rise to nonlinear mathematical equations.

In some cases one wants to draw conclusions about the behaviour of the individual from measurements of the population as a whole, and this might be a third reason for building in some structure. In this thesis we shall pay no attention to this so-called *inverse problem.*

The state of the individual

The first step consists of finding a suitable parameterization of the *i-state* (= state of an individual). The most simple, both practically and conceptually, is the case where the i-state contains only physiological and physical quantities which can be measured, at least in principle, e.g. size, weight, chemical composition, gut content, parasite load etc. It is obvious that one should aim at a description of the i-state which is as simple as possible. This means, among other things, that one should identify i-states which do not give rise to behavioural differences (we shall say below what is meant by the word 'behaviour'), and restrict oneselves to that part of the i-state space $\Omega \subseteq \mathbb{R}^k$ where indeed individuals can occur. We refer to section IV.6 for an example where the computation of the actual i-state space is not completely trivial.

The state of the population

By definition the *p-state* (= state of the population) is the frequency distribution over all i-states $x \in \Omega$; often we assume that at every time instant t it can be represented by a Lebesgue-integrable function $n(t,\cdot):\Omega \to \mathbb{R}$ such that for any measurable set $\Theta \subseteq \Omega$ the integral $\int_\Theta n(t,x)dx$ is the number of individuals at time t with i-state in Θ. An alternative is to represent the p-

state by a Borel measure. An example of this approach can be found in chapter V.

Processes on the individual level

As already mentioned, the incorporation of an i-state makes only sense if this makes it possible to describe the *behaviour* of the individuals. In this context we think of behaviour as everything which has some influence on the p-state, i.e. which has consequences for the number of individuals, now or in the future. First of all there is the movement of the individuals along some trajectories in the (t,x)-plane, the so-called *continuous deterministic i-movement.* This can be described by means of the ordinary differential equation

$$\frac{dx}{dt} = V(x),$$

where $V:\Omega \to \mathbb{R}^k$. Besides on x, V might also depend on environmental factors, such as food resources, the concentration of toxic chemicals etc. If x is the one-dimensional variable size or weight, then V is called the growth of an individual and in that case we rather use the symbol g.

Additionally every individual is subject to discrete chance events, like dying, reproducing and dividing. A consequence of such an event might be that locally in Ω the individual disappears. The same individual, or what has become of it by the event (in the case of division of a cell these are two daughter cells) can reappear somewhere else in Ω (in the interior $\mathring{\Omega}$ or on the boundary $\partial\Omega$). As an illustration we mention the case that the i-state is given by an individual's weight x, and that an individual reproduces (which is a discrete chance event) by giving birth to a young with weight x_0 (where $x_0 \in \partial\Omega$) in such a way reducing its own weight from x to $x - x_0$. We refer to section 3 of Heijmans (1984b) where this example has been discussed in greater detail. Often we describe these discrete chance events by means of a function of x representing the probability per unit of time that the event occurs. We refer to Diekmann, Lauwerier, Aldenberg and Metz (1983) (see also section VI.3) for a different approach.

The balance equation

The function $n(t,x)$, which describes the p-state, has to satisfy a balance equation which can be obtained straight-forward after specification of the i-state and the processes on the individual level. As a matter of fact one only has to do the bookkeeping properly. If only continuous deterministic i-movement occurs, then the equation becomes

$$\frac{\partial n}{\partial t} + \operatorname{div}(Vn) = 0,$$

as follows directly from the divergence theorem. Note that Vn is a *flux*. The disappearance and reappearance of p-mass in the interior of Ω can be described mathematically by adding a sink respectively source term at the right-hand-side of the equation. In addition the equation has to be supplied with a boundary condition for that part of the boundary at which the velocity vector V points inward. A case which is relatively important is the case that the i-state is one-dimensional and all newborns have the same i-state $x_0 \in \partial\Omega$ (for instance most age-structured models belong to this category). This can be described by a boundary condition of the form

$$V(x_0)n(t,x_0) = B(t),$$

where $B(t)$ is the number of newborns per time unit at time t. Often, B takes the form

$$B(t) = \int_{\Omega} b(x)n(t,x)dx,$$

where $b(x)$ is the reproduction rate of individuals with i-state x.

The disappearance of p-mass across (part of) the boundary $\partial\Omega$ (e.g. by instantaneous death of any individual that reaches $\partial\Omega$) is *not* describes by a boundary condition but implicitly by the choice of Ω.

Finally we note that it is sometimes necessary to impose side conditions on the solution in values of x inside Ω: this is e.g. the case if the function which describes the disappearance of p-mass from the interior of Ω contains one or more delta functions. For more details we refer to section III.6 of Metz & Diekmann (to appear).

Throughout this chapter we shall illustrate our expositions with one relatively easy example, which on the other hand, possesses sufficient features to make it interesting.

Communities subject to catastrophes

Consider a collection of communities. In our terminology this collection is called the population and an individual is a community. We assume that each community is completely characterized by the one-dimensional quantity x which we call *size* and which can be thought of as a measure for the number of members of the community. Since we assume x to be large, we may consider x a continuous variable. Every community can be struck by a catastrophe which instantaneously reduces its size from x to x/p where $p > 1$ is a constant. We assume the existence of a function $b(x)$ representing the probability per unit of time that a community with size x is struck by such a catastrophe. During periods that no catastrophes occur a community with size x grows deterministically according to

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

Let there be a threshold value $0<a<1$ such that only communities with size $x>a$ can be struck by a catastrophe, and finally assume that a community cannot grow beyond $x = 1$. This is satisfied (as we will make clear in section 4) if the following conditions on g and b are imposed.

ASSUMPTION E.1

(H_g) g is continuously differentiable on $[a/p, 1]$, $g(x)>0$ on $[1/p, 1)$, $g(1) = 0$ and $g'(1)\neq 0$.

(H_b) b is continuously differentiable on $[a/p, 1]$, $b(x) = 0$ on $[a/p, a]$ and $b(x)>0$ on $(a,1]$.

In the sequel we shall write $\alpha = a/p$, which can be interpreted as a lower-bound for the size of a community.

The model can be described by the first-order partial differential equation

$$\frac{\partial n}{\partial t}(t,x) + \frac{\partial}{\partial x}(g(x)n(t,x)) = -b(x)n(t,x) + \tag{E.1}$$

$$pb(px)n(t,px), t>0,\ \alpha<x<1,$$

where one should read $pb(px)n(t,px) = 0$, $x>1/p$. The fact that there is no influx at $x = \alpha$ is described by the boundary condition

$$n(t,\alpha) = 0,\ t\geqslant 0. \tag{E.2}$$

Here $n(t,x)$ is the so-called size distribution of the population, i.e. $\int_{x_1}^{x_2} n(t,x)dx$ is the number of individuals with size between x_1 and x_2. The first term at the right-hand size of (E.1) describes the (local) disappearance of p-mass at x, and the second term the reappearance of p-mass at x coming from px. The factor p is due to the fact that individuals reappearing in the infinitesimal interval $(x, x+dx)$ come from $(px, px + pdx)$ which is p times as large. We supplement (E.1) - (E.2) with the initial condition

$$n(0,x) = \phi(x). \tag{E.3}$$

So far we did not mention in which space(s) we analyze problems from structured population dynamics. The main reason for this omission is that this depends heavily on the specific problem under consideration. However in most cases we shall work either in the space of Lebesgue-integrable functions or in the space of continuous functions. An important alternative is provided by the space of Borel measures endowed with the weak * topology. We refer to chapter V for an example of this last alternative.

We shall study the model as described by (E.1) - (E.3) in the space $L^1[\alpha,1]$, i.e. the space of Lebesgue- integrable functions on $[\alpha,1]$.

Finally we mention that this example came to our attention by a paper of Gripenberg (1983) who considers a similar problem from a different point of view. □

Mathematical framework

A striking feature of equation (E.1) is the non-local argument px. From the mathematical point of view, it is this phenomenon which makes the problem very interesting. What we are mainly interested in, is the large-time behaviour of solutions. In particular we pose ourselves the question: 'Can we prove the existence of a *stable distribution* as in (SDT)?' It has appeared that the theory of strongly continuous semigroups (see section 4) provides a very powerful and also elegant tool in answering such a question and in the chapters III and V we shall extensively make use of known results from semigroup theory.

The model described by (E.1) - (E.3) has the special feature that it is *linear.* In many realistic models in structured population dynamics the associated mathematical problem is *nonlinear* due to interactions of the population with its environment. One might think of the situation that the food resources are limited. In such situations one should choose the i-state in accordance with these interactions. For instance, if in the case of a limited food supply, the rate of food intake depends on the body size of the individual, then this quantity should be incorporated in the i-state. In the last chapter of this thesis we shall discuss some non-linear models (whereas the chapters II - V are only concerned with linear models). We have found that concepts from *dynamical system theory* can be used to study such non-linear problems, and we shall discuss some of these concepts in section 8.

3. Some concepts from the theory of linear operators

In this section we describe a number of better or less known results from the theory of linear operators, with the emphasis on the spectral theory of closed linear operators. For a detailed exposition we refer to Dunford & Schwarz (1958) and in particular to Taylor & Lay (1979).

In what follows we assume that X is a Banach space with norm $\|\cdot\|$, and we let X^* be its (topological) dual. For $\phi\in X$ and $F\in X^*$ we denote by $<F,\phi>$ the value of F in ϕ. If L is a mapping from a linear subspace D of X into (a subspace of) X satisfying

$$L(\alpha_1\phi_1+\alpha_2\phi_2)=\alpha_1L(\phi_1)+\alpha_2L(\phi_2)\ ,$$

for all scalars α_1, α_2 (c.f. remark 3.1 below) and $\phi_1,\ \phi_2\in D$, then L is called a *linear operator* from X to X with *domain* $\mathfrak{D}(L)=D$. Instead of $L(\phi)$ we shall write $L\phi$. The *graph* $\mathcal{G}(L)$ of a linear operator L is defined by

$$\mathcal{G}(L)=\{(\phi,L\phi)\mid\phi\in\mathfrak{D}(L)\}\ .$$

A linear operator L is called *closed* if $\mathcal{G}(L)$ is a closed linear subspace of $X\times X$. A linear operator L is called *bounded* (or *continuous)* if there exists a constant $M \geqslant 0$ such that

$$\|L\phi\| \leqslant M\|\phi\|, \quad \phi \in \mathfrak{D}(L).$$

The norm $\|L\|$ of a bounded operator L is then defined by

$$\|L\| = \sup_{\phi \in \mathfrak{D}(L)} \|L\phi\| \;/\; \|\phi\| .$$

We denote by $\mathfrak{B}(X)$ the algebra of bounded linear operators L with $\mathfrak{D}(L) = X$ and image (or range) in X. From now on we shall mean a 'linear operator' if we use the word 'operator', and by a 'bounded operator' we mean an element of $\mathfrak{B}(X)$ unless otherwise stated.

REMARK 3.1 Mostly we shall assume that X is a Banach space over the real field $\mathfrak{R}$. Sometimes, however, it is necessary (for instance in spectral theory) to consider X over the complex field $\mathbb{C}$. This transition goes as follows. Let X be a Banach space over $\mathbb{R}$, then its *complexification* $X_{\mathbb{C}}$ is the Banach space consisting of all elements $\phi + i\psi$, where $\phi,\psi \in X$, with norm $\|\phi + i\psi\|_{\mathbb{C}} = \sup_{0 \leqslant \alpha \leqslant 2\pi} \|\phi \cdot \cos\alpha + \psi \sin\alpha\|$, where $\|\cdot\|$ is the norm of X. The complexification $L_{\mathbb{C}}$ of a linear operator L is given by $L_{\mathbb{C}}(\phi + i\psi) = L\phi + iL\psi$. We refer to section II.11 of Schaefer (1974) for a thorough exposition. In the sequel we shall not distinguish between X and $X_{\mathbb{C}}$, and it will turn out that this does not give rise to any confusion.

Let L be a closed operator on X with domain $\mathfrak{D}(L)$. We define the *kernel* (or *nullspace)* $\mathfrak{N}(L)$ of L as

$$\mathfrak{N}(L) = \{\phi \in \mathfrak{D}(L) \mid L\phi = 0\} .$$

The *range* (or *image)* $\mathfrak{R}(L)$ of L is the set

$$\mathfrak{R}(L) = \{L\phi \mid \phi \in \mathfrak{D}(L)\} .$$

The *spectrum* $\sigma(L)$ of L consists of all complex values $\lambda \in \mathbb{C}$ for which $\lambda I - L$ does not possess a bounded inverse, i.e. $(\lambda I - L)U = U(\lambda I - L) = I$ does not have a solution $U \in \mathfrak{B}(X)$. Here I represents the identity operator on X. The spectrum of L can be considered the union of three disjunct subsets:

$$\sigma(L) = P\sigma(L) \cup R\sigma(L) \cup C\sigma(L) .$$

Here $P\sigma(L)$ is the *point spectrum* of L, containing all eigenvalues, i.e. $\lambda \in P\sigma(L)$ iff $\dim \mathfrak{N}(\lambda I - L) > 0$. (For a subspace Y of X we denote by $\dim Y$ its dimension.) The *residual spectrum* $R\sigma(L)$ of L *contains* all complex values λ satisfying $\dim \mathfrak{N}(\lambda I - L) = 0$ and $\mathfrak{R}(\lambda I - L) \neq X$. Finally λ belongs to the *continuous spectrum* $C\sigma(L)$ of L iff $\dim \mathfrak{N}(\lambda I - L) = 0$, $\mathfrak{R}(\lambda I - L) \neq X$ and $\overline{\mathfrak{R}(\lambda I - L)} = X$. The set $\rho(L) = \mathbb{C} \setminus \sigma(L)$ is called the *resolvent set*. For $\lambda \in \rho(L)$ the inverse $R(\lambda, L) = (\lambda I - L)^{-1}$ exists and is called the *resolvent operator*. If L is a bounded operator then $\sigma(L)$ is a compact nonempty subset of $\mathbb{C}$ and in this case the *spectral radius* $r(L)$ of L is defined by

$$r(L) = \sup\{|\lambda| \mid \lambda \in \sigma(L)\}.$$

The following relation holds

$$r(L) = \lim_{n\to\infty} \|L^n\|^{\frac{1}{n}}. \tag{3.1}$$

An important subset of the spectrum of a closed operator is the so-called *Browder-essential spectrum* $\sigma_{ess}(L)$ (see Browder (1961)):

DEFINITION Let L be a closed linear operator. The complex value λ belongs to $\sigma_{ess}(L)$ if at least one of the following conditions is satisfied:
(i) λ is a limit point of $\sigma(L)$
(ii) $\mathcal{R}(\lambda I - L)$ is not closed
(iii) $\dim \bigcup_{k\geq 1} \mathcal{N}((\lambda I - L)^k) = \infty$.

In the literature (see e.g. Kato (1976)) several other definitions of 'essential spectrum' are given, and all of these definitions yield subsets of $\mathbb{C}$ which are contained in $\sigma_{ess}(L)$. We refer to Schappacher (1983) for an overview. The following result proved by Browder (1961) gives a nice characterization of the values $\lambda \in \sigma(L) \setminus \sigma_{ess}(L)$.

THEOREM 3.2 *Let L be a closed, linear operator with densely defined domain (i.e.* $\overline{\mathcal{D}(L)} = X$), *and let* $\lambda_0 \in \sigma(L) \setminus \sigma_{ess}(L)$. *Then* λ_0 *is a pole of the resolvent* $R(\lambda,L)$ *with a residue of finite rank. If p is the order of the pole, then*

$$X = \mathcal{N}((\lambda_0 I - L)^p) \oplus \mathcal{R}((\lambda_0 I - L)^p).$$

Let us here consider the situation described by this theorem more closely. Suppose that $\lambda_0 \in \sigma(L)$ is a pole of $R(\lambda,L)$ of order p. Then we have the following Laurent expansion of $R(\lambda,L)$ in powers of $\lambda - \lambda_0$ (e.g. section V.10 of Taylor & Lay (1979)):

$$R(\lambda,L) = \sum_{k=-p}^{\infty} (\lambda-\lambda_0)^k B_k,$$

where the operators B_k are given by

$$B_k = \frac{1}{2\pi i} \int_{\Gamma} \frac{R(\lambda,L)}{(\lambda-\lambda_0)^{k+1}}\, d\lambda,$$

and where Γ is a counter-clockwise circle $|\lambda-\lambda_0| = \delta$ with δ so small that $\lambda \in \sigma(L)$, $\lambda \neq \lambda_0$ implies that $|\lambda-\lambda_0| \geq \delta_1$, for some $\delta_1 > \delta$. The residue B_{-1} of $R(\lambda,L)$ in $\lambda = \lambda_0$ defines a projection on X (i.e. $B_{-1}^2 = B_{-1}$) with:

$$\mathcal{R}(B_{-1}) = \mathcal{N}((\lambda_0 I - L)^p),\ \mathcal{R}(I - B_{-1}) = \mathcal{R}((\lambda_0 I - L)^p)$$

(actually B_{-1} is the spectral projection associated with the spectral set $\{\lambda_0\}$).

ʼalues $\lambda \in \sigma(L) \setminus \sigma_{ess}(L)$ are sometimes called *normal eigenvalues.* If) then $\sigma_{ess}(L) \neq \emptyset$, and we can define the essential spectral radius ›y

$$r_{ess}(L) = \sup\{|\lambda| \; |\lambda \in \sigma_{ess}(L)\} . \tag{3.2}$$

nt out that for most other definitions of the 'essential spectrum' g in the literature, definition (3.2) yields the same result. In order to ıaracterization of $r_{ess}(L)$ like (3.1) we need some further definitions.

bounded subset V of X we define the *(Kuratowski-) measure of non-ıess* $\alpha(V)$ by (see e.g. Nussbaum (1970), Martin (1976)):

inf$\{d > 0|$ there exist finitely many subsets $V_1,...,V_n$ of X such that the · of V_i is less than d and $V \subset \bigcup_{i=1}^{n} V_i\}$.

e easily seen that $\alpha(V) = 0$ if and only if $\overline{V}$ is compact. The measure ompactness $|L|_\alpha$ of an operator $L \in \mathcal{B}(X)$ is defined by:

$|L|_\alpha = inf\{m \geqslant 0 \mid \alpha(L(V)) \leqslant m \cdot \alpha(V)$ for all bounded subsets V of $X\}$.

ɔn III.8 of this thesis we use a notation different from $\alpha(\cdot)$ and $|\cdot|_\alpha \cdot)$ he following basic result we refer to Nussbaum (1970) or Martin

ʒ.3
$\leqslant \|L\|, \; L \in \mathcal{B}(X)$
$+ L_2|_\alpha \leqslant |L_1|_\alpha + |L_2|_\alpha, \; L_1, L_2 \in \mathcal{B}(X)$.
$+ C|_\alpha = |L|_\alpha$, $L, C \in \mathcal{B}(X)$ *and* C *compact.*

t result implies that $|C|_\alpha = 0$ if C is compact. It follows that $|\cdot|_\alpha$ a semi-norm on $\mathcal{B}(X)$ (e.g. Nussbaum (1970)). The following nice rization of $r_{ess}(L)$ is due to Nussbaum (1970).

$$\cdot_{ess}(L) = \lim_{n \to \infty} |L^n|_\alpha^{\frac{1}{n}} , L \in \mathcal{B}(X) . \tag{3.3}$$

nsequence of lemma 3.3.c we have that $r_{ess}(C) = 0$ and therefore $= \{0\}$ if C is a compact operator.

.BSTRACT CAUCHY PROBLEM AND STRONGLY CONTINUOUS SEMIGROUPS ᴧTORS

· a system of which the evolution in time is described by an initial ɔblem (or Cauchy problem) of the form

$$\frac{du}{dt}(t) = Au(t), \; t > 0 \text{ and } u(0) = \phi , \tag{4.1}$$

where $A:\mathcal{D}(A)\to X$ is a closed, linear operator with domain $\mathcal{D}(A)\subset X$, X being a Banach space and $\phi\in X$. We call $u:[0,\infty)\to X$ a (strong) solution if

(i) u is continuous for $t \geq 0$,

(ii) u is continuously differentiable for $t > 0$,

(iii) $u(t)\in \mathcal{D}(A)$, $t > 0$,

(iv) (4.1) is satisfied.

Note that it follows from (i) and (iii) that (4.1) cannot have a strong solution if $\phi \notin \overline{\mathcal{D}(A)}$.

If for every $\phi \in \mathcal{D}(A)$ the system (4.1) has a unique solution $u(t;\phi)$ depending continuously on the initial function ϕ then we can associate an operator family $\{T(t)\}_{t\geq 0}$ with solutions in the following way

$$T(t)\,\phi = u(t;\phi),\ t\geq 0,\ \phi \in \mathcal{D}(A)\,. \tag{4.2}$$

In what follows we shall assume that A is densely defined, i.e. $\overline{\mathcal{D}(A)} = X$. Then we can extend $T(t)$ to X and $T(t) \in \mathcal{B}(X)$, $t\geq 0$. One sees immediately that

(I) $T(0) = I$.

From $u(t;u(s;\phi)) = u(t+s;\phi)$, $\phi \in \mathcal{D}(A)$ it follows

(II) $T(t+s) = T(t)T(s)$, $t,s\geq 0$,

i.e. $\{T(t)\}_{t\geq 0}$ satisfies the semigroup property. From the fact that the solution $u(t;\phi)$ of (4.1) satisfies $u(0;\phi) = \phi$ it follows that

(III) $\lim_{t\downarrow 0} T(t)\phi = \phi$, $\phi \in X$,

i.e. $\lim_{t\downarrow 0} T(t) = I$ with respect to the strong operator topology. A family of bounded linear operators $\{T(t)\}_{t\geq 0}$ on X is called a *strongly continuous semigroup of operators* (also C_0- *semigroup)* if (I), (II) and (III) are satisfied. The well-known book by Hille & Phillips (1957) is the oldest reference containing a systematic and extensive exposition on semigroups of operators. We also refer to Ladas & Lakshmikantham (1972), and, of more recent date, Davies (1980), Fattorini (1983) and Pazy (1983).

The closed, densely defined operator A from (4.1) is called the *infinitesimal generator* of the semigroup $\{T(t)\}_{t\geq 0}$ defined by (4.2). In general the generator (we shall mostly omit the prefix 'infinitesimal') can be determined from the semigroup in the following way. Let $\{T(t)\}_{t\geq 0}$ be a strongly continuous semigroup, let $\mathcal{D}$ be the subspace of X such that for $\phi\in\mathcal{D}$ the expression $\lim_{t\downarrow 0}\frac{1}{t}\,(T(t)\phi-\phi)$ exists, then

$$A\phi = \lim_{t \downarrow 0} \frac{1}{t}(T(t)\phi - \phi), \quad \phi \in \mathfrak{D}(A) \overset{def}{=} \mathfrak{D}\,. \tag{4.3}$$

We summarize some of these results in the following theorem.

THEOREM 4.1 *Let $\{T(t)\}_{t \geq 0}$ be a strongly continuous semigroup of operators on X and let A be its infinitesimal generator whose domain is $\mathfrak{D}(A)$, then the following holds:*

a) $\overline{\mathfrak{D}(A)} = X$ *and A is a closed operator.*

b) *If $\phi \in \mathfrak{D}(A)$, then $T(t)\phi$ belongs to $\mathfrak{D}(A)$ for $t \geq 0$, $T(t)\phi$ is differentiable with respect to t for $t > 0$ and $\frac{d}{dt}(T(t)\phi) = AT(t)\phi = T(t)A\phi$, $t > 0$.*

c) *The Cauchy problem (4.1) with $\phi \in \mathfrak{D}(A)$ has a unique solution $u(t) = T(t)\phi$, $t \geq 0$.*

If $\phi \in X$, $\phi \notin \mathfrak{D}(A)$, then the initial value problem (4.1) does not have a strong solution if the semigroup $\{T(t)\}_{t \geq 0}$ is not differentiable (see section 2.4 of Pazy (1983)). In this case the function $u(t) = T(t)\phi$, $t \geq 0$, is called a *mild solution* of (4.1) (e.g. section 4.1 of Pazy (1983)).

From the last conclusion of theorem 4.1 it follows immediately that a closed operator with densely defined domain can generate at most one strongly continuous semigroup.

It should be clear now that in practice it is rather important to be able to decide whether or not a closed operator with densely defined domain generates a strongly continuous semigroup. A necessary and sufficient condition is provided by the *Hille-Yosida-Phillips theorem.*

THEOREM 4.2 *A closed operator A with densely defined domain $\mathfrak{D}(A)$ is the generator of a strongly continuous semigroup $\{T(t)\}_{t \geq 0}$ if and only if there exist real numbers ω and M, $M \geq 0$ such that for all $\lambda > \omega$ we have $\lambda \in \rho(A)$ and $\|R(\lambda, A)^n\| \leq M / (\lambda - \omega)^n$, $n \in \mathbb{N}$.*

As to the linear systems describing the dynamics of structured populations we are interested in, this criterium turns out to be rather useless. The following result conforms better to our requirements.

THEOREM 4.3 *Let the closed operator B with dense domain $\mathfrak{D}(B)$ be the generator of a strongly continuous semigroup and let C be a bounded operator. Then the closed operator $A = B + C$ with domain $\mathfrak{D}(A) = \mathfrak{D}(B)$, also generates a strongly continuous semigroup.*

Pazy (1983) proves this result by verifying the conditions in theorem 4.2. An alternative, more constructive method is the following. Consider the Cauchy problem

$$\frac{du}{dt}(t) = Au(t) = Bu(t) + Cu(t), u(0) = \phi \in \mathfrak{D}(A)\,. \tag{4.4}$$

Let $\{T_0(t)\}_{t\geq 0}$ be the semigroup generated by B. Regarding $Cu(t)$ as an inhomogeneous term, a straight-forward application of the variation-of-constants formula yields the integral equation

$$u(t) = T_0(t)\phi + \int_0^t T_0(t-s)Cu(s)\,ds,\ t\geq 0\,, \tag{4.5}$$

and there exists a one-to-one relation between solutions of the differential equation (4.4) and the integral equation (4.5). Defining $T_i(t),\ t\geq 0,\ i = 0,1,2,\cdots$ inductively by

$$T_{i+1}(t)\phi = \int_0^t T_0(t-s)CT_i(s)\phi\,ds,\ t\geq 0,\ i = ,1,2,\cdots\ .$$

we may write the solution of (4.5) as an infinite series

$$u(t) = \sum_{i=0}^{\infty} T_i(t)\phi,\ t\geq 0\ , \tag{4.6}$$

and the semigroup $T(t)$ generated by A is given by

$$T(t) = \sum_{i=0}^{\infty} T_i(t),\ t\geq 0\ .$$

It can be shown by making some straightforward estimates (see section 3.1 of Pazy (1983)) that this series converges in the uniform operator topology, uniformly on bounded t-intervals.

Communities subject to catastrophes

We shall now apply the theory of strongly continuous semigroups as described above to our example. For that purpose we reformulate (E.1) - (E.3) as an abstract Cauchy problem

$$\frac{dn}{dt}(t) = An(t),\ n(0) = \phi\ . \tag{E.4}$$

The underlying Banach space is $L^1[\alpha,1]$, and the differential operator A is given by

$$(A\psi)(x) = -\frac{d}{dx}(g(x)\psi(x)) - b(x)\psi(x) + pb(px)\psi(px)\,, \tag{E.5}$$

(where one should read $pb(px)\psi(px) = 0,\ x > 1/p$) for all ψ in the domain $\mathfrak{D}(A) \subset L^1[\alpha,1]$ of A given by

$$\mathfrak{D}(A) = \{\psi\in L^1[\alpha,1] \mid g\psi \text{ is absolutely continuous and } \psi(\alpha) = 0\}\ . \tag{E.6}$$

It is not difficult to verify that A is a closed operator with densely defined domain. In order to show that indeed A generates a strongly continuous semigroup, we write

$$A = B + C\ , \tag{E.7}$$

where B is the closed operator given by

$$(B\psi)(x) = -\frac{d}{dx}(g(x)\psi(x)) - b(x)\psi(x)\ , \tag{E.8}$$

for $\psi \in \mathcal{D}(B) = \mathcal{D}(A)$, and where the bounded operator C is given by

$$(C\psi)(x) = pb(px)\psi(px)\ , \tag{E.9}$$

for all $\psi \in L^1[\alpha,1]$. Further we define

$$E(x) = \exp(-\int_\alpha^x \frac{b(\xi)}{g(\xi)}\,d\xi),\ \alpha \leqslant x \leqslant 1\ , \tag{E.10}$$

and for $\alpha \leqslant y \leqslant x \leqslant 1$ we can interprete $E(x)\ /\ E(y)$ as the chance that a community with size y reaches size x without being struck by a catastrophe. From assumptions E.1 we obtain that $E(1) = 0$, which supports our assumption that a community cannot grow beyond $x = 1$. Finally we define

$$G(x) = \int_\alpha^x \frac{d\xi}{g(\xi)}\ ,\ \alpha \leqslant x < 1\ , \tag{E.11}$$

$$X(t,x) = G^{-1}(t + G(x))\ ,\ t + G(x) > 0,\ \alpha \leqslant x < 1\ . \tag{E.12}$$

$G(x)$ can be interpreted as the time it takes to grow from size α to x assumed that no catastrophes occur meanwhile. Note that $G(x) \rightarrow \infty$ as $x \uparrow 1$. In (E.12), G^{-1} denotes the inverse of G. We can interprete $X(t,x)$ as the size of a community at time t given that its size at time zero was x, and it is the solution of the ordinary differential equation

$$\frac{d}{dt}X(t,x) = g(X(t,x))\ ,\ X(0,x) = x\ .$$

A straightforward calculation shows that B is the generator of the strongly continuous semigroup $\{T_0(t)\}_{t \geqslant 0}$ given by

$$(T_0(t)\phi)(x) = \frac{E(x)}{g(x)} \cdot \frac{g(X(-t,x))}{E(X(-t,x))} \cdot \phi(X(-t,x)), \tag{E.13}$$

$$t \geqslant 0,\ \alpha \leqslant x \leqslant 1\ ,$$

where one should read

$$(T_0(t)\phi)(x) = 0,\ \text{if}\ X(-t,x) \leqslant \alpha\ \ (i.e.\ t \geqslant G(x))\ .$$

We are ready to apply theorem 4.3, which says that A generates a strongly continuous semigroup $\{T(t)\}_{t \geqslant 0}$. The integral equation (4.5) takes the following form:

$$n(t,x) = \frac{E(x)}{g(x)} \cdot \left\{ \frac{g(X(-\tau,x))}{E(X(-\tau,x))} \cdot \phi(X(-t,x)) + \right. \tag{E.14}$$

$$\left. \int_0^t \frac{g(X(-\tau,x))}{E(X(-\tau,x))} \cdot pb(pX(-\tau x)) \cdot n\ (t-\tau, pX(-\tau,x))d\tau \right\}\ ,$$

with the same convention as in (E.13). As in (4.6) we can write the solution as a series.

$$n(t) = \sum_{i=1}^{\infty} n_i(t) = \sum_{i=1}^{\infty} T_i(t)\,\phi,\ t \geqslant 0\,, \tag{E.15}$$

where $n_i(t) = T_i(t)\phi$, $t \geqslant 0$, $i = 0,1,2,\cdots$. This expansion is called the generation expansion due to the following biological interpretation. $n_0(t)$ represents all communities present at at time zero which have not yet been struck by a catastrophe. Inductively $n_{i+1}(t)$ represents all communities which belonged to the i'th generation at some earlier time, but have been struck once by a catastrophe during the time elapsed.

So we have proved the following result.

THEOREM E.2 *The closed operator A given by $(E.5)-(E.6)$ generates a strongly continuous semigroup $\{T(t)\}_{t\geqslant 0}$.* □

5. Spectral properties of strongly continuous semigroups of operators and stable distributions

Throughout this section we assume that $\{T(t)\}_{t\geqslant 0}$ defines a strongly continuous semigroup of bounded operators on a Banach space X generated by the closed densely defined operator A. There exist real constants ω, M, where $M \geqslant 1$ such that (c.f. theorem I.2.2 of Pazy (1983))

$$\|T(t)\| \leqslant Me^{\omega t}\,,\ t \geqslant 0\,. \tag{5.1}$$

As a matter of fact the semigroup $\{T(t)\}_{t\geqslant 0}$ of theorem 4.2 satisfies (5.1) with the same constants M,ω. We define the t-independent quantity

$$\omega_0 = \omega_0\,(T(t)) = \inf_{t>0} \frac{1}{t} \log \|T(t)\|$$

with the convection that $\log 0 = -\infty$. Then (see Hille & Phillips (1957), section 10.2):

$$\omega_0(T(t)) = \lim_{t\to\infty} \frac{1}{t} \log \|T(t)\|\,. \tag{5.2}$$

We call $\omega_0(T(t))$ the *type* or *growth bound* of the semigroup $T(t)$. An easy calculation shows that the spectral radius of $T(t)$ is given by

$$r(T(t)) = e^{\omega_0 t}\ ,\ t \geqslant 0\,, \tag{5.3}$$

with the convention $e^{\inf} = 0$. The following result follows easily from (5.2).

LEMMA 5.1 *For all $\omega > \omega_0(T(t))$ there is a constant $M(\omega) \geqslant 1$ such that $\|T(t)\| \leqslant M(\omega)e^{\omega t}\ ,\ t \geqslant 0$.*

Analogous to (5.2) we can properly define

$$\omega_{ess} = \omega_{ess}(T(t)) = \inf_{t>0} \frac{1}{t} \log |T(t)|_\alpha = \lim_{t\to\infty} \frac{1}{t} \log |T(t)|_\alpha . \tag{5.4}$$

Again ω_{ess} does not depend on t. We call $\omega_{ess}(T(t))$ the *essential type* or *essential growth bound* of the semigroup $\{T(t)\}_{t\geq 0}$. As an analogon of (5.3) we have

$$r_{ess}(T(t)) = e^{\omega_{ess} t} , t \geq 0 . \tag{5.5}$$

We also have an analogon of lemma 5.1 which we shall not formulate explicitly. The quantity ω_{ess} is, to the knowledge of the author, first defined by Prüss (1981) in the context of age-structured population dynamics. A rather detailed exposition can be found in the book of Webb (1985).

It follows immediately from lemma 3.3a that

$$\omega_{ess}(T(t)) \leq \omega_0 (T(t)) . \tag{5.6}$$

It follows from lemma 3.3c that $\omega_{ess}(T(t)) = -\infty$ if $T(t)$ is compact after finite time, and in that case we have strict inequality in (5.6) if one can show that $\omega_0(T(t)) > -\infty$ which is rather easy in many applications. Later we shall mention weaker conditions on $T(t)$ implying the strict inequality. First we shall return to our example.

Communities subject to catastrophes

If the initial function ϕ in (E.3) satisfies $\phi(x) \geq 0$ almost everywhere on $[\alpha,1]$, then the solution $n(t,\cdot) = T(t)\phi$, $t \geq 0$, has the same property and the following equalities hold (as one obtains by integration of (E.1)).

$$\|T(t)\phi\| = \|n(t)\| = \int_0^1 n(t,x)\mathrm{d}x = \int_0^1 \phi(x)\mathrm{d}x = \|\phi\|, \ t \geq 0 .$$

The positivity of the semigroup $\{T(t)\}_{t\geq 0}$ yields that for arbitrary $\phi \in L^1[\alpha,1]$:

$$\|T(t)\,\phi\,\| \leq \|\phi\,\|, \ t \geq 0,$$

and we conclude that

$$\|T(t)\| = 1, \ t \geq 0,$$

and this yields

$$\omega_0(T(t)) = 0 . \tag{E.16}$$

To estimate $\omega_{ess}(T(t))$ we have to work harder. Let

$$U(t) = \sum_{i=1}^{\infty} T_i(t), \ t \geq 0 ,$$

where $T_i(t)$ is given by (E. 15) . Suppose we can show that $T_1(t)$ is compact for $t \geq 0$, then $T_i(t)$ is compact, $i \geq 2$, $t \geq 0$ since

$$T_{i+1}(t) = \int_0^t T_0(t-s)\, C\, T_i(s)\mathrm{d}s\,,\; t \geqslant 0\,,$$

and the space of compact operators forms a *closed* ideal in the algebra of bounded operators on $L^1[\alpha,1]$. An easy calculation using (E.13) and (E.14) shows that

$$(T_1(t)\phi)(x) = p\cdot\frac{E(x)}{g(x)}\int_0^t \frac{g(X(-\tau,x))}{E(X(-\tau,x))}\cdot(\frac{bE}{g})(pX(-\tau,x))\cdot$$

$$(\frac{g}{E}\cdot\phi)(X(-t+\tau,\, pX(-\tau,x)))d\tau\,.$$

In this expression we substitute for τ

$$\xi = X(-t\; +\; \tau, pX(-\tau,x))\,.$$

It is not difficult to prove from this that $T_1(t)$ is compact for $t \geqslant 0$ if $d\xi\,/\,d\tau \neq 0$ for all relevant values of t,τ and x. Differentiation of ξ with respect to τ yields:

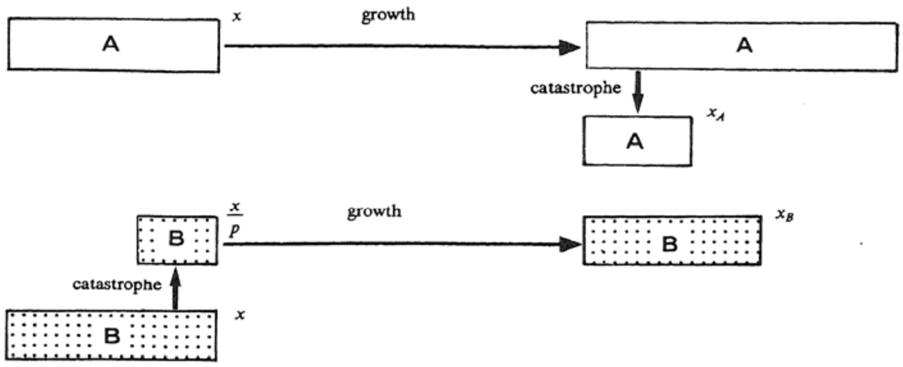
$$\frac{1}{g(\xi)}\cdot\frac{d\xi}{d\tau} = 1 - \frac{pg(z)}{g(pz)}$$

where $z = X(-\tau,x)$. Therefore compactness follows if we impose the following condition on g.

ASSUMPTION E.3

$$g(px) < pg(x),\; x\in[\alpha,\frac{1}{p}]\,.$$

We can give the following biological interpretation of this assumption (see also the figure below). Consider two communities both having size x at time zero. The first community is struck immediately by a catastrophe reducing its size to $x\,/p$. There-upon this community grows during a time t and thus reaches size $X_A = X(t,x\,/p)$. The second community starts growing first and is struck by a catastrophe at time t and thus obtains size $X_B = X(t,x)\,/\,p$. Now assumption E.3 guarantees that $X_B < X_A$. Therefore the combination of growth and catastrophes provides a dispersion mechanism for community size. An important example for which assumption E.3 is never satisfied is $g(x) = cx,\, c>0$. However this g does not obey assumption E.1. (H_g).



We refer to section III.5 and section III.8 where a similar assumption is discussed. From now on we assume that assumption E.3 is satisfied.

THEOREM E.4 *The operator $U(t)$ is compact for all $t \geqslant 0$.*

A combination of (5.4), lemma 3.3, theorem E.4 and (5.2) yields

$$\omega_{ess}(T(t)) = \lim_{t\to\infty} \frac{1}{t} \log |T(t)|_\alpha = \lim_{t\to\infty} \frac{1}{t} \log|T_0(t)|_\alpha \leqslant$$

$$\lim_{t\to\infty} \frac{1}{t} \log\|T_0(t)\| = \omega_0(T_0(t)) .$$

A straightforward computation (c.f Heijmans (1984b)) shows that there is a constant $M > 0$ such that

$$\|T_0(t)\| \leqslant Me^{-b(1)t} , \quad t \geqslant 0 ,$$

hence $\omega_0(T_0(t)) \leqslant -b(1)$ and therefore

$$\omega_{ess}(T(t)) \leqslant - b(1) . \tag{E.17}$$

So we have proved that in our example

$$\omega_{ess}(T(t)) < \omega_0(T(t)) . \tag{E.18}$$

Below it is explained that this is one of the two conditions which are together sufficient to prove the existence of a stable size distribution (compare (SDT) in section 1). □

The strict inequality in (5.6) is of great importance if one wants to determine the spectrum of $T(t)$. This spectrum plays a major role in the characterization of the large time behaviour of solutions of (4.1) (c.f. (SDT)). The spectral mapping theorems below, relating the spectrum of the strongly continuous semigroup to the spectrum of its generator are rather important in this respect. We shall use the following notation. For $V \subseteq \mathbf{C}$ we let $e^{tV} = \{e^{t\lambda} \mid \lambda \in V\}$.

Then

$$e^{tP\sigma(A)} = P\sigma(T(t))\setminus\{0\},\ t \geqslant 0 \tag{5.7.a}$$

$$e^{tR\sigma(A)} = R\sigma(T(t))\setminus\{0\},\ t \geqslant 0 \tag{5.7.b}$$

$$e^{tC\sigma(A)} \subset C\sigma(T(t))\setminus\{0\},\ t \geqslant 0 \tag{5.7.c}$$

and the inclusion in (5.7.c) may be strict. For the essential spectrum a similar result as in (5.7c) holds.

$$e^{t\sigma_{ess}(A)} \subset \sigma_{ess}(T(t))\setminus\{0\},\ t \geqslant 0\,. \tag{5.8}$$

A proof of (5.7) can be found in Pazy (1983) whereas (5.8) was proved by Webb (1985). Finally we define the spectral bound $s(A)$ of the generator A by

$$s(A) = \begin{cases} \sup\{\mathrm{Re}\,\lambda|\ \lambda\in\sigma(A)\}, & \sigma(A) \neq \varnothing, \\ -\infty, & \sigma(A) = \varnothing. \end{cases} \tag{5.9}$$

and obviously $s(A) = \omega_0(T(t))$ if $\sigma(T(t))\setminus\{0\} = e^{t\sigma(A)}$. In general, however, this relation is not satisfied (see also section 7), but one can show that

$$\omega_0(T(t)) = \max\{s(A),\ \omega_{ess}(T(t))\}\,. \tag{5.10}$$

This relation can be found in Prüss (1981) and Webb (1985) in a slightly different formulation.

Now we shall formulate two conditions which together are sufficient to prove that there exists a *stable distribution* of (4.1) (here the use of the word 'distribution' is motivated by the kind of problems we are interested in). A stable distribution can be defined as an element $\overline{u}\in X$ such that for every solution $u(t;\phi)$ of (4.1) the following holds: there is a constant c such that $e^{-\lambda t}u(t;\phi)\to c\overline{u}$ as $t\to\infty$. Here λ is a complex value not depending on ϕ. In most of the applications λ is real.

$[A_1]$ A has a strictly dominant eigenvalue $\lambda_d\in\mathbb{R}$ (i.e. $Re\ \lambda < \lambda_d$ if $\lambda \in \sigma(A)$ and $\lambda \neq \lambda_d$) which is algebraically simple.

$[A_2]$ $\omega_{ess}(T(t)) < \omega_0(T(t))$.

Let us suppose that $[A_1]$ and $[A_2]$ are satisfied. Then (5.10) yields that $\lambda_d = s(A) = \omega_0(T(t))$. Since $\lambda_d > \omega_{ess}\ (T(t))$, (5.8) guarantees that $\lambda_d \in \sigma(A)\ /\ \sigma_{ess}(A)$, and now theorem 3.2 and the algebraic simplicity of λ_d imply.

$$X = \mathcal{N}(\lambda_d I - A) \oplus \mathcal{R}(\lambda_d I - A)\,, \tag{5.11}$$

where $\dim \mathcal{N}(\lambda_d I - A) = 1$. Let $\phi_d \in X$ and $F_d \in X^*$ satisfy

$$A\phi_d = \lambda_d\phi_d\ ,\ A^*\ F_d = \lambda_d\ F_d\ ,\ \langle F_d, \phi_d\rangle = 1\,, \tag{5.12}$$

then the projection P_d on $\mathcal{N}(\lambda_d I - A)$ associated with the decomposition (5.11) of X is given by

$$P_d\,\phi = \langle F_d, \phi\rangle \cdot \phi_d\ ,\quad \phi \in X\ . \tag{5.13}$$

REMARK 5.2. P_d equals the residue B_{-1} of $R(\lambda, A)$ in $\lambda = \lambda_d$ (see section 3), i.e. $P_d = \lim\limits_{\lambda \to \lambda_d} (\lambda - \lambda_d) R(\lambda, A)$.

Suppose there exists a sequence $\{\lambda_n\}_{n \in \mathbb{N}}$, such that $\lambda_n \in \sigma(A)$, $\mathrm{Re}\lambda_{n+1} > \mathrm{Re}\,\lambda_n$ and $\mathrm{Re}\,\lambda_n \to \lambda_d$, $n \to \infty$. Let $t > 0$ be fixed. From (5.7) we conclude that $e^{\lambda_n t} \in \sigma(T(t))$, $|e^{\lambda_{n+1} t}| > |e^{\lambda_n t}|$ and $|e^{\lambda_n t}| \to e^{\lambda_d t}$, $n \to \infty$. This implies that $\sigma(T(t))$ contains a limit point on the circle $\{z \in \mathbb{C} \mid |z| = e^{\lambda_d t}\}$ and therefore

$$\sigma_{ess}(T(t)) \cap \{z \in \mathbb{C} \mid |z| = e^{\lambda_d t}\} \neq \emptyset\ ,$$

from which we conclude that $\omega_{ess}(T(t)) \geq \lambda_d = \omega_0(T(t))$, contradicting $[A_2]$. This proves that there exists an $\eta > 0$ such that

$$\lambda_d - \eta \geq \omega_{ess}(T(t)) \text{ and } \mathrm{Re}\lambda \leq \lambda_d - \eta \text{ if } \lambda \in \sigma(A),\ \lambda \neq \lambda_d\ . \tag{5.14}$$

THEOREM 5.3 *Assume* $[A_1]$ *and* $[A_2]$. *There exists a constant* $\eta > 0$ *such that for all* $\epsilon \in (0,\eta)$ *there is a constant* $M(\epsilon) \geq 1$ *such that*

$$\|T(t)\phi - e^{\lambda_d t}\, P_d\,\phi\,\| \leq M(\epsilon)\, e^{(\lambda_d - \epsilon)t}\ \|\phi\|,\ t \geq 0,\ \phi \in X\ .$$

We point out that this result is stronger than (SDT) since it gives in addition that the rate of convergence is exponential. In this case ϕ_d given by (5.12) is the stable distribution. (We note that ϕ_d is unique up to a multiplicative constant.)

PROOF OF THEOREM 5.3 We define $Z = \mathcal{R}(\lambda_d I - A)$ and denote by $T_Z(t)$ the restriction of $T(t)$ to Z. It follows immediately that $\omega_{ess}(T_Z(t)) = \omega_{ess}(T(t))$ and $\omega_0(T_Z(t)) \leq \lambda_d - \eta$, where η is given by (5.14). Actually we have $\sigma(T_Z(t)) = \sigma(T(t)) \setminus \{e^{\lambda_d t}\}$. Now lemma 5.1 states that for all $\epsilon \in (0,\eta)$ there exists an $M(\epsilon) \geq 1$ such that

$$\|T_Z(t)\phi\| \leq M(\epsilon) e^{(\lambda_d - \epsilon)t}\ \|\phi\|,\ t \geq 0,\ \phi \in Z\ .$$

Let $\phi \in X$, then $\phi = P_d\phi + (I - P_d)\phi$, hence

$$T(t)\phi = T(t)P_d\phi + T_Z(t)(I - P_d)\phi. \text{ Since } T(t)P_d\phi = e^{\lambda_d t}\, P_d\phi\ ,$$

we find

$$\|T(t)\phi - e^{\lambda_d t}\, P_d\phi\| = \|\, T_Z(t)(I - P_d)\,\phi\,\| \leq$$
$$M(\epsilon)e^{(\lambda_d - \epsilon)t}\ \|(I - P_d)\,\phi\,\| \leq M(\epsilon)e^{(\lambda_d - \epsilon)t}\ \|\,\phi\,\|\ .\square$$

In our example $[A_2]$ is indeed satisfied (c.f. (E.18)) . In general, one might say that some kind of compactness property of $T(t)$ has to be established in order to prove $[A_2]$. A useful sufficient condition is:

> $T(t) = T_0(t) + U(t)$, $t \geqslant 0$, $U(t)$ is compact after finite time and there exist constants $\epsilon, C > 0$ such that $\|T_0(t)\| \ / \ \|T(t)\| \leqslant Ce^{-\epsilon t}$ after finite time.

To prove $[A_1]$ at least two closely related methods are available

1. Positive operator theory
In models from structured population dynamics $T(t)\phi$ represents the p-state (see section 2) at time t, and this is a distribution over all i-states. Therefore $T(t)\phi$ is positive (in a sense to be specified later). The resolvent operator $R(\lambda,A)$ can be obtained from the semigroup in the following way

$$R(\lambda,A)\phi = \int_0^\infty e^{-\lambda t}\, T(t)\phi dt \ , \ \ \mathrm{Re}\,\lambda > \omega_0\,(T(t))\ ,$$

(see Pazy (1983)) and it follows that $R(\lambda,A)$ is positive if λ is real and $\lambda > \omega_0(T(t))$. This positivity will be exploited in the following section.

2. Positive semigroup theory
We can also exploit the positivity of the semigroup itself to obtain information about the spectrum of A, in particular about its intersection with the vertical line $\{s(A) + i\nu \mid \nu \in \mathbb{R}\}$. This approach will be discussed in section 7.

At this point we mention that many ideas sketched in the sections 4 to 7 also apply to problems from linear *transport theory*. Some nice references in this respect are Birkhoff (1959), Vidav (1970), Larsen and Zweifel (1974), Kaper, Lekkerkerker and Hejtmanek (1982), Greiner (1984) and Voigt (1984). Thieme (1984) uses positivity arguments to prove renewal theorems for *discrete Volterra equations.*

6. Spectral theory of positive operators

We recall that we do not mention explicitly whether we are working with a real Banach space X or its complexification (see remark 3.1), since this should be clear from the context.

A set $X_+ \subset X$ is called a *cone* if
(i) X_+ is closed

(ii) if $\phi_1, \phi_2 \in X_+$ and $\alpha_1, \alpha_2 \geq 0$ then $\alpha_1 \phi_1 + \alpha_2 \phi_2 \in X_+$
(iii) if $\phi \in X_+$ and $-\phi \in X_+$, then $\phi = 0$.

From (ii) it follows that a cone is convex. We call an element $\phi \in X_+$ *positive* and we write $\phi \geq 0$. If $\phi \geq 0$ and $\phi \neq 0$ then we write $\phi > 0$. The cone X_+ induces a partial ordering on X in the following way: for $\phi_1, \phi_2 \in X$ we have $\phi_1 \geq \phi_2$ if $\phi_1 - \phi_2 \geq 0$. The cone X_+ is called *reproducing* if $\underline{X = X_+ - X_+} = \{\phi_1 - \phi_2 \mid \phi_1, \phi_2 \in X_+\}$. The cone X_+ is called *total* if $\overline{X_+ - X_+} = X$. Finally X_+ is *normal* if there exists a constant $\delta > 0$ such that for all $\phi_1, \phi_2 \in X_+$ with $\|\phi_1\| = \|\phi_2\| = 1$ we have that $\|\phi_1 + \phi_2\| \geq \delta$. For a detailed exposition of the theory of cones in a Banach space we refer to the monograph of Krasnoselskii (1964).

Sometimes we can define the *supremum* $\phi_1 \vee \phi_2$ of two elements $\phi_1, \phi_2 \in X$. The definition goes as follows:

$$\phi = \phi_1 \vee \phi_2 \text{ if } \phi \geq \phi_1, \phi \geq \phi_2$$

$$\text{and } \phi \leq \psi \text{ for all } \psi \in X \text{ satisfying } \psi \geq \phi_1 \text{ and } \psi \geq \phi_2 .$$

The infimum $\phi_1 \wedge \phi_2$ is defined in an analogous way. A *vector lattice* is an ordered vector space such that $\phi_1 \vee \phi_2$ and $\phi_1 \wedge \phi_2$ exist for all pairs $\phi_1, \phi_2 \in X$. If X is a vector lattice then $|\phi| = \phi \vee -\phi$ is called the *modulus* (or *absolute value)* of ϕ. If additionally X is a Banach space with norm $\|\cdot\|$ satisfying: $|\phi_1| \leq |\phi_2|$ implies $\|\phi_1\| \leq \|\phi_2\|$ for all $\phi_1, \phi_2 \in X$, then X is called a *Banach lattice.* We refer to chapter II of Schaefer (1974) for an extensive discussion on the theory of vector and Banach lattices. There it is also explained how one can define the complexification of a Banach lattice. The best known and most frequently used Banach lattices are $C(K)$ where K is a compact space, and $L^p(\mu)$, $1 \leq p \leq \infty$, where (X, Σ, μ) is a measure space.

For the rest of this section we assume, unless otherwise stated, that X is a Banach space with cone X_+. The set X_+^* consists of all functionals $F \in X^*$ satisfying $< F, \phi > \geq 0$, $\phi \in X_+$. If the cone X_+ is total then X_+^* defines a cone in X^* (e.g. Krasnosel'skii (1964)) which we shall call the dual cone of X_+. If X is a Banach lattice then both X_+ and X_+^* are normal. An element $\phi \in X_+$ is called *quasi-interior* if $< F, \phi > \neq 0$ for all $F \in X_+^*$, $F \neq 0$. (Schaefer (1974) gives a different but equivalent definition.) An element $F \in X_+^*$ is called *strictly positive* if $< F, \phi > \neq 0$ for all $\phi \in X_+$, $\phi \neq 0$.

Now let $L: X \to X$ be a bounded, linear operator. We say that L is *positive* ($L \geq 0$) if L leaves the cone X_+ invariant, i.e. $L\,\phi \geq 0$ if $\phi \geq 0$. Krein and Rutman (1948) were the first authors who made a systematic study of positive operators on a Banach space, in particular of their spectral properties. They call a positive operator $L: X \to X$ *strongly positive* if for all $\phi \in X_+$ there exists an integer $p = p(\phi)$ such that $L^p\,\psi \in \mathring{X}_+$, where $\mathring{X}_+$ is the interior of the cone X_+. Obviously a prerequisite is that X_+ has a non-empty interior. One of their main results is the following.

THEOREM 6.1 (Krein & Rutman)

a) *Let X_+ be total and $L: X \to X$ a compact positive operator with spectral radius $r = r(L) > 0$. Then there exist $\phi \in X_+, \phi \neq 0$ and $F \in X^*_+, F \neq 0$ such that*

$$L\,\phi = r\phi\,,\ \ L^*\,F = rF\,.$$

b) *If, moreover, L is strongly positive, then $\phi \in \overset{\circ}{X}_+$, ϕ is (except for positive multiples of ϕ) the only eigenvector of L in X_+ and F is strictly positive. The remaining eigenvalues $\lambda \in \sigma(L)$ satisfy $|\lambda| < r(L)$.*

Although this result has later been generalized by several authors into several directions (e.g. the condition " L is compact " may be replaced by $r_{ess}(L) < r(L)$: see Nussbaum (1980)) it illustrates fairly good what kind of spectral properties a positive operator may have.

It is the strong positivity condition in theorem 6.1 which restricts its applicability. For instance, the standard cones in L^p-spaces have empty interior. As an alternative Krasnosel'skii (1964) introduced u_0- *positive operators* (see chapter II of this thesis for an example). Sawashima (1964) introduced the rarely used but rather useful notion of a *non-supporting operator.*

DEFINITION A positive linear operator $L: X \to X$ is called non-supporting if for every $\phi \in X_+, \phi \neq 0$ and $F \in X^*_+$, $F \neq 0$, there exists an integer p such that $< F, T^n\,\phi > \neq 0$ for all $n \geqslant p$.

We note that Sawashima (1964) uses the adjective "non-support". Sawashima's definition of a non-supporting operator is closely related to Schaefer's definition of an *irreducible operator* (e.g. Schaefer (1974)). For the application to problems from structured populations dynamics Sawashima's concept appears very well suited.

THEOREM 6.2 (Sawashima) *Let the cone X_+ be total and $L: X \to X$ a positive non-supporting operator and suppose that $r = r(L)$ is a pole of the resolvent, then the following holds:*

a) *$r > 0$ and r is an algebraically simple eigenvalue of L.*

b) *The associated eigenvector ϕ is quasi-interior, and the dual eigenvector F is strictly positive.*

c) *If, moreover, X is a Banach lattice and $r_{ess}(L) < r(L)$ then $|\lambda| < r$ if $\lambda \in \sigma(L), \lambda \neq r$.*

Finally we refer to Karlin (1959), Marek (1970) and Nussbaum (1980) where a number of related results can be found.

We shall now try to give an idea how these kind of results can be used in the investigation of problems from structured population dynamics. Therefore we return to our example.

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In section 5 it is indicated that in order to prove a result like (SDT), one has to verify the conditions $[A_1]$ and $[A_2]$ (c.f. theorem 5.3). In our example $[A_2]$ is satisfied (c.f. (E.18)). So let us concentrate on the spectral properties of A. If $\lambda \in \sigma(A)$ and $\mathrm{Re}\,\lambda > -b(1)$, then $e^{\lambda t} \in \sigma(T(t))$ and $|e^{\lambda t}| > e^{-b(1)t} \geq r_{ess}(T(t))$ where we have used (E.17) and (5.5.) Now (5.8) yields that $\lambda \notin \sigma_{ess}(A)$ and we obtain among others that $\lambda \in P\sigma(A)$. So let us consider the eigenvalue problem

$$A\,\psi = \lambda\,\psi\,,\ \ \mathrm{Re}\,\lambda > -b(1)\,. \tag{E.19}$$

This is equivalent to

$$\psi(x) = p\cdot \frac{E(x)e^{-\lambda G(x)}}{g(x)} \cdot \int_{\alpha}^{(x,\frac{1}{p})^-} \frac{b(p\,\xi)}{E(\xi)}\, e^{\lambda G(\xi)}\, \psi(p\,\xi)\mathrm{d}\xi\,. \tag{E.20}$$

Every solution $\psi \in L^1[\alpha,1]$ of (E.20) is of the form

$$\psi(x) = \nu_\lambda(x)\cdot f(x), \tag{E.21}$$

where

$$\nu_\lambda(x) = \frac{E(x)e^{-\lambda G(x)}}{g(x)}\,,\ \ \alpha \leq x < 1\,, \tag{E.22}$$

and $f \in C[\alpha,1]$ with $f(\alpha) = 0$. Substitution of (E.21) in (E.20) yields

$$f(x) = \int_{a}^{(px,1)^-} k_\lambda(\xi) f(\xi)\mathrm{d}\xi\,,\ \ \alpha \leq x \leq 1\,, \tag{E.23}$$

where $(x,y)^-$ denotes the minimum of x and y, and

$$k_\lambda(x) = \frac{b(x)}{g(x)}\,\frac{E(x)}{E(x/p)}\, e^{-\lambda(G(x)-G(x/p))}\,,\ \ \alpha \leq x < 1\,, \tag{E.24}$$

is an integrable function if $\mathrm{Re}\,\lambda > -b(1)$. It is clear from (E.23) that the function $f \in C[\alpha,1]$ is completely determined by its values on the subinterval $[a,1]$. Therefore we study the equation

$$T_\lambda f = f\ ,\ f \in C[a,1]\,, \tag{E.25}$$

where the compact operator $T_\lambda : C[a,1] \to C[a,1]$ is given by

$$(T_\lambda f)(x) = \int_{a}^{(px,1)^-} k_\lambda(\xi) f(\xi)\mathrm{d}\xi\,. \tag{E.26}$$

The following result holds

THEOREM E.5

a) $\sigma_{ess}(A) = \{\lambda \in \mathbb{C} \mid \text{Re}\,\lambda \leqslant -b(1)\}$

b) $\sigma(A) \setminus \sigma_{ess}(A) = \{\lambda \in \mathbb{C} \mid \text{Re}\,\lambda > -b(1) \wedge 1 \in P\sigma(T_\lambda)\}$.

Moreover if $\text{Re}\,\lambda > -b(1)$ *and* $T_\lambda f = f$, $f \in C[a,1]$, *then* $A(\tilde{f}v_\lambda) = \lambda \tilde{f} v_\lambda$ *where* $\tilde{f}$ *is the extension of* f *to* $C[\alpha,1]$ *determined by (E.23), and* v_λ *is given by (E.22).*

We refer to section V.2 for a related result. One sees immediately that for $\lambda \in \mathbb{R}, \lambda > -b(1)$ the operator T_λ is positive with respect to the cone $C_+[a,1]$, consisting of all non-negative functions. Moreover T_λ is strongly positive in the sense of Krein and Rutman (1948). Therefore $r(T_\lambda)$ is an eigenvalue of T_λ if $\lambda > -b(1)$ (see theorem 6.1). Since we are interested in the eigenvalue 1 of T_λ we consider the equation

$$r(T_\lambda) = 1 ,$$

and as in section II.4 and section V.2, we can show that this equation has a unique solution $\lambda_d > -b(1)$. Moreover λ_d is an algebraically simple eigenvalue of A, λ_d is strictly dominant (which is *not* true if assumption E.3 is false for all x), and the corresponding eigenvector $\phi_d \in L^1[\alpha,1]$ and dual eigenvector $F_d \in L^\infty[\alpha,1]$ are quasi-interior and strictly positive respectively. (Note that ϕ_d is of the form as described in theorem E.5.b.) Integration of

$$\lambda_d\, \phi_d(x) + \frac{d}{dx}(g(x)\phi_d(x)) = -b(x)\phi_d(x) + pb(px)\phi_d(px)$$

over $[\alpha,1]$ yields

$$\lambda_d \int_\alpha^1 \phi_d(x)\mathrm{d}x = 0 ,$$

and the positivity of ϕ_d yields that

$$\lambda_d = 0 .$$

This last result also follows from (E.16). We have now proved that condition $[A_1]$ is also satisfied and therefore we can give the following description of the asymptotic behaviour of solutions of (E.1) - (E.3) (c.f. theorem 5.3). Let ϕ_d, F_d be normalized such that $<F_d, \phi_d> = 1$.

THEOREM E.6 *There exists a constant* $\eta > 0$ *such that for all* $\epsilon \in (0,\eta)$ *there is a constant* $M(\epsilon) \geqslant 1$ *such that*

$$\|T(t)\phi - <F_d,\phi>\phi_d\| \leqslant M(\epsilon)\, e^{-\epsilon t}\, \|\phi\|,\ t \geqslant 0,\ \phi \in L^1[\alpha,1] .$$

We call ϕ_d the stable size distribution. □

This example illustrates nicely how the positivity of the resolvent operator

$R(\lambda,A)$ for $\lambda \in \mathbb{R}$ sufficiently large (where A is the infinitesimal generator of a strongly continuous semigroup) can be used to verify condition $[A_1]$. In chapter II and section V.2 we shall discuss two slightly different examples.

7. SPECTRAL THEORY OF POSITIVE SEMIGROUPS

In the previous section we described on the basis of our example how the positivity of the resolvent can be exploited to prove condition $[A_1]$. In this section we shall indicate how positivity properties of the semigroup can provide an alternative proof.

Throughout this section we assume that X is a Banach lattice with cone X_+ and that $\{T(t)\}_{t\geq 0}$ defines a strongly continuous semigroup of operators whose generator is A. The *peripheral spectrum* $\sigma_+(A)$ of A is defined by

$$\sigma_+(A) = \begin{cases} \{\lambda \in \sigma(A) | \mathrm{Re}\lambda = s(A)\} & \text{if} \quad s(A) > -\infty \\ \varnothing & \text{if} \quad s(A) = -\infty \,, \end{cases}$$

where the spectral bound $s(A)$ is given by (5.9). The semigroup $\{T(t)\}_{t\geq 0}$ is called *positive* if $T(t)$ is positive for every $t \geq 0$. Greiner, Voigt & Wolff (1981) showed that $s(A) \in \sigma(A)$ if $\{T(t)\}_{t\geq 0}$ is a positive semigroup and $\sigma(A) \neq \varnothing$. Derndinger (1979) has proved that $s(A) = \omega_0(T(t))$ (compare this to (5.10)) if X is an AL-space, e.g. $L^1(\mu)$, or an AM-space with unit, e.g. $C(K)$ (see Schaefer (1974)), but in general this relation is not true. Greiner et al (1981) give an example of a positive semigroup whose spectrum is the whole unit disk and whose generator has empty spectrum. Below we shall formulate a number of results characterizing the peripheral spectrum of a positive semigroup. The first result is proved by Greiner (1981).

$\{T(t)\}_{t\geq o}$ be a positive semigroup and suppose that $s(A) > -\infty$ is a pole of the resolvent. Then $\sigma_+(A)$ is additively cyclic, i.e. $s(A) + i\nu \in \sigma(A)$ implies that $s(A) + ik\nu \in \sigma_+(A)$ for all $k \in \mathbb{Z}$.

An easy consequence of this result and the spectral mapping theorems (5.7) - (5.8) is the following result.

THEOREM 7.2 *Let* $\{T(t)\}_{t\geq 0}$ *be a positive semigroup with* $\omega_{ess}(T(t)) < \omega_0(T(t))$. *Then* $\sigma_+(A) = \{s(A)\}$.

PROOF First we note that $s(A) = \omega_0(T(t) > -\infty$ because of (5.10). Next suppose that $s(A) + i\,\nu \in \sigma(A)$ for some $\nu \neq 0$. Then $s(A) + i\,k\,\nu \in \sigma(A)$ for all $k \in \mathbb{Z}$, hence $e^{ts(A)}\, e^{ik\nu t} \in \sigma(T(t))$ for $t \geq 0$. If we choose $t > 0$ such that $\nu t / 2\pi$ is irrational, we obtain that $\{z \in \mathbb{C} |\, |z| = e^{t \cdot s(A)}\} \subset \sigma(T(t))$ and therefore $r_{ess}(T(t)) \geq e^{t\cdot s(A)}$ or equivalently $\omega_{ess}(T(t)) \geq s(A) = \omega_0(T(t))$ which is a contradiction. □

To establish the algebraic simplicity of $\lambda_d = s(A)$, the positivity of the semigroup is not sufficient.

DEFINITION The positive semigroup $\{T(t)\}_{t\geq 0}$ is called *irreducible* if for every $\phi \in X_+$, $\phi \neq 0$ and $F \in X_+^*$, $F \neq 0$ there exists a $t = t(\phi, F) \geq 0$ such that $<F, T(t)\phi> > 0$.

This definition is quite different from the original definition given by Schaefer (1974) but from Proposition III.8.3 in Schaefer (1974) it follows that these definitions are equivalent (see also proposition 3.8 of Greiner et al (1981)). For the following result we refer to Greiner (1982). See also Greiner et al (1981) and Greiner (1984).

THEOREM 7.3 *Let* $\{T(t)\}_{t\geq 0}$ *be a positive irreducible semigroup and suppose that* $s(A) > -\infty$ *is a pole of the resolvent of* A. *Then* $\sigma_+(A) = s(A) + i\nu\mathbb{Z}$ *for some* $\nu \geq 0$ *and every element of* $\sigma_+(A)$ *is a simple pole of the resolvent with a residue of rank one.*

Combination of theorem 7.2 and theorem 7.3 yields that condition $[A_1]$ is automatically satisfied if $[A_2]$ is satisfied and $\{T(t)\}_{t\geq 0}$ is a positive irreducible semigroup. Moreover ϕ_d and F_d determined by (5.12) can be chosen quasi-interior and strictly positive respectively, since

$$T(t)\phi_d = e^{\lambda_d t}\,\phi_d \quad \text{and} \quad T(t)^*\,F_d = e^{\lambda_d t}\,F_d,\; t \geq 0\,,$$

and $T(t)$ is irreducible (see Schaefer (1974), section V.5).

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The positivity of the semigroup $\{T(t)\}_{t\geq 0}$ in this example (and other examples in structured population dynamics) is obvious. We shall now state a lemma which implies the irreducibility of the semigroup. Since we have already proved $[A_2]$ we obtain $[A_1]$ from this lemma and this provides an alternative proof of theorem E.6.

LEMMA E.7 *Let* $\phi \in L^1_+[\alpha,1]$, $\phi \neq 0$, *then there exists a* $t^* > 0$ *such that* $n(t,x) > 0$, $\alpha < x < X(t-t^*, \alpha)$.

SKETCH OF THE PROOF (c.f. Heijmans (1984b)). We assume that ϕ is continuous and $\phi(x) > 0$, $x \in (\xi_0^-, \xi_0^+)$, where $1/p < \xi_0^- < \xi_0^+ < 1$. (It is not difficult to see that $n(t,x) = n_0(t,x) + n_1(t,x)$, and $n_1(t,x)$ satisfies these assumptions if t is large enough.) Now let

$$\xi^-(t) = X(t, \xi_0^-)\,,\; \xi^+(t) = X(t, \xi_0^+),\, t \geq 0\,,$$

where $X(t,x)$ is defined in (E.12). With (E.14) it follows directly that $n(t,x) > 0$ if $x \in (\xi^-(t), \xi^+(t))$, $t \geq 0$. It can also be shown from (E.14) that $n(t,x) > 0$, $x \in (x_1, x_2)$ where $a < x_1 < x_2 < 1$ implies that

$n(t,x) > 0$, $x \in (x_1/p, x_2/p)$. Now choose $k \in \mathbb{N}$ such that $p^{-k} \leqslant a$ and $p^{-k+1} > a$, and $t_0 \geqslant 0$ such that $\xi^-(t_0) \cdot p^{-k+1} > a$ (note that $\xi^-(t) \to 1$ as $t \to \infty$). Then $n(t,x) > 0$, $x \in (\xi^-(t) \cdot p^{-k}, \xi^+(t) \cdot p^{-k}) \subseteq (\alpha, a)$ if $t \geqslant t_0$. Now let $t^* = t_0 + G(a) - G(\xi^+(t) \cdot p^{-k})$, then one can easily show that with this choice of t^* the lemma is satisfied. □

Now the following result is clear.

COROLLARY E.8 $\{T(t)\}_{t \geqslant 0}$ *defines a positive irreducible semigroup.*

There is a more direct way to prove condition $[A_1]$ from lemma E.7, exploiting the fact that $T(t)$ obeys a stronger condition than irreducibility, namely: for all $t > 0$, the operator $T(t)$ is nonsupporting. Now $[A_1]$ follows immediately from theorem 6.2 if $\omega_{ess}(T(t)) < \omega_0(T(t))$. We refer to Nussbaum (1984) for a related result. □

It depends on the nature of the problem whether the positivity of the resolvent or the positivity of the semigroup should be used to prove the existence of a strictly dominant algebraically simple eigenvalue of A. If, for instance, generations (see section 4) die out after a finite time then it is a rather difficult job to prove irreducibility of the semigroup. An unmistakable advantage of working with the semigroup, is that extensions to non-autonomous problems (e.g. the case of time-periodic rates) are possible. We refer to Diekmann, Heijmans and Thieme (1985) for an example.

8. Nonlinear models and dynamical systems

In the first section we noted that in reality biological populations do not grow unlimited (= exponential), since an increase of the population has a negative effect on its environment e.g. by the limited availibility of food. Such negative feedback effects can be built into the model in a biologically significant way by looking what is the effect of these interactions on the individual level and this underlines once more the necessity of incorporating some structure. The mathematical equations that one finds are *nonlinear*.

The theory of nonlinear structured population dynamics has hardly been developed with the exception of age-structured models (see Prüss (1981, 1983a, 1983b), Gyllenberg (1982), Cushing (1980) and Webb (1985)). In the last chapter of this thesis we consider some nonlinear models for cell growth, which have in common that they can be analyzed with existing mathematical machinery, mainly originating from *dynamical system theory*. For that reason we shall discuss in this section some better or less known results from this field, which we need in chapter VI. For a detailed exposition we refer to the book of Walker (1980).

Let X be a Banach space and C a closed subset of X. A *dynamical system* on C is a mapping $u:\mathbb{R}_+ \times C \to C$ with the following properties:

(i) $u(\cdot;\phi):\mathbb{R}_+ \to C$ is continuous for all $\phi \in C$
(ii) $u(t;\cdot):C \to C$ is continuous for all $t \geqslant 0$
(iii) $u(0;\phi) = \phi$, $\phi \in C$
(iv) $u(t + s;\phi) = u(t;u(s;\phi))$, $t,s \in \mathbb{R}_+$, $\phi \in C$.

Strictly spoken we ought to call u a semi-dynamical system in this case, since u is defined on the positive time-axis only. For convenience we shall omit the prefix 'semi'. Note that, if the system is linear, i.e.

$$u(t;\alpha_1\phi_1 + \alpha_2\phi_2) = \alpha_1 u(t;\phi_1) + \alpha_2 u(t;\phi_2),\ \phi_1,\phi_2 \in C,\ \alpha_1,\alpha_2 \in \mathbb{R}\ ,$$

then we can extend the system to span(C) being the linear subspace of X spanned by C.

Let the family of mappings $T(t):C \to C$, $t \geqslant 0$ be defined by

$$T(t)\phi = u(t;\phi),\ t \geqslant 0,\ \phi \in C\ , \tag{8.1}$$

then $\{T(t)\}_{t \geqslant 0}$ defines a strongly continuous semigroup of (not necessarily linear) operators on C, i.e. $\{T(t)\}_{t \geqslant 0}$ satisfies the following conditions:

(i) $t \mapsto T(t)\,\phi$ is continuous from $\mathbb{R}_+$ to C for all $\phi \in C$
(ii) $T(t)$: $C \to C$ is continuous for all $t \geqslant 0$
(iii) $T(0) = I$ (where I is the identity on C)
(iv) $T(t + s) = T(t)T(s)$, $t,s \in \mathbb{R}_+$.

Often we shall call $\{T(t)\}_{t \geqslant 0}$ the dynamical system, which is allowed because (8.1) defines a one-to-one relation between a (semi-) dynamical system on C, and a strongly continuous semigroup on C. In (8.1) ϕ is called the initial state and $T(t)\phi$ the state at time t.

It is a first task of the investigator of a problem in structured population dynamics (and many other problems) to show that it 'generates' a dynamical system: at this point it is very likely that the choice of the state space C plays an important role.

An obvious next step is the examination of the behaviour of solutions. Although often the applied biologist is interested in both the transient and asymptotic behaviour of solutions, most mathematicians restrict themselves to the second problem, probably because the first problem is much more difficult in general. This, however, does not mean that the characterization of the large time behaviour of solutions involving the questions *do there exist equilibria?, do there exist periodic solutions?, what about stability?, can methods from bifurcation theory be applied?, is chaotic behaviour possible?* is an easy problem, not even if the underlying Banach space X is finite dimensional (see Guckenheimer and

Holmes (1983)). All that we can do at this point is to give some tools which can be of some help in trying to answer them.

For $\phi \in C$, we call the set

$$\Gamma^+(\phi) = \{T(t)\phi \mid t \geqslant 0\}, \tag{8.2}$$

the *orbit* starting in ϕ. The omega-limit set $\Omega(\phi)$ of $\phi \in C$ is defined by

$$\Omega(\phi) = \{\psi \in C \mid \text{there exists a sequence } \{t_k\}_{k=1}^{\infty} \text{ such that } t_k \to \infty \text{ and } T(t_k)\phi \to \psi,\ k \to \infty\}. \tag{8.3}$$

One always has that $\Omega(\phi)$ is *closed* and *positively invariant*, i.e. $T(t)\Omega(\phi) \subset \Omega(\phi)$, $t \geqslant 0$.

DEFINITION A subset $\mathfrak{M} \subset C$ is called *invariant* if there exists a mapping $F: \mathbb{R} \times \mathfrak{M} \to \mathfrak{M}$ such that $F(0,\phi) = \phi$ and $F(t+s,\phi) = T(t)F(s,\phi)$ for all $\phi \in \mathfrak{M}$, $s \in \mathbb{R}$ and $t \geqslant 0$.

A well-known result (e.g. Walker (1980)) says:

THEOREM 8.1 *If $\phi \in C$, and $\Gamma^+(\phi)$ is precompact, then $\Omega(\phi)$ is non-empty, compact, connected and invariant, and moreover* $\lim_{t\to\infty} d(T(t)\phi, \Omega(\phi)) = 0$.

Here, for $\phi \in X$ and $V \subset X$, $d(\phi, V)$ denotes the distance from ϕ to V, i.e. $d(\phi,V) = \inf_{\psi \in V} \|\phi - \psi\|$.

Theorem 8.1. can be used to characterize the asymptotic behaviour of $u(t;\phi) = T(t)\phi$ provided that one is able to prove precompactness of the orbit $\Gamma^+(\phi)$ and to determine the omega-limit set of ϕ. As to this last aspect, *Lyapunov functions* are extremely useful.

Let $\mathcal{V}: C \to \mathbb{R}$ be a continuous function. For $\phi \in C$ we define

$$\dot{\mathcal{V}}(\phi) = \liminf_{t \downarrow 0} \frac{1}{t} \{\mathcal{V}(T(t)\phi) - \mathcal{V}(\phi)\}, \tag{8.4}$$

where it is permitted that $\dot{\mathcal{V}}(\phi) = -\infty$. The function $\mathcal{V}$ is called a (continuous) *Lyapunov function* for $T(t)$ on C if

$$\dot{\mathcal{V}}(\phi) \leqslant 0, \ \phi \in C . \tag{8.5}$$

The following theorem, which can be found in Walker (1980) is called the *invariance principle.*

THEOREM 8.2 (Invariance Principle) *Let $\mathcal{V}$ be a continuous Lyapunov function for $T(t)$ on C and let $\mathcal{E}$ be the largest invariant subset of $\{\phi \in C \mid \dot{\mathcal{V}}(\phi) = 0\}$. If $\phi \in C$ and $\Gamma^+(\phi)$ is precompact then* $\lim_{t\to\infty} d(T(t)\phi, \mathcal{E}) = 0$.

Walker (1980) proves a more general version of the invariance principle, but for our purposes theorem 8.2 suffices. In practice there do not always exist Lyapunov functions, and even if they do exist, it is usually impossible to find them without the kind help of Dame Fortune.

Finally we note that it is sometimes possible to prove monotonicity of the dynamical system $T(t)$ on C (i.e. $T(t)\phi \leqslant T(t)\psi$, $t \geqslant 0$ if $\phi \leqslant \psi$) or some invariant subset of C. An illustration of this technique can be found in section VI.4. We refer to Hirsch (1984) and Matano & Hirsch (in prep.) for a systematic approach.

9. About the thesis

The field of structured population dynamics has several aspects. There is the experimental stage consisting of observations on the level of both the individual and the population. Then there is the model-building stage during which modelling assumptions, based on experimental observations, are translated into mathematical problems. The analysis of these problems and the translation of the mathematical results into biological language form a third stage. These stages, which are equally important, should certainly not be performed in a strict order, but should mutually influence each other.

This thesis is mainly concerned with the third stage (but we made some remarks on model building in section 2 of this introductory chapter). Although we have tried to consider only problems which are biologically relevant, the accent of this thesis lies on mathematics and not on biology. This might explain how it can happen that not less than four chapters (namely II - IV and VI) are concerned with cell division models, and one chapter (namely V) with a model for the predatory behaviour of an invertebrate predator, without making the whole unbalanced, at least to the author's view.

Our main objective is to indicate what sort of techniques apply to structured population models. In that respect this introductory chapter plays an important role, and it has missed its goal if it doesn't give the reader an impression of what structured population dynamics is all about. All the other chapters (except the last, which plays a somewhat different role) are more or less variations on a theme. At this point we note that in the near future a book in the series Lecture Notes in Biomathematics, edited and partially written by Hans Metz and Odo Diekmann (see Metz and Diekmann (to appear)) will appear, containing a wealth of information and ideas, and discussing several aspects of the field of structured population dynamics, which are not mentioned in this thesis.

Besides this introductory chapter, this thesis contains five chapters, which can be read independently. In chapter II, III and IV the starting point is the Bell-Anderson model (see Bell & Anderson (1967) and Bell (1968)) describing the age-size distribution of a cell population reproducing by fission into two equal parts. Here we shall give a short description of the model. Consider a population of single cells of which the individuals can be distinguished according to their *age* a and *size* x (here size can mean weight, length, DNA-content etc). In the language of section 2 this means that the i-state of a cell is given by the two-dimensional quantity (a,x). Let $\Omega \subset \mathbb{R}_+ \times \mathbb{R}_+$ be the i-state space and let the p-*state* at time $t \geq 0$ be described by the integrable function

$$n(t,\cdot,\cdot):\Omega \to \mathbb{R} \ ,$$

i.e. for any measurable set $\Theta \subset \Omega$ the integral $\int_\Theta n(t,a,x)\mathrm{d}a\,\mathrm{d}x$ is the number of cells at time t with i-state in Θ. Let $b(a,x)$ and $\mu(a,x)$ be the chance per unit of time that a cell with i-state (a,x) divides respectively dies. We assume further that the continuous deterministic i-movement is described by

$$\frac{da}{dt} = 1\ , \ \frac{dx}{dt} = g(a,x)\ , \ (a,x) \in \Omega\ .$$

The function $V:\Omega \to \mathbb{R}^2$ of section 2 is given by $V(a,x) = (1,g(a,x))$. We call g the *individual growth rate.*

We can write down the following balance equation for n:

$$\frac{\partial n}{\partial t}(t,a,x) + \frac{\partial n}{\partial a}(t,a,x) + \frac{\partial}{\partial x}(g(a,x)n(t,a,x)) = \tag{9.1}$$

$$-(\mu(a,x) + b(a,x))n(t,a,x)\ ,$$

Note that the left-hand-side of this equation equals $\frac{\partial n}{\partial t} + \mathrm{div}(V\cdot n)$. A dividing cell with age a and size x gives birth to two daughters both having age 0 and size $\frac{1}{2}x$. This results in the boundary condition

$$n(t,0,x) = 4\int_0^\infty b(a,2x)\, n(t,a,2x)\mathrm{d}a\ . \tag{9.2}$$

The factor 4 can be explained as follows: $4 = 2\times 2$ where the first factor 2 is due to the fact that a cell divides into $\underline{2}$ parts, whereas the second factor 2 is due to the fact that daughters with size in $(x,x+dx)$ come from mother cells in the size interval $(2x,2x+\underline{2}dx)$.

On that part of the boundary $\partial\Omega$ of Ω where $a>0$ and V points inward we have to impose the condition $(Vn\cdot\nu)(t,a,x) = 0$, where ν is the normal vector on $\partial\Omega$. See chapter III of Metz and Diekmann (to appear) for more details.

In chapter IV we study (9.1)$-$(9.2), the main assumption being that g does only depend on x. By integrating (9.1) along the characteristics we obtain an integral equation for the birth function $B(t,x) = n(t,0,x)$, which we might call an *abstract renewal equation:* it has the same form as the integral equation derived by Lotka (1907) (c.f. section 1), but the underlying space is not $\mathbb{R}$ but an infinite-dimensional Banach space. The main techniques exploited in chapter IV are Laplace transformation and positive operator theory.

If we assume that neither g nor μ nor b depend on a, then the i-state of a cell is given by its size x and in this case (9.1) - (9.2) can be simplified considerably. We define $N(t,x) = \int_0^\infty n(t,a,x)da$, and now $N(t,\cdot)$ represents the new p-state at time t. Integration of (9.1) from $a = 0$ to $a = \infty$ and substitution of $g = g(x)$, $\mu = \mu(x)$, $b = b(x)$ and the boundary condition (9.2) leads to

$$\frac{\partial N}{\partial t}(t,x) + \frac{\partial}{\partial x}(g(x)N(t,x)) = -(\mu(x) + b(x))N(t,x) + \qquad (9.3)$$
$$4b(2x)N(t,2x).$$

This partial differential equation has to be supplemented with a boundary condition of the form

$$g(x)N(t,x)|_{x=x_{min}} = 0, \qquad (9.4)$$

where x_{min} is the smallest possible cell size.

In chapter II, which is a revision of Heijmans (to appear a), we investigate the eigenvalue problem associated with (9.3) - (9.4). There our main tool is formed by the spectral theory of positive operators as discussed in section 6.

In chapter III, which is joint work with O. Diekmann and H.R. Thieme, we consider the initial problem (9.3) - (9.4) supplemented with an initial condition

$$N(0,x) = N_0(x). \qquad (9.5)$$

We reformulate the problem as an abstract Cauchy problem and show that we can associate a strongly continuous semigroup of operators with the problem (see section 4). Using the results from chapter II, where the spectrum of the generator is characterized, we are able to determine the asymptotic behaviour of solutions (see also section 5).

REMARKS 9.1.

a) In Heijmans (1984b) we exploit the positivity properties of the semigroup to obtain the same results under slightly different assumptions (see also section 7). In Diekmann, Heijmans and Thieme (1985) we use positivity properties of the *evolution operators* (see e.g. Tanabe (1979) and Pazy (1983)) to find the asymptotic behaviour of solutions of (9.3) - (9.5) if the rates g,μ and b depend periodically on time.

b) In Gyllenberg and Heijmans (1985) we consider a variant of (9.3) - (9.5), where we assume that there is a fixed time r between the onset of division and the division moment itself. In that case (9.3) becomes

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

$$-(\mu(x) + b(x))n(t,x) + 4b(2x)n(t-r,2x).$$

(In Gyllenberg and Heijmans (1985) a slightly more general problem is investigated.)

We anticipate the subsequent chapters by mentioning that the relation

$$g(2x) \neq 2g(x), \quad \text{for all } x ,$$

plays an important role in chapters II - IV (compare this to assumption E.3).

In chapter V we shift our attention to a model originally formulated by Hans Metz, who in his turn had been inspired by the celebrated work of Holling (1966), concerning the functional response of an invertebrate predator. Together with Eeke van Batenburg he wrote three papers (Metz and van Batenburg (1984a, 1984b, 1984c)), discussing the full model and a number of simplifications (obtained by limiting procedures), and their extensive work is completed by a number of simulation results. Metz and van Batenburg (1984a, 1984b, 1984c) started from the assumption that the i-state of the predator (the praying mantid *Hierodula crassa* is one of their examples) is given by its *satiation* s (which we shall identify with gut content) and the *handling time of the prey* τ, being the total time which the predator still needs to catch and, in case of a successful strike, swallow the prey. Again the p-state at time t is given by a function $p(t,s,\tau)$, which in this case describes the state of *one* predator, i.e. for a measurable subset Θ of the i-state space Ω the integral $\int_\Theta p(t,s,\tau)\mathrm{d}s\,\mathrm{d}\tau$ is the chance that the predator's i-state at time t belongs to Θ. One of the simplifications mentioned by Metz and van Batenburg (1984a, 1984b, 1984c) is the case where the handling time τ is negligable and can be omitted. This is also the model that we discuss in chapter V. Below we shall give a short description.

Let s denote satiation and let $p(t,s)$ be the satiation distribution at time t, i.e. $\int_{s_1}^{s_2} p(t,s)\mathrm{d}s$ is the chance that the predator has satiation between s_1 and s_2 at time t. Between two prey catches satiation decreases according to

$$\frac{ds}{dt} = -as, \; s > 0,$$

where $a > 0$ is a constant. The rate of prey catch of a predator with satiations s is $xg(s)$ where x denotes prey density. Finally it is assumed that every prey brings about the same increase w of satiation when swallowed. Now the dynamics of $p(t,s)$ is described by

$$\frac{\partial p}{\partial t}(t,s) - \frac{\partial}{\partial s}(asp(t,s)) = -xg(s)p(t,s) + xg(s-w)p(t,s-w) \quad (9.6)$$

supplied with the boundary condition

$$p(t,s_{\max}) = 0\,, \quad (9.7)$$

where s_{max} is the maximum attainable satiation. In chapter V it is explained why it is advantageous to study the *backward* (or *adjoint) equation* of (9.6) instead of the *forward equation* (9.6) itself. The solutions of the forward equation are characterized by the solutions of the backward equation via a duality relation. In this context the weak $\star$ topology plays a very important role.

If the prey weight w is very small in reality, then it makes sense to "idealize" and let w tend to zero in equation (9.6). This limit transition makes only biological sense if we let at the same time tend the prey density to infinity (otherwise there would be nothing left to eat). In chapter V we consider the case

$$w \to 0,\ x \to \infty,\ xw = \xi\ ,$$

where ξ is a constant. Then formally (9.6) transfers into (for the details we refer to chapter V):

$$\frac{\partial p}{\partial t}(t,s) + \frac{\partial}{\partial s}((\xi g(s)-s)p(t,s)) = 0\ , \tag{9.8}$$

which is a much simpler problem. In chapter V we show that a *Trotter-Kato theorem* can be used to give a mathematical justification of this formal limiting procedure (which was performed by Metz and van Batenburg (1984a, 1984b, 1984c)). By this we mean that we can show that solutions of (9.8) approximate the corresponding solutions of (9.6) if w is small.

From the equilibrium solution of (9.6) (which does exist because the dominant eigenvalue is zero) we can find an expression for the so-called *functional response*, which happens to be the quantity which biologists are interested in. An easy computable approximation of the functional response is found if the equilibrium solution of (9.8) (which is a delta-function) is substituted.

So far only linear problems have been discussed. There are two reasons for this. The first is that linear models in structured population dynamics form a class of problems which is interesting enough to be investigated extensively. Secondly, a rather general approach to nonlinear problems is lacking. In chapter VI we consider three nonlinear problems which we could solve completely. The first two problems are concerned with two rather different models for the growth of a cell population in a *chemostat*. Except for the fact that both problems can in some sense be reduced to a two-dimensional system of ODE's, and that in both cases the concept of an omega-limit set is used to characterize the large-time behaviour of solutions, the problems are rather different from a mathematical as well as a biological point of view. The third model that we discuss describes the bone marrow stem cell population which supplies the blood population with new cells. There we use a Lyapunov function, the Invariance Principle (theorem 8.2) and monotonicity of the associated dynamical system to prove global stability of equilibria. Finally we added a section stating some open problems.

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An eigenvalue problem associated with a model for size-dependent cell growth

by

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ABSTRACT

A model for the growth of a size-structured cell population is formulated, and the spectrum of the associated differential operator is investigated. This is done by transforming the eigenvalue problem into an integral equation. The main tool is provided by the spectral theory of positive operators on a Banach space.

Keywords & phrases size distribution, cell division, cone in a Banach space, positive operator, u_0-positive operator, non-supporting operator, Krein-Rutman theorem, dominant eigenvalue.

1. Introduction

We consider a cell population whose members can be distinguished from one another according to their size, which we denote by the parameter x. In stead of size one may also read volume, mass, amount of protein or any other quantity which obeys a physical conservation law. The individual 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 $dx = g(x)dt$. In other words: during periods of growth the size $x = x(t)$ of an individual obeys the ordinary differential equation

$$\frac{dx}{dt} = g(x). \tag{1.1}$$

We call $g(x)$ the (deterministic) individual growth rate.

We assume that a mother always divides into two equal daughters both having half the size of the mother. In [6] (see also chapter VI of this thesis) 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 & Anderson [1,2]. As a matter of fact, they formulated a more general model incorporating both size and age dependence. A similar model was applied by Sinko & Streifer [12] to populations of the planarian worm *Dugesia Tigrina*. The present paper is concerned with a rigorous investigation of the spectral properties of the differential operator associated with our model. The main question is whether or not 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 [3] (see also chapter III of this thesis) 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 is that the existence of a strictly dominant eigenvalue heavily depends on properties of 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 2 we present the model, and put it in a more tractable form by means of some elementary transformation. In section 3 the associated eigenvalue problem is reduced to an integral equation. In section 4 we use methods from positive operator theory (such as discussed in the Introduction of this thesis) to prove the existence of a dominant eigenvalue, i.e. an eigenvalue with largest real part. It turns out that the eigenvector belonging to this dominant eigenvalue is positive. The characteristic equation (which provides a tool for computing all eigenvalues) is derived in section 5. In section 6 and 7 we consider the essentially different cases $g(2x) < 2g(x)$ and $g(2x) = 2g(x)$ for all x, respectively. Finally in section 8 some remarks on the adjoint eigenvalue problem are made.

2. The equation and its interpretation

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

$$\frac{\partial n}{\partial t}(t,x) + \frac{\partial}{\partial x}(g(x)n(t,x)) = -\mu(x)n(t,x) - b(x)n(t,x) + 4b(2x)n(t,2x) \tag{2.1}$$

which describes the dynamics of a population (for instance algae or bacteria) reproducing by fission into two equal parts. Here t denotes time, x the size of an individual, $n(t,x)$ is the size distribution at time t, 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, μ is the death rate, b the division rate and g the individual growth rate (c.f. section 1).

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

$$n(t,\tfrac{1}{2}a) = 0. \tag{2.2}$$

In the subsequent analysis it will become clear that the cases $a = 0$ and $a > 0$ are essentially different. As to the biology this is obvious. We assume further that cells have to be divided before reaching a maximal size which is normalized to be 1. This is satisfied if the following condition holds:

$$\int_a^1 \frac{b(x)}{g(x)}\, dx = \infty. \tag{2.3}$$

It is explained below why this is sufficient. Throughout this paper we make the following assumptions on g, μ and b:

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

(H_μ) μ is a non-negative integrable function on $[\frac{1}{2}a, 1]$.

(H_b) b is integrable on $[a, 1-\epsilon]$ for all $\epsilon > 0$, $b(x) = 0$ a.e. (almost everywhere) on $(\frac{1}{2}a, a)$, $b(x) > 0$ a.e. on $(a, 1)$ and $\lim_{x \uparrow 1} \int_a^x b(\xi) d\xi = \infty$.

Let

$$E(x) = \exp\left[-\int_{\frac{1}{2}a}^{x} \frac{\mu(\xi) + b(\xi)}{g(\xi)} d\xi\right]. \tag{2.4}$$

$E(x)$ 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. The assumptions (H_g) and (H_b) imply that (2.3) is fulfilled, hence $E(1) = 0$, which means that cells with size greater than 1 do not exist. Therefore the last term at the right-hand-side of (2.1) must be interpreted as zero for $x \geqslant \frac{1}{2}$.

Remark 2.1 The choice that we made here is not the only possible one. For instance (2.3) is also satisfied if b is bounded and $g(x) \sim c(1-x)$, $x \uparrow 1$. This situation is discussed in [7].

Substitution of

$$g(x)n(t,x) = E(x)m(t,x) \tag{2.5}$$

into equation (2.1) leads to

$$\frac{\partial m}{\partial t} + g(x)\frac{\partial m}{\partial x} = k(x)m(t,2x), \tag{2.6}$$

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

$$k(x) = 4\,\frac{g(x)}{E(x)}\,\frac{b(2x)}{g(2x)}\,E(2x). \tag{2.7}$$

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

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

Equation (2.6) is to be supplemented with the boundary condition

$$m(t, \tfrac{1}{2}a) = 0. \tag{2.8}$$

From a mathematical point of view, the time-dependent equation (2.6) is more tractable than (2.1) because of the integrability of k, and from now on we will restrict our attention to (2.6). A precise relation between solutions of (2.1) and (2.6) can be found in section 7 of chapter III of this thesis.

3. Reduction of the eigenvalue problem to an integral equation

The inhomogeneous eigenvalue problem associated with (2.6), (2.8) is given by

$$\lambda\psi(x) + g(x)\frac{d\psi}{dx} - k(x)\psi(2x) = f(x), \tag{3.1}$$

$$\psi(\tfrac{1}{2}a) = 0. \tag{3.2}$$

We shall study this problem in $L_1[\frac{1}{2}a,1]$, so we assume that $f \in L_1[\frac{1}{2}a,1]$ and look for L_1-solutions ψ of (3.1) - (3.2).

Remark 3.1 The eigenvalue problem (3.1) - (3.2) 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 in stead of L_1-functions. Moreover for both cases one finds the same set of eigenvalues and eigenvectors. These eigenvectors are continuous functions. This is shown below.

An abstract way of writing (3.1) - (3.2) is

$$\lambda\psi - A\psi = f\ , \tag{3.3}$$

where A is the unbounded, linear operator given by

$$(A\psi)(x) = -g(x)\frac{d\psi}{dx} + k(x)\psi(2x)\ , \tag{3.4}$$

having a domain

$$\mathfrak{D}(A) = \{\psi \in L_1[\tfrac{1}{2}a,1] \mid \psi \text{ is absolutely continuous and } \psi(\tfrac{1}{2}a) = 0\}. \tag{3.5}$$

Theorem 3.2. *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 $\psi_n \in \mathfrak{D}(A)$, $\psi_n \to \psi$, $n\to\infty$ and $A\psi_n \to f$, $n\to\infty$. We must prove that $\psi\in\mathfrak{D}(A)$ and $A\psi = f$. Let $r \in \mathbf{R}$ be such that $\int_{a/2}^{1/2} k(\xi)e^{-r\xi}d\xi < 1$. Obviously $-\frac{d\psi_n}{dx} - r\psi_n(x) + k(x)\psi_n(2x) \to f(x) - r\psi(x)$ in L_1-sense. Let ϕ_n be given by $\phi_n(x) = e^{rx}\psi_n(x)$. Substitution yields

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

If we integrate from $\frac{1}{2}a$ to x we obtain $-\phi_n + L\phi_n \to F$, $n\to\infty$ in the sup-norm, where L defines a bounded linear operator on the space of continuous functions (notice that ϕ_n is continuous because $\psi_n \in \mathfrak{D}(A)$), given by $(L\phi)(x) = \int_{a/2}^{x} k(\xi)e^{-r\xi}\phi(2\xi)d\xi$, and $F(x) = \int_{a/2}^{x}\{f(\xi) - r\psi(\xi)\}e^{r\xi}d\xi$ 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 supnorm. 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 ϕ is absolutely continuous and $\phi(\frac{1}{2}a) = 0$. The same result holds for ψ. If we differentiate again we obtain $A\psi = f$, and the result is proved. □

Let

$$G(x) = \int_{\frac{1}{2}a}^{x} \frac{d\xi}{g(\xi)}. \tag{3.6}$$

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

$$\psi(x) = e^{-\lambda G(x)}\phi(x), \tag{3.7}$$

in (3.1), we obtain

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

where

$$k_\lambda(x) = \frac{k(x)}{g(x)}\, e^{-\lambda(G(2x)-G(x))}. \tag{3.8}$$

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

$$\phi(x) - \int_{\frac{1}{2}a}^{(\frac{1}{2},x)^-} k_\lambda(\xi)\phi(2\xi)d\xi = \int_{\frac{1}{2}a}^{x} \frac{f(\xi)}{g(\xi)} e^{\lambda G(\xi)} d\xi, \tag{3.9}$$

where $(\alpha,\beta)^-$ denotes the minimum of α and β. In order that ψ can be a solution of (3.1) - (3.2) we must have $\psi \in \mathfrak{D}(A)$ which implies that ψ is continuous and $\psi(\frac{1}{2}a) = 0$. This should also be true for ϕ. Let X be the Banach space

$$X = \{\phi \in C[\tfrac{1}{2}a,\, 1] \| \, \phi(\tfrac{1}{2}a) = 0\} \tag{3.10}$$

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

$$(T_\lambda\phi)(x) = \int_{\frac{1}{2}a}^{(\frac{1}{2},x)^-} k_\lambda(\xi)\phi(2\xi)d\xi\,,\ \phi \in X\,, \tag{3.11}$$

$$(U_\lambda f)(x) = \int_{\frac{1}{2}a}^{x} \frac{f(\xi)}{g(\xi)}\, e^{\lambda G(\xi) d\xi}\,,\ \ f \in L_1[\tfrac{1}{2}a,1]. \tag{3.12}$$

Theorem 3.3. *For all $\lambda \in \mathbf{C}$, the linear operators $T_\lambda : X \to X$ and $U_\lambda : L_1[\frac{1}{2}a,1] \to L_1[\frac{1}{2}a,1]$ are compact.*

The proof uses Arzéla-Ascoli-like arguments. See e.g. [13]. Let

$$\Sigma := \{\lambda \in \mathbf{C} | 1 \in P\sigma(T_\lambda)\}. \tag{3.13}$$

(We refer to the Introduction of this thesis for an explanation of the used notation). We can prove the following result.

Theorem 3.4. $\sigma(A) = P\sigma(A) = \Sigma$. *For all $\lambda \in \mathbf{C} \setminus \sigma(A)$ the resolvent $(\lambda I - A)^{-1}$ is compact.*

Proof. Putting $f = 0$ in (3.1) it follows that $A\psi = \lambda\psi$ if and only if $T_\lambda\phi = \phi$, where ϕ is given by (3.7). This yields that $P\sigma(A) = \Sigma$. Now suppose that $\lambda \notin P\sigma(A)$. Then we have that $I - T_\lambda$ is invertible. Let $f \in L_1[\frac{1}{2}a,1]$ and let ϕ be the solution of $\phi - T_\lambda\phi = U_\lambda f$. Then ϕ is well-defined because $U_\lambda f$ is (absolutely) continuous and can be regarded as an element of X (more precisely: as an element of the embedding of X in $L_1[\frac{1}{2}a,1]$). It follows immediately that ϕ is absolutely continuous. (This is yielded by the fact that $U_\lambda f$ and $T_\lambda\phi$ are absolutely continuous.) Now ψ, 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, ψ 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 which can be determined by means of the equation

$$T_\lambda \phi = \phi \ , \ \phi \in X.$$

Theorem 3.5. *All points of $\sigma(A)$ are isolated.*

Proof. Since $\|T_\lambda\| \to 0$ as $\mathrm{Re}\lambda \to \infty$ we have that $\lambda \in \rho(A)$ if $\mathrm{Re}\lambda$ is large enough. Now the result follows from the compactness of $(\lambda I - A)^{-1}$ (e.g. [13]). □

4. The dominant eigenvalue

Intuïtively it is clear that the operators T_λ defined by (3.11) are positive if λ is real. We shall make this more precise below. We assume during the rest of this section that λ is real unless otherwise stated.

Definition Let the cones $X_+, X_{++} \subseteq X$ be defined as

$$X_+ = \{\phi \in X | \phi(x) \geqslant 0 \ , \ \tfrac{1}{2} a \leqslant x \leqslant 1\},$$

$$X_{++} = \{\phi \in X_+ | \phi \text{ is non-decreasing}\}.$$

Note that $\phi_1 \leqslant \phi_2$ with respect to X_+ means something else than $\phi_1 \leqslant \phi_2$ with respect to X_{++}. We have confidence that this will not give rise to confusion.

The following result is almost trivial. For b) we refer to [11].

Lemma 4.1.

a) $X_{++} \subseteq X_+$.

b) *X_+ is reproducing. The space X with the ordering induced by X_+ defines a Banach lattice.*

c) *T_λ is positive with respect to X_+ and X_{++} for all $\lambda \in \mathbf{R}$.*

d) *$T_\lambda X_+ \subseteq X_{++}$ for all $\lambda \in \mathbf{R}$.*

This last assertion implies among others that if ϕ is an eigenvector of T_λ belonging to X_+ then automatically $\phi \in X_{++}$. Let X^* be the dual space of X, then X^* can be represented by all bounded variation functions on $[\frac{1}{2}a, 1]$ which are continuous from the left and zero in $\frac{1}{2}a$. For elements $\phi \in X$, $F \in X^*$, we denote the duality pairing by $\langle F, \phi \rangle$, i.e. $\langle F, \phi \rangle = \int_{a/2}^{1} \phi(x) dF(x)$. Obviously X^*_+ contains all nondecreasing elements of X^*.

In section 2 we noticed already that the cases $a > 0$ and $a = 0$ are essentially different. This difference becomes perfectly clear if we try to prove some strong positivity result for T_λ. First let us give a definition due to Krasnoselskii (see [8]).

Definition. Let L be a bounded operator on a Banach space Y with cone Y_+ and let $u_0 \in Y_+$. Then L is called u_0-positive if for all $\phi \in Y_+, \phi \neq 0$, there exists an integer n and positive constants α and β such that $\alpha u_0 \leqslant L^n \phi \leqslant \beta u_0$.

Now for $\lambda \in \mathbf{R}$ we define $u_\lambda \in X_{++}$ by

$$u_\lambda(x) = \int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} k_\lambda(\xi) d\xi \ , \ \tfrac{1}{2}a \leqslant x \leqslant 1 \ . \tag{4.1}$$

Theorem 4.2. *If $a > 0$ then T_λ is u_λ-positive with respect to the cone X_{++}.*

Proof Let $\phi \in X_{++}$, $\phi \neq 0$. A straightforward computation shows that $(T_\lambda^n \phi)(x) > 0$, for all $(2^{-n}, \frac{1}{2}a)^+ \leqslant x \leqslant 1$, where $(\alpha, \beta)^+ = \max\{\alpha, \beta\}$. If n is so large that $2^{-n} \leqslant \frac{1}{2} a$, then we have $T_\lambda^n \phi \in X_{++}$ and $(T_\lambda^n \phi)(x) > 0, \frac{1}{2}a < x \leqslant 1$. Therefore

$$(T_\lambda^{n+1}\phi)(x)-(T_\lambda^n\phi)(a).u_\lambda(x) = \int_{a/2}^{(1/2,x)^-} k_\lambda(\xi).\{(T_\lambda^n\phi)(2\xi)-(T_\lambda^n\phi)(a)\}d\xi\in X_{++}$$

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 $T_\lambda^{n+1}\phi-\ (T_\lambda^n\phi)(a).u_\lambda\in X_{++}$. For all $\psi\in X_{++}$, $\psi\neq 0$, we have

$$\psi(1).u_\lambda(x)-(T_\lambda\psi)(x) = \int_{\frac{1}{2}a}^{(\frac{1}{2},x)^-} k_\lambda(\xi).\{\psi(1)-\psi(2\xi)\}d\xi,$$

which implies that $\psi(1).u_\lambda - T_\lambda\psi\in X_{++}$, because $\psi(1)-\psi(2\xi)\geqslant 0$ for all ξ with $\frac{1}{2}a\leqslant\xi\leqslant\frac{1}{2}$. As a consequence $T_\lambda\psi\leqslant\psi(1).u_\lambda$. If we substitute $\psi = T_\lambda^n\phi$ we find $T_\lambda^{n+1}\phi\leqslant(T_\lambda^n\phi)(1).u_\lambda$, and this completes the proof. □

Theorem 4.3 *If $a = 0$ then T_λ is non-supporting with respect to the cone X_+.*

Proof Let $\phi\in X_+$, $\phi\neq 0$ and $F\in X_+^*$, $F\neq 0$. The fact that $F\neq 0$ implies that there exists an $\bar{x}$ with $0 < \bar{x} \leqslant 1$ such that $F(\bar{x}-\epsilon)<F(\bar{x})$ for all $0<\epsilon<\bar{x}$. Let p be an integer such that $2^{-p} < \bar{x}$. Then $(T_\lambda^n\phi)(x) > 0$, $x\in(2^{-p},1]$ for all $n\geqslant p$. Hence $< F,T_\lambda^n\phi > \geqslant \int_{2^{-p}}^{\bar{x}} (T_\lambda^n\phi)(x)dF(x) >0$ if $n\geqslant p$, and this proves the result. □

Now the following result holds.

Theorem 4.4 *Let $\lambda\in\mathbf{R}$ and $r_\lambda = r(T_\lambda)$, then*

a) *r_λ is an algebraically simple eigenvalue of T_λ.*

b) *There exists a non-trivial eigenvector $\phi_\lambda\in X_{++}$ such that $T_\lambda\phi_\lambda = r_\lambda\,\phi_\lambda$.*

c) *There exists a strictly positive (with respect to X_+) eigenfunctional $F_\lambda\in X_+^*$ such that $T_\lambda^*F_\lambda = r_\lambda\,F_\lambda$.*

Proof. (i) Let $a>0$. Then the results (a) and (b) follow from the u_λ-positivity of T_λ (e.g. [8]). However, we should make the remark that Krasnoselskii proves the result in case that the underlying cone is reproducing which is not true for the cone X_{++}. However it follows directly that his result remains valid if the following weaker condition on the cone is satisfied: for every $\phi\in X$ there exist $\phi_1,\phi_2\in X_{++}$ such that $T_\lambda\phi = \phi_1-\phi_2$, and in our case this follows from the fact that X_+ is reproducing and $T_\lambda X_+\subseteq X_{++}$. The strict positivity of the functional F_λ, whose existence is guaranteed by a result of Krein and Rutman (see [9]), can be proved in the following way. Suppose $< F_\lambda,\phi > = 0$ for some $\phi\in X_+\setminus\{0\}$. Since $\alpha\,u_\lambda\leqslant T_\lambda^n\phi\leqslant\beta u_\lambda$ for some $n\in\mathbb{N}$ and $\alpha,\beta>0$ we have that $\alpha< F_\lambda,u_\lambda > \leqslant\ < F_\lambda,T_\lambda^n\phi> = r_\lambda^n <F_\lambda,\phi> = 0$. Consequently $<F_\lambda,u_\lambda> = 0$ which implies that $<F_\lambda,\psi> = 0$ for all $\psi\in X_+$ (since $T_\lambda^m\psi\leqslant\beta u_\lambda$). But now the fact that X_+ is reproducing yields that $F_\lambda = 0$, which is a contradiction.

(ii) For $a = 0$ the proof follows from a result of Sawashima on non-supporting operators; (see [10] or the Introduction of this thesis). □

Remark 4.5 i) There is a more elegant and transparant way to obtain the results for $a>0$. The basic idea is to study the integral equation $T_\lambda\phi = \phi$ on the subinterval [a, 1].

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

The values of $T_\lambda\phi$, for $\phi\in X$, on the interval $[\frac{1}{2}a,a]$ are completely determined by the values of $\tilde{\phi} = \phi|_{[a,1]}\in\tilde{X}\overset{def}{=}C[a,1]$, i.e. the restriction of ϕ to [a, 1]. Suppose $\tilde{\phi}\in\tilde{X}$ is a solution of $\tilde{T}_\lambda\tilde{\phi} = \tilde{\phi}$, where $\tilde{T}_\lambda$ is given by (*), and let the extension ϕ of $\tilde{\phi}$ on $[\frac{1}{2}a,1]$, be defined by

$$\phi(x) = \tilde{\phi}(x), \quad a \leq x \leq 1,$$

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

Then $\phi \in X$ and ϕ is a solution of the original equation $T_\lambda\phi = \phi$. The advantage of this method is, that it permits us to work in the cone $\tilde{X}_+ = \{\phi \in \tilde{X} \mid \phi(x) \geq 0\}$, which has non-empty interior $\mathring{\tilde{X}}_+$. The operator $\tilde{T}_\lambda$ is strongly positive with respect to $\tilde{X}_+$, i.e. for all $\phi \in \tilde{X}_+$ there exists an integer $n = n(\phi)$ such that $\tilde{T}_\lambda^n\ \phi \in \mathring{\tilde{X}}_+$. Now the unicity of the positive eigenvector is given by theorem 6.3. of Krein and Rutman in [9].
ii) If $a > 0$ then T_λ is *not* non-supporting, neither with respect to X_+ nor with respect to X_{++}.

As mentioned before we are only interested in those values of λ for which 1 is an eigenvalue of T_λ. This motivates us to look for real solutions of

$$r(T_\lambda) = 1.$$

Theorem 4.6. *There exists a unique real solution λ_d of the equation $r(T_\lambda) = 1$.*

Proof. Let $\lambda, \mu \in \mathbf{R}$, $\lambda < \mu$ and let ϕ_λ, ϕ_μ, F_λ and F_μ be as in theorem 4.4. Then

$$r_\mu = \frac{<T_\mu^* F_\mu, \phi_\lambda>}{<F_\mu, \phi_\lambda>} = \frac{<F_\mu, T_\mu\phi_\lambda>}{<F_\mu, \phi_\lambda>} = \frac{<F_\mu, T_\lambda\phi_\lambda>}{<F_\mu, \phi_\lambda>} - \frac{<F_\mu, (T_\lambda - T_\mu)\phi_\lambda>}{<F_\mu, \phi_\lambda>} = r_\lambda - \Delta,$$

where $\Delta = \Delta(\lambda,\mu) = \dfrac{<F_\mu, (T_\lambda - T_\mu)\phi_\lambda>}{<F_\mu, \phi_\lambda>} > 0$, because $(T_\lambda - T_\mu)\phi_\lambda > 0$ and F_μ is strictly positive. Therefore $r_\mu < r_\lambda$, which implies that $r_\lambda = r(T_\lambda)$ is strictly monotone decreasing in λ. Moreover $\lim_{\mu\to\lambda} \Delta(\lambda,\mu) = 0$, which yields the continuity of r_λ. Now suppose that $\|\phi_\lambda\| = 1$. Clearly

$$(T_\lambda\phi_\lambda)(1) = \|T_\lambda\ \phi_\lambda\| = r_\lambda\|\phi_\lambda\| = r_\lambda = \int_{\frac{1}{2}a}^{\frac{1}{2}} k_\lambda(\xi)\phi_\lambda(2\xi)d\xi,$$

where we have used that $\|\psi\| = \psi(1)$ if $\psi \in X_{++}$. One also sees that $\phi_\lambda(x) = \phi_\lambda(1) = \|\phi_\lambda\| = 1$, $\frac{1}{2} \leq x \leq 1$, and we obtain that

$$\int_{\frac{1}{4}}^{\frac{1}{2}} k_\lambda(\xi)d\xi \leq r_\lambda \leq \int_{\frac{1}{2}a}^{\frac{1}{2}} k_\lambda(\xi)d\xi, \ \lambda \in \mathbf{R}, \tag{4.2}$$

and from these inequalities we conclude that $\lim_{\lambda\to-\infty} r(T_\lambda) = \infty$, $\lim_{\lambda\to\infty} r(T_\lambda) = 0$, and now the result follows immediately. □

Remark 4.7. If $a > 0$ then one can easily obtain the following estimates: let $\lambda, \mu \in \mathbf{R}$, $\lambda < \mu$, then

$$e^{(\mu-\lambda)m}\, T_\mu\, \phi \leq T_\lambda\, \phi \leq e^{(\mu-\lambda)M}\, T_\mu\, \phi, \ \phi \in X_+,$$

where $m = \min_{\frac{1}{2}a \leq x \leq \frac{1}{2}} \{G(2x) - G(x)\}$, $M = \max_{\frac{1}{2}a \leq x \leq \frac{1}{2}} \{G(2x) - G(x)\}$. Obviously $0 < m \leq M < \infty$. Note that $a = 0$ implies that $m = 0$. Now substituting $\phi = \phi_\mu$ and taking the duality pairings with F_λ yields

$$e^{(\mu-\lambda)m}.r_\mu \leq r_\lambda \leq e^{(\mu-\lambda)M}\ .\ r_\mu,$$

and this also gives the conclusion of theorem 4.6.

Now we have proved that there exists a unique $\lambda_d \in \mathbf{R}$ and (except for a constant) a unique

$\phi_d = \phi_{\lambda_d} \in X_{++}$ and $F_d = F_{\lambda_d} \in X^*_+$ (which is strictly positive) such that

$$T_{\lambda_d}\phi_d = \phi_d \, , \, T^*_{\lambda_d}F_d = F_d \, , \tag{4.3}$$

and the eigenvalue 1 of T_{λ_d} is algebraically simple. Now let $\psi_d \in X_+$ be defined by

$$\psi_d(x) = e^{-\lambda_d G(x)}.\phi_d(x) \, , \tag{4.4}$$

then the following result holds.

Theorem 4.8. *$A\psi_d = \lambda_d \psi_d$ and the eigenvalue λ_d of A is algebraically simple.*

Proof The first conclusion follows from the results in section 3. The geometric simplicity of the eigenvalue λ_d of A follows directly from the geometric simplicity of the eigenvalue 1 of T_{λ_d}.
Now suppose that $(\lambda_d - A)^2\psi = 0$, for some $\psi \in \mathfrak{D}(A^2)$. Let $\bar{\psi} \overset{def}{=} (\lambda_d - A)\psi$, then $A\bar{\psi} = \lambda_d \bar{\psi}$ and $\bar{\psi} \neq 0$, from which we conclude that $\bar{\psi} = \alpha.\psi_d$ for some constant α, which we may assume to be 1. In section 3 we showed that the equation $\lambda_d\psi - A\psi = \psi_d$ can be rewritten as $\phi - T_{\lambda_d}\phi = U_{\lambda_d}\psi_d$, where $\phi(x) = e^{\lambda_d G(x)}\psi(x)$. Taking duality pairings with F_d yields $< F_d, U_{\lambda_d}\psi_d > = 0$ which is a contradiction because $U_{\lambda_d}\psi_d \in X_+ \setminus \{0\}$, and F_d is strictly positive. This proves the result. □

5. The characteristic equation.

In this section we deduce the so-called characteristic equation, i.e. the equation from which the eigenvalues of A can be computed (at least numerically). This equation happens to be a very tractable one if $a \geq \frac{1}{2}$, but it becomes more and more intractable according as a becomes smaller.
Let the Banach space Y be the space of all continuous functions on $[\frac{1}{2}a, 1]$ with the supnorm. Clearly X is a closed subspace of Y. For every $\lambda \in \mathbf{C}$ the operator $T_\lambda : X \rightarrow X$ can be extended to the larger space Y. This extension is also denoted by the symbol T_λ.

$$(T_\lambda\phi)(x) = \int_{\frac{1}{2}a}^{(\frac{1}{2},x)^-} k_\lambda(\xi)\phi(2\xi)d\xi, \ \phi \in Y. \tag{5.1}$$

One sees immediately: $T_\lambda Y \subset X$. As a consequence $T_\lambda\phi = \phi$, $\phi \in Y$, implies that $\phi \in X$. Using theorem 3.4, we obtain

$$\lambda \in \sigma(A) \Leftrightarrow 1 \in P\sigma(T_\lambda|_X) \Leftrightarrow 1 \in P\sigma(T_\lambda) \tag{5.2}$$

where $T_\lambda|_X$ denotes the restriction of $T_\lambda : Y \rightarrow Y$ to the subspace X. Let $e_1 \in Y$ defined by:

$$e_1(x) = 1, \ \tfrac{1}{2}a \leq x \leq 1. \tag{5.3}$$

$T_\lambda : Y \rightarrow Y$ can be decomposed in the following way. Let $\phi \in Y$:

$$(T_\lambda\phi)(x) = \int_{\frac{1}{2}a}^{\frac{1}{2}} k_\lambda(\xi)\phi(2\xi)d\xi - \int_{(\frac{1}{2},x)^-}^{\frac{1}{2}} k_\lambda(\xi)\phi(2\xi)d\xi = H_\lambda(\phi)e_1 + N_\lambda\phi, \tag{5.4}$$

where H_λ is a bounded linear functional on Y,

$$H_\lambda(\phi) \overset{def}{=} \int_{\frac{1}{2}a}^{\frac{1}{2}} k_\lambda(\xi)\phi(2\xi)d\xi \, , \tag{5.5}$$

and N_λ is a bounded linear operator on Y,

$$(N_\lambda\phi)(x) \overset{def}{=} - \int_{(\frac{1}{2},x)^-}^{\frac{1}{2}} k_\lambda(\xi)\phi(2\xi)d\xi. \tag{5.6}$$

The reason that we have embedded X in the larger space is clear now: Y is invariant under N_λ, whereas X isn't. We make a distinction between the cases $a > 0$ and $a = 0$.

I. $a > 0$

Lemma 5.1. *The operator N_λ is compact and nilpotent, for all $\lambda \in \mathbb{C}$, i.e. $N_\lambda^p = 0$ for some $p \in \mathbb{N}$. (Here p does not depend on λ.)*

Proof. Compactness is trivial. Let $p \in \mathbb{N}$ be such that $2^{-p+1} \leqslant a < 2^{-p+2}$. Then we have $N_\lambda^{p-1} \neq 0$ and $N_\lambda^p = 0$. This follows from the observation that $(N_\lambda^i \phi)(x) = 0$, $x \geqslant 2^{-i}$ for all $\phi \in Y$ and $i = 0, 1, \cdots$. □

Substitution of $T_\lambda \phi$ in (5.4) yields

$$T_\lambda^2 \phi = H_\lambda(T_\lambda \phi) e_1 + N_\lambda(T_\lambda \phi) = H_\lambda(T_\lambda \phi) e_1 + H_\lambda(\phi) N_\lambda e_1 + N_\lambda^2 \phi. \tag{5.7}$$

We define

$$e_j := N_\lambda e_{j-1}, \; j = 2, \cdots, p. \tag{5.8}$$

Notice that

$$N_\lambda e_p = N_\lambda^p e_1 = 0. \tag{5.9}$$

Lemma 5.2. *$e_1, \cdots, e_p$ are linearly independent in Y. Furthermore $\Re(T_\lambda^p) \subset span < e_1, \cdots, e_p >$, where $span < e_1, \cdots, e_p >$ is the subspace of Y spanned by the functions $e_1, \cdots, e_p$.*

Proof. $e_2(x) = (N_\lambda e_1)(x) \neq 0$, if $x < \frac{1}{2}$. A straightforward computation shows that for all i, with $1 \leqslant i \leqslant p$, we have $e_i(x) \neq 0$ if $x < 2^{-i+1}$. Now suppose that for certain $\alpha_i \in \mathbb{C}$, $i = 1, \cdots, p$, $\alpha_1 e_1 + \cdots + \alpha_p e_p = 0$. 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 $i = 2, \cdots, p$. This proves the linear independence of $e_1, \cdots, e_p$. Recursion of (5.7) yields

$$T_\lambda^p \phi = H_\lambda(T_\lambda^{p-1}\phi) e_1 + H_\lambda(T_\lambda^{p-2}\phi) e_2 + \cdots + H_\lambda(\phi) e_p \tag{5.10}$$

for all $\phi \in Y$, where we have used that $N_\lambda^p = 0$. This completes the proof. □

Defining

$$f_j \stackrel{def}{=} H_\lambda(e_j), \; j = 1, \cdots, p \tag{5.11}$$

we have

$$T_\lambda e_j = H_\lambda(e_j) e_1 + N_\lambda e_j = f_j e_1 + e_{j+1}, \; j = 1, \cdots, p, \text{ where } e_{p+1} \stackrel{def}{=} 0. \tag{5.12}$$

Remark 5.3. One should keep in mind that e_j and f_j both depend on λ.

Now suppose that $\lambda \in \sigma(A)$. This implies that $1 \in P\sigma(T_\lambda)$. Therefore $T_\lambda \phi = \phi$ for some $\phi \in Y, \phi \neq 0$. Consequently $T_\lambda^p \phi = \phi$. In other words $\phi \in \Re(T_\lambda^p) \subset span < e_1, \cdots, e_p >$. Hence we can write $\phi = \phi_1 e_1 + \cdots + \phi_p e_p$. Using (5.12) we find

$$\sum_{i=1}^{p} \phi_i e_i = \phi = T_\lambda \phi = \sum_{i=1}^{p} \phi_i (f_i e_1 + e_{i+1}).$$

Using the linear independence of the functions e_i we conclude

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

$\phi \neq 0$ 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 5.4. *$\lambda \in \sigma(A)$ if and only if $H_\lambda(e_1 + \cdots + e_{p-1}) = 1$.*

$H_\lambda(e_1 + \cdots + e_{p-1}) = 1$ is called the characteristic equation. If $a \geq \frac{1}{2}$ then it takes the following simple form:

$$\int_{\frac{1}{2}a}^{\frac{1}{2}} k_\lambda(x)dx = 1.$$

II. $a = 0$

Let H_λ and N_λ be defined by (5.5) and (5.6) where $\frac{1}{2}a$ is replaced by 0.

$$T_\lambda \phi = H_\lambda(\phi)e_1 + N_\lambda \phi, \ \phi \in Y. \tag{5.13}$$

Let e_j be defined by (5.8) for all $j \geq 1$.

Lemma 5.5. *N_λ is compact and quasinilpotent.*

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

Lemma 5.6. *Let $\eta_\lambda = \sum_{k=1}^{\infty} e_k$, then $\eta_\lambda \in Y$ and $\|\eta_\lambda\|$ is uniformly bounded in every vertical strip $s \leq \mathrm{Re}\lambda \leq t$.*

Proof. Let $\lambda \in \mathbf{C}$ be such that $s \leq \mathrm{Re}\lambda \leq t$, where $s, t \in \mathbf{R}$, $s \leq t$. Obviously $\|e_1\| = 1$. For e_2 we have

$$|e_2(x)| \leq \int_{(\frac{1}{2}x)}^{\frac{1}{2}} |k_\lambda(\xi)| d\xi < \int_0^{\frac{1}{2}} |k_\lambda(\xi)| d\xi < \infty,$$

and therefore $e_2(x) = 0$, $x \geq \frac{1}{2}$, $|e_2(x)| \leq M$, $x \leq \frac{1}{2}$, where $M := \max_{s \leq \mathrm{Re}\lambda \leq t} (\int_0^{\frac{1}{2}} |k_\lambda(\xi)| d\xi)$. Likewise

$$|e_3(x)| \leq \int_0^{\frac{1}{4}} |k_\lambda(\xi)| M d\xi \leq \tfrac{1}{4} L\ M,$$

where

$$L := \max\{|k_\lambda(\xi)| \mid 0 \leq \xi \leq \tfrac{1}{4}, s \leq \mathrm{Re}\lambda \leq t\}. \tag{5.14}$$

By induction we find that

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

and the proof follows. □

Theorem 5.7. *$T_\lambda\phi = \phi$ has a solution if and only if $H_\lambda(\eta_\lambda) = 1$. In that case η_λ is the unique solution (except for a constant).*

Proof.

(i)Suppose $T_\lambda\phi = \phi$. Inserting (5.13) we obtain $N_\lambda\phi = \phi - H_\lambda(\phi)e_1$. If we put $\hat{\phi} = H_\lambda(\phi)\eta_\lambda$ then $N_\lambda(\phi-\hat{\phi}) = \phi - H_\lambda(\phi)e_1 - H_\lambda(\phi)N_\lambda\eta_\lambda = \phi - H_\lambda(\phi)e_1 - H_\lambda(\phi)\ (e_2+e_3+....) = \phi-\hat{\phi}$. Now the quasinilpotency of N_λ 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 $H_\lambda(\eta_\lambda) = 1$. Then $T_\lambda\eta_\lambda = H_\lambda(\eta_\lambda)e_1 + N_\lambda\eta_\lambda = \eta_\lambda$. □

In this case $H_\lambda(\eta_\lambda) = 1$ is called the characteristic equation. From the above construction it should be clear that it makes no sense to write down the explicit expression.

6. 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 λ_d. It appears that the outcome depends heavily on the individual growth rate $g(x)$. The following arguments show why this is so.

The kernel $k_\lambda(x)$ of the integral operator T_λ (c.f (3.8)) can be written as

$$k_\lambda(x) = \frac{k(x)}{g(x)}e^{-\lambda r(x)},\ \tfrac{1}{2}a \leqslant x \leqslant \tfrac{1}{2}, \tag{6.1}$$

where

$$r(x) = G(2x) - G(x). \tag{6.2}$$

Obviously $\frac{dr}{dx} = \frac{2g(x)-g(2x)}{g(x)g(2x)}$. Hence, if $2g(x) = g(2x)$ for all $x \in[\frac{1}{2}a,\frac{1}{2}]$, 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 position of the eigenvalues of A. In this section we shall restrict ourselves to the case

$$g(2x) < 2g(x),\ \tfrac{1}{2}a \leqslant x \leqslant \tfrac{1}{2}, \tag{6.3}$$

and from now on we assume that this relation is satisfied. However we emphasize that all results carry over to the case $g(2x)>2g(x)$,$\frac{1}{2}a\leqslant x \leqslant \frac{1}{2}$.

We have seen that the operator A has exactly one positive eigenvector corresponding to an eigenvalue $\lambda_d\in\mathbb{R}$ (see section 4). Now we shall prove that λ_d is the strictly dominant value of A, i.e. all the other eigenvalues of A have a real part which is strictly less than λ_d. We need the following elementary lemma.

Lemma 6.1. *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 $u(x) \underset{def}{=} \mathrm{Re}\{\alpha f(x)\}$ 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 $\mathrm{Im}\{\alpha f(x)\}\neq 0$. 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. Obviously

$$|\int_a^b f(x)dx| = |z| = \alpha z = \int_a^b \alpha f(x)dx = \mathrm{Re}\{\int_a^b \alpha f(x)dx\} = \int_a^b \mathrm{Re}\{\alpha f(x)\}dx = \int_a^b u(x)dx\ .$$

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 6.2. *If* $\lambda \in P\sigma(A)$ *and* $\lambda \neq \lambda_d$ *then* $\mathrm{Re}\lambda < \lambda_d$.

Proof (i) Suppose $\lambda \in \sigma(A)$ and $\mathrm{Re}\lambda > \lambda_d$. Then $1 \in P\sigma(T_\lambda)$ which implies that $T_\lambda \phi = \phi$ for some $\phi \in X$. Thus

$$\phi(x) = \int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} k_\lambda(\xi)\phi(2\xi)d\xi = \int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} \frac{k(\xi)}{g(\xi)} e^{-\lambda r(\xi)}\phi(2\xi)d\xi.$$

Taking absolute values on both sides, we find $\int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} \frac{k(\xi)}{g(\xi)} e^{-\mathrm{Re}\lambda r(\xi)} |\phi(2\xi)|d\xi \geq |\phi(x)|$, which can be written as: $T_{\mathrm{Re}\lambda}|\phi| \geq |\phi|$ (with respect to X_+) where $|\phi| \in X$ is defined by $|\phi|(x) := |\phi(x)|$. Using theorem 6.2. of Krein and Rutman [9] we obtain $T_{\mathrm{Re}\lambda}\psi = \rho\psi$ for some $\psi \in X_+ / \{0\}$ and $\rho \geq 1$. Consequently $r(T_{\mathrm{Re}\lambda}) \geq 1$. On the other hand, theorem 4.6. states that $r(T_{\mathrm{Re}\lambda}) < 1$. Now we have proved that $\lambda \in \sigma(A)$ implies that $\mathrm{Re}\lambda \leq \lambda_d$.
(ii) Suppose that $\lambda = \lambda_d + i\eta$ and $\lambda \in \sigma(A)$. This implies that $T_\lambda \psi = \psi$ for some $\psi \in X$ and as in (i) we deduce $T_{\mathrm{Re}\lambda}|\psi| \geq |\psi|$, i.e. $T_{\lambda_d}|\psi| \geq |\psi|$. Suppose $T_{\lambda_d}|\psi| \neq |\psi|$. This yields $T_{\lambda_d}|\psi| - |\psi| \in X_+ \setminus \{0\}$. Let F_d be the strictly positive eigenfunctional satisfying $T^*_{\lambda_d} F_d = F_d$. Then $0 < \langle F_d, T_{\lambda_d}|\psi| - |\psi| \rangle = \langle T^*_{\lambda_d} F_d - F_d, |\psi| \rangle = 0$, which is a contradiction. Consequently $T_{\lambda_d}|\psi| = |\psi|$, which means, by the simplicity of the eigenvalue 1 of T_{λ_d} that $|\psi| = \gamma\phi_d$, for some constant $\gamma \in \mathbf{C}$, which we may assume to be one without loss of generality. As a consequence $|\psi(x)| = \phi_d(x)e^{i\alpha(x)}$, where $\alpha(x) \in \mathbf{R}$, $x \in [\frac{1}{2}a, 1]$. Using $|T_\lambda \psi| = |\psi| = T_{\mathrm{Re}\lambda}|\psi| = T_{\lambda_d}\phi_d$, we find

$$\int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} k_{\lambda_d}(\xi)\phi_d(2\xi)d\xi = |\int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} k_\lambda(\xi)\psi(2\xi)d\xi| = |\int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} e^{-i\eta r(\xi)} k_{\lambda_d}(\xi)\phi_d(2\xi)e^{i\alpha(2\xi)}d\xi|.$$

Using lemma 6.1. 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

$$\int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} k_\lambda(\xi)\psi(2\xi)d\xi = \psi(x) = \int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} e^{-i\eta r(\xi)} k_{\lambda_d}(\xi)\phi_d(2\xi)e^{i\alpha(2\xi)}d\xi = \phi_d(x)e^{i\alpha(x)},$$

we obtain $e^{iC}\int_{\frac{1}{2}a}^{(\frac{1}{2}x)^-} k_{\lambda_d}(\xi)\phi_d(2\xi)d\xi = \phi_d(x)e^{iC + i\eta r(\frac{1}{2}x)}$, which implies $\phi_d(x) = \phi_d(x)e^{i\eta r(\frac{1}{2}x)}$ a.e. on [a,1].
Because r is a continuous increasing function on $[\frac{1}{2}a, \frac{1}{2}]$ we obtain $\eta = 0$, which implies that $\lambda = \lambda_d$. □

In section 3 we noticed that all elements of $\sigma(A)$ are isolated (c.f theorem 3.5). Now we are going to show that in every vertical strip $s \leq \mathrm{Re}\lambda \leq t$, there are only finitely many of them.

Theorem 6.3. *Suppose* $s < t$. *In the vertical strip* $s \leq \mathrm{Re}\lambda \leq t$, *there are only finitely many points of* $\sigma(A)$.

Proof. (i) Let $a > 0$. Suppose $\lambda \in \sigma(A)$. From theorem 5.4 we conclude that $H_\lambda(e_1 + \dots + e_{p-1}) = 1$.

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

where we have used (6.1). Because $r'(\xi)\neq 0$ the well-known Riemann-Lebesque lemma states that

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

Using the same arguments for $i > 1$, we find $\lim_{\mathrm{Im}\lambda\to\pm\infty} H_\lambda(e_1+\cdots+e_{p-1}) = 0$, uniformly in $s \leqslant \mathrm{Re}\lambda \leqslant t$. This together with the fact that all elements of $\sigma(A)$ are isolated (see theorem 3.5) proves the result for $a > 0$.

(ii) Let $a = 0$. Let $\lambda\in\sigma(A)$ and $s \leqslant \mathrm{Re}\lambda \leqslant t$. According to lemma 5.6 there exists a constant $M_1 > 0$ such that $||\eta_\lambda|| \leqslant M_1$. Theorem 5.7 yields that $H_\lambda(\eta_\lambda) = 1$. We have

$$H_\lambda(\eta_\lambda) = \int_0^1 k_\lambda(\xi)\eta_\lambda(2\xi)d\xi = \int_0^\epsilon k_\lambda(\xi)\eta_\lambda(2\xi)d\xi + \int_\epsilon^1 k_\lambda(\xi)\eta_\lambda(2\xi)d\xi.$$

Now $|\int_0^\epsilon k_\lambda(\xi)\eta_\lambda(2\xi)d\xi| \leqslant M_1\int_0^\epsilon|k_\lambda(\xi)|d\xi \leqslant LM_1\epsilon$, where L is defined by (5.14). We choose $\epsilon < \frac{1}{4}$ such that $\epsilon LM_1 \leqslant \frac{1}{2}$. Hence

$$|H_\lambda(\eta_\lambda)| \leqslant \tfrac{1}{2} + |\int_\epsilon^{\frac{1}{2}} k_\lambda(\xi)\eta_\lambda(2\xi)d\xi|$$

for all λ satisfying $s \leqslant \mathrm{Re}\lambda \leqslant t$. There exists a $j_0\in\mathbb{N}$ such that $j > j_0$ implies $e_j(x) = 0$ if $x \geqslant \epsilon$. This yields

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

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

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

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

$$\sum_{j=1}^{j_0}|\int_\epsilon^{\frac{1}{2}} k_\lambda(\xi)e_j(2\xi)d\xi| \leqslant \tfrac{1}{4}.$$

For these values of λ we obtain $|H_\lambda(\eta_\lambda)|\leqslant\frac{3}{4}$ and we conclude from theorem 5.7 that $\lambda\notin\sigma(A)$. Again, the result follows from the fact that all elements of $\sigma(A)$ are isolated. □

We call $n_d(x) = \dfrac{E(x)}{g(x)}.\psi_d(x)$ (c.f. (2.5)) the stable size distribution. In chapter III of this thesis it becomes clear why.

7. Position of the eigenvalues for the case $g(2x) = 2g(x)$

In this section we shall investigate what happens if

$$g(2x) = 2g(x),\ \tfrac{1}{2}a \leqslant x \leqslant \tfrac{1}{2}. \tag{7.1}$$

Then we have

$$r(x) = G(2x)-G(x) = r,\ \tfrac{1}{2}a \leqslant x \leqslant \tfrac{1}{2}, \tag{7.2}$$

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

$$T_\lambda = e^{-\lambda r} T_0. \tag{7.3}$$

Because T_0 defines a compact operator, its spectrum is the union of $\{0\}$ and a set containing at most countably many non-zero eigenvalues $\sigma_1, \ldots, \sigma_q$, where q is allowed to be ∞.

Remark 7.1. If $a > 0$ it can be shown that $q \leqslant p-1$ where p is the integer determined by lemma 5.1, i.e. $2^{-p+1} \leqslant a < 2^{-p+2}$.

Using (7.3) it follows immediately that $\lambda \in \Sigma$ if and only if $e^{-\lambda r}\sigma_j = 1$ for some $1 \leqslant j \leqslant q$. Let λ_{j0} be a solution of $e^{-\lambda r}\sigma_j = 1$, then

$$\Sigma = \{\lambda_{j0} + i.\frac{2k\pi}{r} \mid 1 \leqslant j \leqslant q, k \in \mathbb{Z}\}. \tag{7.4}$$

As a consequence there does not exist a strictly dominant eigenvalue.

Remark 7.2. The above results can also be obtained from the characteristic equation. If $a > 0$ it can be proved that $H_\lambda(e_1 + \cdots + e_{p-1}) = C_1.e^{-\lambda r} + C_2 . (e^{-\lambda r})^2 + \cdots + C_{p-1} . (e^{-\lambda r})^{p-1}$ (see theorem 5.4) where C_i, $i = 1, \cdots, p-1$ are real coefficients. If $a = 0$ we find $H_\lambda(\eta_\lambda) = \Phi(e^{-\lambda r})$ (see theorem 5.7) where Φ 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 whose mother belonged to the cohort, will have a size which equals exactly half the size of an undivided member of the cohort, 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 unvalid if a mother cell not necessarily divides into two equal daughters. In [6] (see also chapter VI of this thesis), we study the situation that division occurs into unequal parts, more precisely, the ratio $\frac{\text{birth size of daughter}}{\text{division size of mother}}$ is a random variable satisfying a smooth probability density function, and in that case we find indeed that there 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 γ is some constant. In the literature, this is called the case of "exponential individual growth". (See e.g. [1, 2].) This nomenclature becomes clear if one observes that the solution of (1.1) is $x(t) = x(0)e^{\gamma t}$, if $g(x) = \gamma x$.

Remark 7.3. If the relation $g(2x) = 2g(x)$ is satisfied on a nontrivial subset of $[\frac{1}{2}a, \frac{1}{2}]$, then the question concerning the existence of a strictly dominant eigenvalue is more difficult to answer. In [3, part II] it is shown that indeed there does exist a strictly dominant eigenvalue in this case (see also chapter III of this thesis).

8. 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 shall be omitted.

The adjoint operator A^* is given by

$$(A^* f)(x) = \frac{d}{dx}(g(x)f(x)) + \tfrac{1}{2}k(\tfrac{1}{2}x)f(\tfrac{1}{2}x) \tag{8.1}$$

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

$$\mathfrak{D}(A^*) = \{f \in L_\infty[\tfrac{1}{2}a, 1] \mid gf \text{ is absolutely continuous,} \tag{8.2}$$

the function $x \rightarrow \frac{d}{dx}(g(x)f(x)) + \frac{1}{2}k(\frac{1}{2}x)f(\frac{1}{2}x)$ belongs to $L_\infty[\frac{1}{2}a, 1]$ and $f(1) = 0\}$.

Here $L_\infty[\frac{1}{2}a, 1]$ is the dual space of $L_1[\frac{1}{2}a, 1]$, i.e. the Banach space of essentially bounded, measurable functions. The eigenvalue problem $A^* f = \lambda f$ can be rewritten as

$$h(x) = \int_{(\frac{1}{2}x, \frac{1}{2}a)'}^{1} k_\lambda(\xi) h(\xi) d\xi \tag{8.3}$$

where h is given by

$$h(x) = e^{-\lambda G(x)} g(x) f(x) \ . \tag{8.4}$$

Notice that every solution h of (8.3) is a continuous function. Let h_d be the solution of (8.3) for $\lambda = \lambda_d$. Then $h_d(x) > 0$ for $\frac{1}{2}a \leq x < 1$. Let f_d be given by

$$f_d(x) = \frac{h_d(x)}{g(x)} e^{-\lambda_d G(x)} , \tag{8.5}$$

then we have

$A^* f_d = \lambda_d f_d$,

f_d is continuous on $[\frac{1}{2}a, 1]$,

$f_d(x) > 0$, $\frac{1}{2}a \leq x < 1$, $f_d(1) = 0$.

Because of the algebraic simplicity of the eigenvalue λ_d, and the compactness of the resolvent of A (see theorem 3.4) we can give the following decomposition of the space $L_1[\frac{1}{2}a, 1]$:

$$L_1[\tfrac{1}{2}a, 1] = \mathcal{N}(\lambda_d I - A) \oplus \mathcal{R}(\lambda_d I - A) \ , \tag{8.6}$$

where $\mathcal{N}(\lambda_d I - A)$ is the null space of $\lambda_d I - A$ and $\mathcal{R}(\lambda_d I - A)$ denotes the range.

Let P be the projection on $\mathcal{N}(\lambda_d I - A)$ with respect to this decomposition, then we have

$$P\phi = \int_{\frac{1}{2}a}^{1} f_d(x) \phi(x) dx . \psi_d ,$$

where the pair f_d, ψ_d is normalized by the condition

$$\int_{\frac{1}{2}a}^{1} f_d(x) \psi_d(x) dx = 1.$$

Remark 8.1. The properties of f_d mentioned above can also be found using the positivity of the resolvent operator $(\lambda I - A)^{-1}$ for $\lambda > \lambda_d$.

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On the stability of the cell size distribution

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Abstract. A model for the growth of a size-structured cell population reproducing by fission into two identical daughters is formulated and analysed. The model takes the form of a linear first order partial differential equation (balance law) in which one term has a transformed argument. Using semigroup theory and compactness arguments we establish the existence of a stable size distribution under a certain condition on the growth rate of the individuals. An example shows that one cannot dispense with this condition.

Key words: Size-dependent population growth — Reproduction by fission — Balance equation — First-order partial differential equation — Transformed arguments — Stable size distribution

1. Introduction

In their paper "A model for populations reproducing by fission" [19], J. W. Sinko and W. Streifer presented a deterministic model decribing the dynamics of single species populations of organisms reproducing by binary fission. Starting from the assumption that the important physiological characteristics of these organisms can be described by their size alone, they derived a complicated nonlinear evolution equation which they solved numerically (moreover, the model is applied to populations of the planarian worm *Dugesia tigrina* and theory and experiments are compared with each other). Similar models for the growth of procaryotic cell populations have been formulated by A. G. Fredrickson, D. Ramkrishna and H. M. Tsuchiya [6].

Although our long-term objective is the analysis of such complicated systems of nonlinear equations describing the dynamics of structured populations, we shall here concentrate on some aspects of a related but much simpler linear problem. More precisely, we study a variant of the Bell–Anderson [2, 3] model for size-dependent cell population growth when reproduction occurs by fission into two equal parts. (Here one may replace "size" by weight, volume, length or, in fact, by any quantity which obeys a physical conservation law.) The environment is supposed to be unlimited and all possible (nonlinear) feedback mechanisms are ignored. It is well-known that under such circumstances the solution of the initial value problem for *age-dependent* population growth behaves asymptotically for $t \to \infty$ as

$$n(t, a) \sim C e^{\sigma t} \bar{n}(a)$$

where (i) σ is the Malthusian parameter (intrinsic rate of natural increase), (ii) $\bar{n}(a)$ is the so-called stable age-distribution, (iii) σ and $\bar{n}(a)$ do not depend on the initial condition (iv) C is a constant which depends on the initial condition only (see [11, 12, 17]). Here we address the question whether reproduction by fission results similarly in convergence towards a stable size-distribution. As anticipated by Bell and Anderson [1, 2, 3] we find that the answer depends heavily on the functional relationship (described by a function g, see eq. (2.1)) between the growth of organisms and their size x. For instance, the answer is yes if $g(2x) < 2g(x)$ for all relevant x, but no if $g(2x) = 2g(x)$. Two of us conjecture that the answer remains yes, if the relation $g(2x) < 2g(x)$ is satisfied for values of x in a set of nonzero measure. This conjecture is proved for a special case.

The organization of the paper is as follows. In Sect. 2 we present the balance law for size dependent reproduction by fission into two identical parts and we rewrite it as a linear evolution problem in a Banach space. In Sect. 3 we prove the existence and uniqueness of a solution and we reformulate that result in terms of a strongly continuous semigroup of bounded linear operators. In Sect. 4 we find a representation of the solution in terms of a *finite* sum of generations. In Sect. 5 we show that the semigroup is compact after finite time if $g(2x) < 2g(x)$. In Sect. 6 we discuss the eigenvalues of the infinitesimal generator and we derive a characteristic equation for an important special case (the general case is treated in [9]). In Sect. 7 we reap the fruits of our preparations and prove the existence of a stable size distribution under the condition $g(2x) < 2g(x)$. In Sect. 8 we investigate what happens if the condition $g(2x) < 2g(x)$ is not satisfied for all x. Finally in Sect. 9, we make some concluding remarks.

2. The equation and its interpretation

The subject of our investigation is the equation

$$\frac{\partial n}{\partial t}(t, x) + \frac{\partial}{\partial x}(g(x)n(t, x)) = -\mu(x)n(t, x) - b(x)n(t, x) + 4b(2x)n(t, 2x). \quad (2.1)$$

Here the independent variables t and x denote, respectively, time and size. The unknown n is a density function: $\int_{x_1}^{x_2} n(t, \xi)\, d\xi$ is the number of cells with size between x_1 and x_2 at time t. The functions μ, b and g (which are assumed to be known) are the rates at which cells of size x die, divide and grow, respectively. The second term at the left hand side describes changes due to the growth of individuals and the first term at the right hand side describes changes due to death or dilution. The last two terms describe the reproduction process. At first sight the factor 4 in the source term may seem strange. But a moment of reflection should bring about that $4 = 2 \times 2$, where the first factor accounts for the doubling of numbers and the second for the doubling of intervals (those who originate from splitting in $(2x, 2x+2\,dx)$ enter into $(x, x+dx)$); a convincing check can be made as follows: multiply by the size x and integrate, then the contributions of the last two terms have to cancel each other because of conservation of "size". For the sake of completeness we present a derivation of (2.1) in the Appendix.

We assume that the cells cannot divide before they have reached a minimal size $a > 0$. Consequently, cells with size less than $\frac{1}{2}a$ cannot exist. Mathematically we express this fact by the boundary condition

$$n(t, \tfrac{1}{2}a) = 0 \tag{2.2}$$

which supplements (2.1).

From each "cohort" passing size y a fraction $E(x)/E(y)$ will reach size x, where

$$E(x) = M(x)\Gamma(x), \tag{2.3}$$

$$M(x) = \exp - \int_{a/2}^{x} \frac{\mu(\xi)}{g(\xi)}\, d\xi, \tag{2.4}$$

$$\Gamma(x) = \exp - \int_{a}^{x} \frac{b(\xi)}{g(\xi)}\, d\xi. \tag{2.5}$$

Note that M describes the loss due to mortality and Γ the "loss" due to splitting. Since we want to describe that the cells have to divide before they reach a maximal size, which we normalize to be $x = 1$, we are led to require that the integral $\int_a^x b(\xi)/g(\xi)\, d\xi$ diverges for $x \uparrow 1$ and to interpret the term $4b(2x)n(t, 2x)$ in equation (2.1) as zero whenever $x \geq \frac{1}{2}$. Clearly we now require $a < 1$. If $a \geq \frac{1}{2}$ the maximal size of a daughter is less than the minimal size of a mother. This realistic case is relatively easy and we will pay special attention to it. However, at this point we do not yet exclude the case $a < \frac{1}{2}$ in which a large cell can undergo two divisions immediately after each other so that effectively a division into four parts occurs.

Clearly we now choose the domain of x to be the interval $[\frac{1}{2}a, 1]$. Concerning the growth, death and division rates we assume

H_g: g is a strictly positive continuous function

H_μ: μ is a nonnegative continuous function

H_b: $b(x) = 0$ for $x \in [\frac{1}{2}a, a]$ and $b(x) > 0$ for $x \in (a, 1)$.

Moreover b is continuous and satisfies $\lim_{x\uparrow 1} \int_a^x b(\xi)\, d\xi = +\infty$.

In all these assumptions we can weaken the continuity requirement at the expense of some small technical difficulties.

Strictly speaking the interpretation suggests no other condition on $n(t, x)$ as a function of x than the integrability of the functions $b(\cdot)n(t, \cdot)$ and $n(t, \cdot)$. Nevertheless we shall assume that the initial condition n_0 in

$$n(0, x) = n_0(x) \tag{2.6}$$

is such that $n_0(\cdot)/\Gamma(\cdot)$ is continuous (in particular this assumption requires that $n_0(x) \to 0$ at a certain rate as $x \uparrow 1$) and we shall show that $n(t, \cdot)$ inherits this property. Here we are guided by the interpretation of Γ and by the desire to avoid technical details. As a side remark we mention that the smoothing properties of (2.1) hinge upon properties of $g(2x) - 2g(x)$ on the one hand (cf. Sects. 5 and 8) and the behaviour of $\Gamma'(x)$ for $x \uparrow 1$ on the other.

The transformation

$$m(t, x) = \frac{g(x)}{E(x)} n(t, x) \tag{2.7}$$

leads to the evolution problem

$$(EP)\begin{cases} \dfrac{\partial m}{\partial t} = -g(x)\dfrac{\partial m}{\partial x}(t, x) + k(x)m(t, 2x) \\ m(t, \tfrac{1}{2}a) = 0 \\ m(0, x) = \phi(x) \end{cases}$$

where by definition $\phi(x) = [g(x)/E(x)]n_0(x)$ and

$$k(x) = 4\frac{g(x)}{E(x)}\frac{b(2x)}{g(2x)}E(2x) \tag{2.8}$$

and where, here and in the following, one should interpret $k(x)m(t, 2x)$ as zero for $x \geq \frac{1}{2}$. Note that $g(x)n(t, x)$ is the flux of individuals at (t, x) and that $E(x)$ is a factor which, in some sense, accounts for the "loss" due to mortality and fission.

Although b has a non-integrable singularity, k is integrable and we shall exploit this property in, e.g. the proof of Lemma 3.1. In fact this "reduction of the singularity" is an extra motivation for the transformation (2.7).

Our approach will be to look for solutions as functions of t with values in the space

$$X = \{\psi \in C[\tfrac{1}{2}a, 1] \mid \psi(\tfrac{1}{2}a) = 0\}$$

provided with the supremum norm. Thus we can rewrite (EP) as the abstract Cauchy problem

$$(ACP)\begin{cases} \dfrac{dm}{dt} = Am \\ m(0) = \phi \end{cases}$$

where A is the unbounded operator defined by

$$\begin{cases} (A\psi)(x) = -g(x)\psi'(x) + k(x)\psi(2x) \\ \mathcal{D}(A) = \{\psi \in X \mid \psi \text{ is } C^1 \text{ on } [\tfrac{1}{2}a, \tfrac{1}{2}) \cup (\tfrac{1}{2}, 1]; \text{ the limits} \\ \lim_{x\uparrow\frac{1}{2}} [-g(x)\psi'(x) + k(x)\psi(2x)] \text{ and } \lim_{x\downarrow\frac{1}{2}} [-g(x)\psi'(x)] \text{ exist and} \\ \text{equal each other; } -g(\tfrac{1}{2}a)\psi'(\tfrac{1}{2}a) + k(\tfrac{1}{2}a)\psi(a) = 0\}. \end{cases} \tag{2.9}$$

A is a closed, densely defined operator on X. Now we are ready to apply the theory of semigroups of operators [13, 16].

3. Existence and uniqueness of a solution

One possibility to show that A generates a strongly continuous semigroup of bounded linear operators on X is to verify the Hille–Yosida conditions [13, 14]. Although this is not too difficult (one can use the results of [9]) we prefer another approach. Formally $A = B + C$ where

$$(B\psi)(x) = -g(x)\psi'(x) \tag{3.1}$$

$$(C\psi)(x) = k(x)\psi(2x). \tag{3.2}$$

We consider B as an unbounded operator from $L_1[\frac{1}{2}a, 1]$ into itself, with domain of definition

$$\mathcal{D}(B) = \{\psi|\psi \text{ is absolutely continuous and } \psi(\tfrac{1}{2}a) = 0\}$$

and C as a bounded operator from X into $L_1[\frac{1}{2}a, 1]$. Clearly B generates the semigroup e^{Bt} defined by $(e^{Bt}\psi)(x) = \psi(\Gamma(-t, x))$, where $\Gamma(t, x)$ is the solution operator of $\dot{x} = g(x)$. Explicitly we have

$$(e^{Bt}\psi)(x) = \psi(G^{-1}(G(x) - t)) \tag{3.3}$$

where by definition

$$G(x) = \int_{a/2}^{x} \frac{d\xi}{g(\xi)} \tag{3.4}$$

and G^{-1} is the inverse of the monotone function G on $[0, G(1)]$ and defined to be $\frac{1}{2}a$ on $(-\infty, 0]$. Note that $G(x)$ is the time which a cell needs to grow from $\frac{1}{2}a$ to x and that $G^{-1}(t)$ is the size at time t when the cell had size $\frac{1}{2}a$ at time zero; so $G^{-1}(t)$ is the solution of $du/dt = g(u)$ with initial condition $u(0) = \frac{1}{2}a$.

We observe that e^{Bt} leaves (the embedding of) X invariant. Moreover, $(e^{Bt}\phi)(x) = 0$ for $t \geq G(x)$ and so, in particular, $e^{Bt} = 0$ for $t \geq G(1)$.

Again formally the problem

$$\frac{dm}{dt} = (B + C)m$$

$$m(0) = \phi$$

leads to the integral equation (variation-of-constants formula)

$$m(t) = e^{Bt}\phi + \int_0^t e^{B(t-\tau)}Cm(\tau)\, d\tau. \tag{3.5}$$

Our plan is as follows. First we shall show that (3.5) has a unique solution $m = m(t; \phi)$. Next we prove that $T(t)\phi = m(t; \phi)$ defines a semigroup on X and, finally, that A is the generator of $T(t)$.

If m is an X-valued function then $e^{B(t-\tau)}Cm(\tau)$ is an L_1-valued function. It turns out that the integration with respect to τ produces a continuous function of x:

Lemma 3.1. *The formula*

$$(Lm)(t) = \int_0^t e^{B(t-\tau)}Cm(\tau)\, d\tau \tag{3.6}$$

defines a bounded linear operator from $C([0, T]; X)$ into itself. For T sufficiently small, the norm of L is less than one.

Proof. Explicitly we have the following expressions for $(Lm)(t)(x)$:

$$\int_{G^{-1}(G(x)-t)}^{x} k(\xi)m(G(\xi)-G(x)+t,2\xi)\frac{d\xi}{g(\xi)}, \quad \text{for } x\leq\tfrac{1}{2}$$

$$\int_{G^{-1}(G(x)-t)}^{1/2} k(\xi)m(G(\xi)-G(x)+t,2\xi)\frac{d\xi}{g(\xi)}, \quad \text{for } x\geq\tfrac{1}{2} \text{ and } t\geq G(x)-G(\tfrac{1}{2}),$$

$$0, \quad \text{for } x\geq\tfrac{1}{2} \text{ and } t\leq G(x)-G(\tfrac{1}{2})$$

(here we used the transformation $\xi=G^{-1}(G(x)-t+\tau)$). Hence it follows that:

(i) for fixed t this is a continuous function of x (which is zero for $x=\frac{1}{2}a$);

(ii) the supremum norm with respect to x depends continuously on t;

(iii) for $T\downarrow 0$ the supremum norm with respect to x and t goes to zero uniformly for m in the unit-ball of $C([0,T];X)$. □

A standard contraction mapping and continuation argument yields

Corollary 3.2. *For arbitrary $\phi\in X$ and $T>0$ equation* (3.5) *has a unique solution in $C([0,T];X)$. This solution depends continuously on ϕ.*

On the basis of this result we define bounded linear operators $T(t)$ on X by

$$T(t)\phi=m(t;\phi), \tag{3.7}$$

where $m(t;\phi)$ is the solution of (3.5). If we take in (3.5) the argument $t+s$ and subsequently rearrange the terms, we arrive at the identity

$$m(s+t)=e^{Bt}m(s)+\int_0^t e^{B(t-\tau)}Cm(s+\tau)\,d\tau.$$

Consequently, uniqueness of solutions implies the semigroup relation

$$T(t+s)=T(t)T(s).$$

Corollary 3.3. *$\{T(t)\}$ forms a strongly continuous semigroup of bounded linear operators on X.*

Theorem 3.4. *A is the infinitesimal generator of $T(t)$.*

Proof. Let $\tilde{A}$ be the infinitesimal generator of $T(t)$. In order to show that $A=\tilde{A}$, we let $u\in D(\tilde{A})$, $\tilde{A}u=v$. Then, if $\operatorname{Re}\lambda$ is large enough, $u=(\lambda I-\tilde{A})^{-1}(\lambda u-v)=\int_0^\infty e^{-\lambda t}T(t)(\lambda u-v)\,dt$. (See [16]). The Laplace transform of (3.5) with $\phi=\lambda u-v$ yields

$$u=(\lambda I-B)^{-1}(\lambda u-v)+(\lambda I-B)^{-1}Cu$$

with B and C regarded as operators from X to L_1. Thus $u\in\mathcal{D}(B)$ and $(B+C)u=v$. Since $v\in X$, $u\in\mathcal{D}(A)$ and $Au=v$. This consideration implies that $\mathcal{D}(\tilde{A})\subset\mathcal{D}(A)$ and $\tilde{A}u=Au$ for $u\in\mathcal{D}(\tilde{A})$.

$\mathcal{D}(A)\subset\mathcal{D}(\tilde{A})$ is proved by reading these arguments backwards. □

Thus we showed that A generates a semigroup which corresponds exactly to solving the integral equation (3.5).

The solution $m(t, x)$ is not necessarily differentiable with respect to t and x separately. So the question arises in what sense it satisfies the first-order p.d.e. The following two observations clarify the situation:

(i) the solution is differentiable along the characteristics $t - G(x) = \text{constant}$,

(ii) but in $x = \frac{1}{2}$ one has to distinguish between the right- and left derivative since $k(x)m(t, 2x)$ (interpreted as zero for $x \geq \frac{1}{2}$) is not necessarily continuous in $x = \frac{1}{2}$.

Mathematically this amounts to the relation:

$$\lim_{\varepsilon \to 0} \frac{m(t+\varepsilon, G^{-1}(G(x)+\varepsilon)) - m(t, x)}{\varepsilon} = k(x)m(t, 2x)$$

where for $x = \frac{1}{2}$ the two limits $\varepsilon \uparrow 0$ and $\varepsilon \downarrow 0$ have to be taken separately if $k(\frac{1}{2}) \neq 0$.

4. Representation of the solution: The generation expansion

Defining $m_0(t) = e^{Bt}\phi$ we can rewrite (3.5) as

$$m = m_0 + Lm. \tag{4.1}$$

By the method of successive approximations we find formally

$$m = m_0 + \sum_{n=1}^{\infty} L^n m_0. \tag{4.2}$$

It turns out that the infinite sum contains, in fact, a finite number of terms only.

Lemma 4.1. *Fix $T > 0$. L, as an operator from $C([0, T]; X)$ into itself, is nilpotent. More precisely, $L^n = 0$ for $n \geq 2T|g|_\infty / a + k$ where k is such that*

$$2^{-k} \leq \frac{a}{2} < 2^{-k+1}$$

and $|g|_\infty := \max\{|g(x)| \mid \frac{1}{2}a \leq x \leq 1\}$.

Proof. We shall first deal with the special case that g is identically one. We split the iterative procedure into two steps:

$$w_n(t) = Cm_n(t), \qquad n = 0, 1, 2, \ldots,$$

$$m_n(t) = \int_0^t e^{B(t-\tau)} w_{n-1}(\tau)\, d\tau, \qquad n = 1, 2, 3, \ldots.$$

From (3.2) and (3.3) we deduce that

$$w_0(t)(x) = 0 \text{ for } x \geq \tfrac{1}{2} \Rightarrow m_1(t)(x) = 0 \text{ for } x \geq \tfrac{1}{2} + t$$

$$\Rightarrow w_1(t)(x) = 0 \text{ for } x \geq \tfrac{1}{4} + \tfrac{1}{2}t \Rightarrow m_2(t)(x) = 0 \text{ for } x \geq \tfrac{1}{4} + t$$

$$\ldots \qquad \ldots$$

$$\Rightarrow w_{l-1}(t)(x) = 0 \text{ for } x \geq 2^{-l} + \tfrac{1}{2}t \Rightarrow m_l(t)(x) = 0 \text{ for } x \geq 2^{-l} + t.$$

So $w_k(t)(x) = 0$ for $x \geq a/4 + \frac{1}{2}t$. But, since also $w_k(t)(x) = 0$ for $x \leq a/2$, it follows that

$$w_k(t) = 0 \text{ for } x \geq \frac{a}{4} + \tfrac{1}{2}t \text{ and for } t \leq \frac{a}{2}.$$

Hence $m_{k+1}(t)(x)=0$ for those combinations of x and t for which $x-t+\tau \geq a/4+\frac{1}{2}\tau$ for all $\tau \in [a/2, 1] \cap [0, t]$, i.e. for $x \geq t$ and for $t \leq a/2$. Continuing like above we find that $m_{k+l}(t)(x)=0$ for $x \geq t-(l-1)a/2$ and for $t \leq l(a/2)$. As soon as $l(a/2) \geq T$, m_{k+l} is identically zero. For the special case this concludes the proof.

In the general case we have

$$m_n(t)(x) = \int_0^t w_{n-1}(\tau)(G^{-1}(G(x)-t+\tau))\,d\tau.$$

We claim that for $t \geq \tau$ and $x \geq |g|_\infty(t-\tau)+\xi$, the inequality $G^{-1}(G(x)-t+\tau) \geq \xi$, holds. Indeed, the definition (3.4) of G implies that

$$G(x)-G(\xi) \geq |g|_\infty^{-1}(x-\xi) \quad \text{for } x \geq \xi$$

and consequently

$$G(x)-G(\xi)-t+\tau \geq |g|_\infty^{-1}(x-\xi)-t+\tau \geq 0$$

from which it follows that

$$G^{-1}(G(x)-t+\tau) \geq \xi.$$

Using this result one can repeat the induction steps above. In all (intermediate) formulas one has to replace t and τ by $|g|_\infty t$ and $|g|_\infty \tau$. □

We conclude that (4.2) gives a valid and useful representation of the solution. Moreover, each term has a clear interpretation which we now describe.

The contribution to the solution of those cells which were present at $t=0$, but have not yet divided, is given by m_0, the zero'th generation. Inductively the l'th generation $m_l = L^l m_0$ gives the contribution of those organisms which arose from divisions of the $(l-1)$'th generation and have not yet divided themselves. Lemma 4.1 expresses the intuitively obvious fact that at each time instant at most finitely many generations are present in the population. We note that each generation will go extinct in finite time, but that still the number of generations present in the population becomes unbounded as $t \to +\infty$.

5. Compactness

From the generation expansion (4.2) one can compute the solution for finite (and especially small) times, but this does not give any information about the asymptotic behaviour for $t \to +\infty$. In order to obtain such information we shall try to characterize the spectrum of $T(t)$ in terms of the spectrum of A, about which we know a lot (see [9] and the next section). It is known that this characterization is easy when there is compactness in the problem [8, 16].

Somewhat imprecisely one can say that growth and division lead to shift and multiplication operators, and these are not compact. However, when division occurs distributed, some kind of smoothing may (but need not to) take place. We shall show that the way in which the growth rate g depends on x has a decisive influence.

Lemma 5.1. *Assume that* $2g(x) > g(2x)$ *for* $\frac{1}{2}a \le x \le \frac{1}{2}$. *Fix* $t > 0$. *The mapping*

$$\phi \mapsto \int_0^t e^{B(t-\tau)} C\, e^{B\tau} \phi \, d\tau$$

from X *into itself is compact.*

Proof. Let $F = F(x, \phi)$ and $\alpha = \alpha(x, t)$ be defined by

$$F(x, \phi) = \int_0^t (e^{B(t-\tau)} C\, e^{B\tau} \phi)(x) \, d\tau,$$

$\alpha(x, t) = G^{-1}(G(x) - t)$. (This quantity has a clear biological interpretation: it is the size of an individual at time 0 given that its size at time t equals x.) By definition $\alpha(x, t) = \frac{1}{2}a$ if $G(x) < t$. Now

$$F(x, \phi) = \int_0^t k(\alpha(x, t-\tau))\phi(G^{-1}(G(2\alpha(x, t-\tau)) - \tau)) \, d\tau,$$

where the integrand should be interpreted as zero whenever $\alpha \le \frac{1}{2}a$ or $\alpha \ge \frac{1}{2}$. Putting

$$\xi = G(2\alpha(x, t-\tau)) - \tau$$

we find

$$\frac{d\xi}{d\tau} = \frac{2g(\alpha)}{g(2\alpha)} - 1 > 0.$$

So we can use ξ as a new integration variable:

$$F(x, \phi) = \int_{G(2G^{-1}(G(x)-t))}^{G(2x)-t} k(\alpha(x, t-\tau(\xi)))\phi(G^{-1}(\xi)) \times \frac{g(2\alpha(x, t-\tau(\xi)))}{2g(\alpha(x, t-\tau(\xi))) - g(2\alpha(x, t-\tau(\xi)))} \, d\xi.$$

Since now x does not appear in the argument of ϕ anymore, it is easy to show, using the continuity of g, G, G^{-1} and α and the fact that $k \in L_1$, that

$$|F(x_1, \phi) - F(x_2, \phi)| \le \|\phi\| \, \varepsilon(x_1, x_2)$$

where $\varepsilon(x_1, x_2) \downarrow 0$ as $|x_1 - x_2| \downarrow 0$. (In view of the proof of Lemma 5.2 we remark that for each $T > 0$, $\varepsilon(x_1, x_2)$ can be chosen such that the estimate holds for any $t \in [0, T]$.) Hence, on account of the Arzela–Ascoli theorem, we conclude that each bounded set is mapped onto a precompact set. □

Lemma 5.1 gives a compactness criterion for the first generation $m_1(t, \phi) = \int_0^t e^{B(t-\tau)} C\, e^{B\tau} \phi \, d\tau$. Essentially the same argument leads to

Lemma 5.2. *Assume that* $2g(x) > g(2x)$ *for* $\frac{1}{2}a \le x \le \frac{1}{2}$. *Define, as before, the* nth *generation by*

$$m_n(t, \phi) = \int_0^t e^{B(t-\tau)} C m_{n-1}(\tau, \phi) \, d\tau, \qquad n \ge 1.$$

Fix $t>0$ and $n\in\mathbb{N}$. The mapping

$$\phi\mapsto m_n(t,\phi)$$

from X into itself is compact.

Corollary 5.3. *If $g(2x)<2g(x)$ for all $x\in[\frac{1}{2}a,\frac{1}{2}]$, then $T(t)$ is compact for $t\geqslant G(1)$.*

Proof. For $t\geqslant G(1)$, $m_0(t,\cdot)=0$ and consequently $T(t)$ equals a finite sum of compact operators. □

Precisely the same conclusion follows from the biologically unrealistic assumption $2g(x)<g(2x)$ for all x. The importance of such a condition on g becomes clear in Sect. 8.

6. The spectrum of A

In this section we restrict our attention to the case $a\geqslant\frac{1}{2}$ (i.e. the maximal size of a daughter cell is less than the minimal size of a mother cell). We refer to Heijmans [9] for a detailed study of the general case, which turns out to be essentially the same but computationally much more difficult.

The inhomogeneous equation $(A-\lambda I)\psi=f$ can be rewritten as

$$-g(x)\psi'(x)-\lambda\psi(x)=f(x),\qquad \tfrac{1}{2}\leqslant x\leqslant 1,$$

$$-g(x)\psi'(x)-\lambda\psi(x)=f(x)-k(x)\psi(2x),\qquad \tfrac{1}{2}a\leqslant x\leqslant\tfrac{1}{2},\qquad \psi(\tfrac{1}{2}a)=0.$$

The solution of the first equation is given by

$$\psi(x)=\psi(\tfrac{1}{2})\,e^{\lambda(G(\frac{1}{2})-G(x))}-\int_{1/2}^{x}e^{\lambda(G(\xi)-G(x))}\frac{f(\xi)}{g(\xi)}\,d\xi,\qquad \tfrac{1}{2}\leqslant x\leqslant 1.\tag{6.1}$$

Using this expression we can solve the second equation:

$$\psi(x)=\int_{a/2}^{x}e^{\lambda(G(\xi)-G(x))}\left\{\psi(\tfrac{1}{2})\,e^{\lambda(G(\frac{1}{2})-G(2\xi))}k(\xi)\right.$$
$$\left.-f(\xi)-k(\xi)\int_{1/2}^{2\xi}e^{\lambda(G(\eta)-G(2\xi))}\frac{f(\eta)}{g(\eta)}\,d\eta\right\}\frac{d\xi}{g(\xi)}.\tag{6.2}$$

Finally, the requirement of continuity in $x=\frac{1}{2}$ yields the compatibility condition

$$(\pi(\lambda)-1)\psi(\tfrac{1}{2})=\zeta(\lambda,f)\tag{6.3}$$

where

$$\pi(\lambda)=\int_{a/2}^{1/2}e^{\lambda(G(\xi)-G(2\xi))}\frac{k(\xi)}{g(\xi)}\,d\xi\tag{6.4}$$

$$\zeta(\lambda,f)=\int_{a/2}^{1/2}e^{\lambda(G(\xi)-G(\frac{1}{2}))}\left\{f(\xi)+k(\xi)\int_{1/2}^{2\xi}e^{\lambda(G(\eta)-G(2\xi))}\frac{f(\eta)}{g(\eta)}\,d\eta\right\}\frac{d\xi}{g(\xi)}.\tag{6.5}$$

If $\pi(\lambda)\neq 1$ we can solve (6.3) for $\psi(\frac{1}{2})$ and for that special value of $\psi(\frac{1}{2})$ the function ψ defined by (6.1)–(6.2) is a solution of $(A-\lambda I)\psi=f$ which depends continuously on f. Hence λ is an element of the resolvent set if $\pi(\lambda)\neq 1$. If, on the other hand, $\pi(\lambda)=1$ then (6.1)–(6.2) with $f\equiv 0$ defines for arbitrary $\psi(\frac{1}{2})$ a solution of $(A-\lambda I)\psi=0$. It follows that λ is an eigenvalue if $\pi(\lambda)=1$. For obvious reasons we shall call the equation

$$\pi(\lambda)=1 \tag{6.6}$$

the *characteristic equation.* Since π is analytic its roots are isolated points.

Using the definitions (2.3)–(2.5) and (2.8) we can rewrite the definition of $\pi(\lambda)$ as follows

$$\begin{aligned}\pi(\lambda) &= 2\int_a^1 \frac{b(\xi)}{g(\xi)}\exp\left(-\int_{\xi/2}^{\xi}\frac{\lambda+\mu(\eta)+b(\eta)}{g(\eta)}\,d\eta\right)d\xi \\ &= 2\int_a^1 \exp\left(-\int_{\xi/2}^{\xi}\frac{\lambda+\mu(\eta)}{g(\eta)}\,d\eta\right)d(1-\Gamma(\xi))\end{aligned} \tag{6.7}$$

(here we also used that the support of b is contained in $[a, 1]$). As an intermezzo we now show that $\pi(0)$ admits a simple biological interpretation. Clearly any newborn cell has to pass size a before it can possibly produce offspring. So the contribution of an arbitrary cell passing size a to the growth of the population can be effectively measured by the number of her daughters that will grow up to at least size a. If we consider cells passing size a, the average number of daughters which grow up safely to size a can be calculated as follows:

(i) The chance that the potential mother reaches size ξ is given by

$$\exp\left(-\int_a^{\xi}\frac{\mu(\eta)+b(\eta)}{g(\eta)}\,d\eta\right).$$

(ii) The chance density that fission occurs at ξ is given by $b(\xi)/g(\xi)$ (here the factor $1/g(\xi)$ accounts for the conversion of chance per unit of time to chance per unit of size). The number of daughters is exactly two.

(iii) The chance that a daughter born with size $\frac{1}{2}\xi$ does not die before reaching size a is given by

$$\exp\left(-\int_{\xi/2}^{a}\frac{\mu(\eta)}{g(\eta)}\,d\eta\right).$$

Summing all contributions with respect to $a<\xi<1$ we find that the average number of daughters at a is precisely $\pi(0)$.

The characteristic function π is monotone decreasing as a function of real λ. Since $\pi(-\infty)=+\infty$ and $\pi(+\infty)=0$ there exists precisely one real root of the characteristic equation, which we shall call λ_d. Clearly $\lambda_d>0$ if $\pi(0)>1$ and $\lambda_d<0$ if $\pi(0)<1$. Other roots occur in complex conjugate pairs. Their position relative to λ_d depends heavily on the function $g(x)$ (see Sect. 8).

If $g(2x)<2g(x)$, one can use the transformation $\tau=G(\xi)-G(\frac{1}{2}\xi)$ to rewrite $\pi(\lambda)$ as the Laplace transform of a nonnegative function and, consequently, all complex roots satisfy $\operatorname{Re}\lambda\leq\lambda_d-\varepsilon$ for some $\varepsilon>0$ (and, moreover, there are at most finitely many roots in any vertical strip).

A straightforward computation based on (6.1)–(6.5) shows that a root of $\pi(\lambda)=1$ corresponds to an algebraically simple eigenvalue of A if and only if $\pi'(\lambda)\neq 0$. Hence λ_d is a simple eigenvalue. The corresponding eigenvector of A which we denote by ψ_d is positive. One can decompose the whole space as the direct sum of the null space and the range of $A-\lambda_d I$:

$$X=\mathcal{N}(A-\lambda_d I)\oplus\mathcal{R}(A-\lambda_d I) \tag{6.8}$$

(here we use that A has a compact resolvent: if $\pi(\lambda)\neq 1$, (6.1)–(6.2) with $\psi(\frac{1}{2})$ the solution of (6.3) defines a compact inverse of $A-\lambda I$). ψ_d can be found from (6.1)–(6.2) with $\lambda=\lambda_d$ and $f\equiv 0$. We normalize ψ_d by the condition $\psi_d(\frac{1}{2})=e^{-\lambda_d G(\frac{1}{2})}$. Then $\mathcal{N}(A-\lambda_d I)$ is the one-dimensional subspace spanned by ψ_d and the projection on this subspace according to (6.8) is given by

$$P\phi=-\frac{\zeta(\lambda_d,\phi)}{\pi'(\lambda_d)}\psi_d. \tag{6.9}$$

This formula follows directly from our explicit calculations, but a more systematic derivation can be based on the theory of adjoint operators. See [9, Sect. 7]. In that paper it has been shown that there exists an L_∞-function ψ_d^* which is positive almost everywhere, such that

$$P\phi=\left(\int_{a/2}^{1}\psi_d^*(x)\phi(x)\,dx\right)\psi_d. \tag{6.10}$$

As a side remark we mention that Sudbury [20] has studied related models starting from the adjoint formulation. (He considers the backward equation whereas our starting point has been the forward equation, cf. Feller [5, Ch. X]).

We summarize those results of this section which remain true if the restriction on a is dropped.

Theorem 6.1 [9]. *The spectrum of A consists of isolated points which are eigenvalues. On the real axis there is a greatest eigenvalue λ_d, which is algebraically simple. The corresponding eigenvector ψ_d is positive on $(\frac{1}{2}a, 1]$ and no other eigenvector has this property. The decomposition* (6.8) *holds. If* $2g(x)>g(2x)$ *all other eigenvalues satisfy* $\operatorname{Re}\lambda\leq\lambda_d-\varepsilon$ *for some* $\varepsilon>0$ *and in each vertical strip there are at most finitely many of them.*

7. The stable size distribution

Let, as before, ψ_d denote the eigenvector spanning $\mathcal{N}(A-\lambda_d I)$ and let P denote the projection operator on ψ_d according to the decomposition (6.8). Then P commutes with $T(t)$ and one can study the action of $T(t)$ on the two invariant subspaces separately. The action on ψ_d is

$$T(t)\psi_d=e^{\lambda_d t}\psi_d.$$

Our aim is to deduce an exponential estimate for the action of $T(t)$ on $\mathcal{R}(A-\lambda_d I)$ from information about the position of the remaining eigenvalues of A relative to λ_d.

Theorem 7.1. *Assume* $g(2x)<2g(x)$ *then there exist positive constants* ε *and* K *such that*

$$\|(I-P)T(t)\phi\|\leq K\,e^{(\lambda_d-\varepsilon)t}\|\phi\|.$$

Proof. Take some $s \geq G(1)$. Corollary 5.3 implies that $T(s)$ is compact. It follows that the nonzero part of the spectrum of $T(s)$ consists of eigenvalues. Eigenvalues of $T(s)$ are necessarily of the form $e^{\lambda s}$ with λ some eigenvalue of A (the point spectrum of the semigroup is "faithful" to the point spectrum of the generator; see [16, Sect. 2.2]). Theorem 6.1 implies that for the restriction to $\mathcal{R}(A-\lambda_d I)$ the inequality $\operatorname{Re}\lambda \leq \lambda_d - \varepsilon$ holds for some $\varepsilon > 0$. Exploitation of the semigroup property then yields the required estimate, see Hale [8, Sect. 7.4]. □

The constant ε has to be estimated by analysing the characteristic function $\pi(\lambda)$.

Corollary 7.2. *Assume* $g(2x) < 2g(x)$ *then*

$$m(t, \cdot\,; \phi) = T(t)\phi = e^{\lambda_d t}(P\phi + o(1)), \qquad t \to +\infty.$$

In words this says that the dominant term in the asymptotic expansion for $t \to +\infty$ is factorized as the product of an exponential function of t, a function $\psi_d(x)$ and a scalar factor. The initial function manifests itself in the scalar factor only. Note that for nonnegative ϕ, $P\phi \neq 0$ unless $\phi = 0$ (see (6.9) or [9]). Since $e^{-\lambda_d t} m(t, \cdot\,; \phi)$ converges to a multiple of ψ_d we call ψ_d the *stable size distribution* of m. If $a \geq \frac{1}{2}$ then ψ_d is given by (6.1)–(6.2) with $f \equiv 0$ and $\lambda = \lambda_d$ the real root of (6.6). The computation of ψ_d for $a < \frac{1}{2}$ is presented in [9]. From ψ_d one can compute the stable size distributions Ψ_d of n: $\Psi_d = (E/g)\psi_d$ (see (2.7)).

Let $n(t, x; n_0)$ be the solution of our original equation (2.1) supplied with the boundary condition (2.2) and initial condition (2.6) where n_0 is such that $n_0(\cdot)/\Gamma(\cdot)$ is continuous on $[\frac{1}{2}a, 1]$, then we have the following result.

Corollary 7.3. *Assume* $g(2x) < 2g(x)$ *for all* $x \in [\frac{1}{2}a, \frac{1}{2}]$, *then* $n(t, \cdot\,; n_0) = e^{\lambda_d t}(C \cdot \Psi_d + o(1))$, $t \to \infty$, *where C is a constant depending on the initial condition only.*

Since the total population size behaves like $\exp(\lambda_d t)$ we call λ_d the Malthusian parameter.

Remark 1. The relation between n and m can be formulated more precisely in the following way. A function $\psi \in X$ is called E-bounded if $\psi(\cdot)/E(\cdot)$ is a bounded function. (This is equivalent to saying that $\psi(\cdot)/\Gamma(\cdot)$ is bounded). Let X_0 be the space of E-bounded functions in X supplied with the norm

$$\|\psi\|_E = \sup\left\{\frac{|\psi(x)|}{E(x)} \,\middle|\, \tfrac{1}{2}a \leq x \leq 1\right\}.$$

Then X_0 is a Banach-space and the linear mapping $H: X_0 \to X$ given by

$$(H\psi)(x) = \frac{g(x)\psi(x)}{E(x)}$$

is an isomorphism. Now the transformation from n to m can be written abstractly as $m(t, \cdot) = Hn(t, \cdot)$. Now $\tilde{T}(t) = H^{-1}T(t)H$, $t \geq 0$, defines a strongly continuous semigroup on X_0 and the solution of the original equation is $n(t, \cdot\,; n_0) = \tilde{T}(t)n_0$, if $n_0 \in X_0$.

(2) Using expression (6.10) the constant C in Corollary 7.3 can be computed explicitly

$$C = \int_{a/2}^{1} \frac{g(x)}{E(x)} \psi_d^*(x) n_0(x)\, dx.$$

(3) From a mathematical point of view we are dealing with *positive* semigroups. We refer to [21, 22] for a number of relevant general results in this area.

8. Exponential individual growth

In Corollary 5.3 it has been proved that the semigroup $T(t)$ is compact after finite time if g satisfies the condition $g(2x) < 2g(x)$, $\frac{1}{2}a \leq x \leq \frac{1}{2}$ (or $g(2x) > 2g(x)$). In this section we shall investigate what happens if this condition is not satisfied for all x. We will distinguish between two cases

(A) $g(2x) = 2g(x)$, all $x \in [\frac{1}{2}a, \frac{1}{2}]$

(B) $g(2x) = 2g(x)$, $x \in Q_1$

$g(2x) < 2g(x)$, $x \in Q_2$

where $Q_1 \cup Q_2 = [\frac{1}{2}a, \frac{1}{2}]$ and both sets have a non-zero measure.

The general solution of the functional equation $g(2x) = 2g(x)$ is $g(x) = x\Phi(\ln x)$ where Φ is a $\ln 2$-periodic function. We restrict ourselves to a special solution, namely $g(x) = cx$ where c is some constant. By scaling the time we may set $c = 1$. This case which is characterized by exponential individual growth seems to be the most relevant from a biological point of view. See [1, 2, 3]. (However, our method of proof works equally well in the general case.)

Let us first deal with case (A).

$$g(x) = x, \qquad \tfrac{1}{2}a \leq x \leq 1.$$

Clearly

$$G(x) = \ln \frac{2x}{a} \quad \text{and} \quad G^{-1}(t) = \frac{a}{2} e^t.$$

For the 0th and 1st generation of the population we find, respectively, (see Sect. 4) $m_0(t, x; \phi) = \phi(x\, e^{-t})$ and

$$m_1(t, x; \phi) = \phi(2x\, e^{-t}) \int_0^t k(x\, e^{-\tau})\, d\tau$$

where by definition $\phi(x) = 0$ if $x \leq \frac{1}{2}a$. Similar expressions for higher generations show that the solution is related to the initial condition by periodic continuation and multiplication. No information is lost, no smoothing occurs. Although non-negativity is preserved, it is not reinforced: the solution has zeros for arbitrary large time if it has zeros initially.

The exceptional position of exponential individual growth is found once more if one looks at the characteristic equation. A straightforward calculation shows that for $a \geq \frac{1}{2}$ (see (6.7)):

$$\pi(\lambda) = 2^{-\lambda} C$$

where

$$C = 2\int_a^1 \exp\left(-\int_{\xi/2}^{\xi} \frac{\mu(\eta)}{g(\eta)}\,d\eta\right) d(1-\Gamma(\xi))$$

and all roots $\lambda = (1/\ln 2)(\ln C + 2k\pi i)$, $k \in \mathbb{Z}$ lie on the vertical line $\operatorname{Re}\lambda = \lambda_d = \ln C/\ln 2$; in other words, there is no distance $\varepsilon > 0$ between the dominant (real) eigenvalue λ_d and the real parts of the other eigenvalues of A. The total population size still behaves like $\exp \lambda_d t$ but convergence in shape does not take place. Instead the initial size distribution turns around and around while numbers are multiplied.

This striking behaviour in the case of exponential individual growth has already been noticed by Bell and Anderson [2, 3]. The following Gedanken experiment illustrates the biological reason. Consider two cells A and B with equal size and assume that at some time instant t_0 cell A splits into a and a. During the time interval $[t_0, t_1]$, a, a and B grow and at t_1 cell B splits into b and b. If $g(x) = cx$, the daughter cells a and b will have equal sizes just as their mothers A and B. In other words, the relation "equal size" is hereditary and extends over the generations. The growth model behaves like a multiplicating machine which copies the size distribution.

Of course the situation changes if we abandon the point of view that fission results into two exactly equal daughters. One of us (Heijmans) currently investigates a model with $g(x) = cx$ and a smooth probability density function for the mother-daughter size ratio [10].

Now a very interesting question arises: what happens in situation B, i.e. the situation that the functional equation $g(2x) = 2g(x)$ is satisfied on a subset of $[\frac{1}{2}a, \frac{1}{2}]$?

Heuristic reasoning in terms of probabilities can give some insight (the characteristic equation appears to be very helpful. See below).

To begin, let us restrict ourselves to the following situation.

(B′) $a \geqslant \frac{1}{2}$; $\quad g(x) = x \;\text{ for } \frac{1}{2}a \leqslant x \leqslant \beta, \qquad g(x) < x \;\text{ for } \beta < x \leqslant 1,$

where β is some value between a and 1. We shall prove that in this case there exists a stable size distribution.

The idea is the following. Suppose $\lambda_d = 0$, then the average cell which undergoes fission has one viable descendant (i.e. a daughter which undergoes fission as well). The population can be seen as the union of two distinct groups. A cell is a member of the first group iff all of its ancestors have been dividing before reaching the size $x = \beta$. If at least one of its ancestors has divided at a size $x > \beta$, then it is a member of the second group. The semigroup $T(t)$ corresponding to the total population never becomes compact because the first group (the reproduction of those members should be compared to a copying-machine, as mentioned in the first part of this section) never goes extinct (assumed that it had members at $t = 0$). The membership in the first group, however, decreases to zero as $t \to \infty$, because the probability that a member's descendant n generation afterwards is also member of the first group is p^n, where p is the probability that a daughter cell born at a size smaller than β will divide before reaching size β. Note that there is only a one-way traffic from the first to the second group. Members of the second group have at least one ancestor which has run through the dispersion-machine generated by the non-exponential individual growth, which is enough "to make this group compact".

The rest of this section is devoted to the precise elaboration of this idea. Let us assume that $\lambda_d = 0$. (This can always be achieved by the transformation $\tilde{n}(t, x) = e^{-\lambda_d t} n(t, x)$ in the original equation (2.1) and replacement of $\mu(x)$ by $\mu(x) + \lambda_d$.)

We are going to investigate solutions $m(t, x)$ of the evolution problem (EP). At each instant t the population is composed of two so-called subpopulations

$$m(t, x) = \bar{m}(t, x) + \hat{m}(t, x) \tag{8.1}$$

where $\bar{m}(t, x)$ represents the members of the first group and $\hat{m}(t, x)$ the members of the second group. As has been done in Sect. 4 we can write down a generation expansion for both $\bar{m}(t, x)$ and $\hat{m}(t, x)$

$$\bar{m}(t, x) = \sum_{i=0}^{\infty} \bar{m}_i(t, x) \tag{8.2a}$$

$$\hat{m}(t, x) = \sum_{i=1}^{\infty} \hat{m}_i(t, x). \tag{8.2b}$$

Note that the 0th generation is not present in the subpopulation $\hat{m}(t, x)$. Thus

$$\bar{m}_0(t, x) = \phi(G^{-1}(G(x) - t)). \tag{8.3}$$

We can write down the following recurrent relations for $\bar{m}_i$ and $\hat{m}_i$. Let, as in Sect. 5

$$\alpha(x, t) = G^{-1}(G(x) - t)$$

then

$$\bar{m}_{i+1}(t, x) = \int_0^{(t, t+G(\frac{1}{2}\beta) - G(x))^-} k(\alpha(x, t-\tau))\bar{m}_i(\tau, 2\alpha(x, t-\tau))\, d\tau \tag{8.4}$$

$$\begin{aligned} \hat{m}_{i+1}(t, x) = &\int_0^t k(\alpha(x, t-\tau))\hat{m}_i(\tau, 2\alpha(x, t-\tau))\, d\tau \\ &+ \int_{(t, t+G(\frac{1}{2}\beta) - G(x))^-}^t k(\alpha(x, t-\tau))\bar{m}_i(\tau, 2\alpha(x, t-\tau))\, d\tau \end{aligned} \tag{8.5}$$

where $(t_1, t_2)^- = \min(t_1, t_2)$. Note that $\tau \geq t + G(\frac{1}{2}\beta) - G(x)$ implies $\alpha(x, t-\tau) \leq \frac{1}{2}\beta$. Note that the second term at the right-hand side of (8.5) is identically zero if $x < \frac{1}{2}\beta$. The assumption $\lambda_d = 0$ together with (6.7) yields

$$\int_{\alpha/2}^{1/2} \frac{k(\xi)}{g(\xi)}\, d\xi = 1.$$

Now let

$$p = \int_{\alpha/2}^{\beta/2} \frac{k(\xi)}{g(\xi)}\, d\xi, \tag{8.6}$$

then $p < 1$.

Lemma 8.1. $|\bar{m}_i(t,x)| \leq p^i \|\phi\|$, $i=0,1,2,\ldots$ *and* $\bar{m}_i(t,x)=0$ (*i.e. the* ith $\bar{m}$ *generation goes extinct*) *for*

$$t \geq \ln\left(\frac{2^{i+1}\beta}{a}\right) + \int_\beta^1 \frac{d\xi}{g(\xi)}.$$

Proof: Let $\bar{u}_i(t,x)$ be the restriction of $\bar{m}_i(t,x)$ to the subinterval $[\frac{1}{2}a, \beta]$. Let $\bar{u}(t,x) = \sum_{i=0}^{\infty} \bar{u}_i(t,x)$ then $\bar{u}(0,x) = \bar{\phi}(x)$ where $\bar{\phi}$ is the restriction of ϕ to $[\frac{1}{2}a, \beta]$. Using the recurrence relation (8.4) we find

$$\bar{u}_1(t,x) = \bar{\phi}(2x\,e^{-t}) \int_0^t \bar{k}(x\,e^{-\tau})\,d\tau,$$

where $\bar{k}(x) = k(x)$ if $x \leq \frac{1}{2}\beta$ and $\bar{k}(x) = 0$ elsewhere.

By iteration we find

$$\bar{u}_i(t,x) = \bar{\phi}(2^i x\,e^{-t})\bar{k}_i(t,x), \qquad i=0,1,2,\ldots$$

where $\bar{k}_0(t,x) = 1$ and

$$\bar{k}_i(t,x) = \int_0^t \bar{k}(x\,e^{-\tau})\bar{k}_{i-1}(t-\tau, 2x\,e^{-\tau})\,d\tau.$$

Using these expressions for $\bar{u}_i$ we find

$$|\bar{u}_0(t,x)| \leq \|\bar{\phi}\|, \qquad |\bar{u}_1(t,x)| \leq \|\bar{\phi}\| \int_{a/2}^{\beta/2} \frac{\bar{k}(\xi)}{\xi}\,d\xi = p\|\bar{\phi}\|$$

and by iteration we find

$$|\bar{u}_i(t,x)| \leq p^i \|\bar{\phi}\|. \tag{8.7}$$

One can also see from the expressions above that $\bar{u}_i(t,x)$ vanishes identically from time

$$t_i = \ln\left(\frac{2^{i+1}\beta}{a}\right) \text{ on.} \qquad \text{Let } i \geq 1.$$

All individuals contained in $\bar{m}_i(t,x)$ are daughters of individuals contained in $\bar{u}_{i-1}(t,x)$. From (8.4) we find

$$\bar{m}_i(t,x) = \int_0^{(t,t+G(\frac{1}{2}\beta)-G(x))^-} k(\alpha(x,t-\tau))\bar{u}_{i-1}(\tau, 2\alpha(x,t-\tau))\,d\tau$$

and this together with (8.7) gives us

$$|\bar{m}_i(t,x)| \leq p^{i-1}\|\bar{\phi}\| \cdot \int_{a/2}^{\beta/2} \frac{k(\xi)}{g(\xi)}\,d\xi = p^i \|\bar{\phi}\| \leq p^i \|\phi\|.$$

The generation $\bar{m}_i$ goes extinct *a* time $\int_\beta^1 d\xi/g(\xi)$ after $\bar{u}_i$. This proves the lemma. □

Now we are able to prove that the contribution of $\bar{m}(t,x)$ to the total population becomes very small for large t.

Theorem 8.2. $\|\bar{m}(t,\cdot\,;\phi)\| \leq M\,e^{-qt}\|\phi\|$, $t \geq 0$, *where* $M>0$ *is some constant not depending on* t *or* ϕ *and* $q=-\ln p/\ln 2>0$.

Proof: Suppose $t>0$. There are finitely many generations $i, i+1, \ldots, j$ present in the sub-population $\bar{m}(t,x)$ where i is larger or equal to the smallest integer ν satisfying

$$\ln\left(\frac{2^{\nu}\beta}{a}\right)+\int_{\beta}^{1}\frac{d\xi}{g(\xi)} \geq t.$$

(The precise value of j is not important for our purposes). Hence $\bar{m}(t,x)=\sum_{l=i}^{j}\bar{m}_l(t,x)$ from which it follows that

$$|\bar{m}(t,x)| \leq \sum_{l=\nu}^{\infty}\|\bar{m}_l(t,\cdot)\| \leq \sum_{l=\nu}^{\infty}p^l\|\phi\| = \frac{p^{\nu}}{1-p}\|\phi\|.$$

The definition of ν yields

$$\nu-1 \leq \frac{t}{\ln 2}+\theta \leq \nu \quad \text{where } \theta=\frac{\ln a/\beta}{\ln 2}$$

and the result follows. □

For the remaining sub-population $\hat{m}(t,x)$ we can prove a compactness result.

Theorem 8.3. *The linear map* $\phi \mapsto \hat{m}(t,\cdot\,;\phi)$ *is compact for all* $t \geq 0$.

Proof. $\hat{m}_0(t,x)=0$ by assumption. (8.3) and (8.5) yield that

$$\hat{m}_1(t,x)=\int_{(t,t+G(\frac{1}{2}\beta)-G(x))^-}^{t} k(\alpha(x,t-\tau))\phi(G^{-1}(G(2\alpha(x,t-\tau))-\tau))\,d\tau.$$

As in Lemma 5.1 we substitute

$$\xi=G(2\alpha(x,t-\tau))-\tau$$

and find that $d\xi/d\tau>0$ for all values of x, t and τ where $\alpha(x,t-\tau) \geq \frac{1}{2}\beta$. Now arguments similar to those used to prove Lemma 5.1 yield the result. □

Corresponding to the subpopulations $\bar{m}(t,x)$ and $\hat{m}(t,x)$ we define two families of operators $\bar{T}(t)$ and $\hat{T}(t)$:

$$\bar{T}(t)\phi=\bar{m}(t,\cdot\,;\phi), \qquad \hat{T}(t)\phi=\hat{m}(t,\cdot\,;\phi).$$

One should note that neither of them defines a semigroup. Theorem 8.2 states

$$\|\bar{T}(t)\| \leq M\,e^{-qt} \tag{8.8}$$

and Theorem 8.3 can be summarized by saying that

$$\hat{T}(t) \text{ is compact for all } t \geq 0. \tag{8.9}$$

Now we introduce the notion of a measure of non-compactness. We refer to [15] for more details.

Let B be a Banach-space, and V be a bounded subset of B. The measure of non-compactness (or Kuratowski-measure) $\gamma(V)$ of V is defined to be

$$\gamma(V)=\inf\{d>0 \mid \text{there exist a finite number of sets } S_1,\ldots,S_n \text{ such that diameter } (S_i)\leq d \text{ and } V=\textstyle\bigcup_{i=1}^n S_i\}.$$

Two important properties are

$$\gamma(V)=0 \text{ iff } V \text{ has a compact closure} \tag{8.10a}$$

$$\gamma(V+W)\leq\gamma(V)+\gamma(W) \text{ where } V+W=\{v+w \mid v\in V \text{ and } w\in W\} \text{ and } V, W \text{ are bounded subsets of } B. \tag{8.10b}$$

The measure of non-compactness of a bounded operator $L: B\to B$ is defined to be

$$\hat{\gamma}(L)=\inf\{\varepsilon\geq 0 \mid \gamma(L(V))\leq\varepsilon\gamma(V), \text{ for all bounded sets } V\subset B\}. \tag{8.11}$$

(8.10a) and (8.10b) yield

$$\hat{\gamma}(L)=0 \quad \text{iff } L \text{ is compact,} \tag{8.12a}$$

$$\hat{\gamma}(L_1+L_2)\leq\hat{\gamma}(L_1)+\hat{\gamma}(L_2), \quad \text{where } L_1, L_2 \text{ are bounded operators on } B. \tag{8.12b}$$

Moreover, it is obvious that

$$\hat{\gamma}(L)\leq\|L\|. \tag{8.12c}$$

The Browder essential spectrum $\sigma_{ess}(L)$ of the operator L is defined by $\lambda\in\sigma_{ess}(L)$ if at least one of the following conditions holds

(1) $\mathcal{R}(\lambda I-L)$ is not closed
(2) λ is a limit point of $\sigma(L)$
(3) $\bigcup_{k\geq 1}\mathcal{N}((\lambda I-L)^k)$ is infinite dimensional.

It can be proved that

$$\lambda\in\sigma(L)\backslash\sigma_{ess}(L)\Rightarrow\lambda\in P\sigma(L). \tag{8.13}$$

(These are called normal eigenvalues).

Let $r_{ess}(L)$ be the radius of the essential spectrum

$$r_{ess}(L)=\sup\{|\lambda| \mid \lambda\in\sigma_{ess}(L)\}.$$

Nussbaum [15] proved the following result.

Lemma 8.4. $r_{ess}(L)=\lim_{n\to\infty}(\hat{\gamma}(L^n))^{1/n}$.

Now we return to the original problem. We can prove the following important result on the semigroup $T(t)$.

Theorem 8.5. *Assume B' holds. Suppose $\mu\in\sigma(T(t))$ and $|\mu|>e^{-qt}$ then there exists a $\lambda\in P\sigma(A)$ such that $\mu=e^{\lambda t}$.*

Proof: $r_{ess}(T(t))=\lim_{n\to\infty}(\hat{\gamma}(T(nt)))^{1/n}$. $\hat{\gamma}(T(nt))\leq\hat{\gamma}(\bar{T}(nt))+\hat{\gamma}(\hat{T}(nt))=\hat{\gamma}(\bar{T}(nt))\leq\|\bar{T}(nt)\|\leq M e^{-qnt}$, where we have used (8.8), (8.9) and (8.12a, b, c). Consequently $r_{ess}(T(t))\leq e^{-qt}$. Now suppose $\mu\in\sigma(T(t))$ and $|\mu|>e^{-qt}$, then it must be that $\mu\in P\sigma(T(t))$, and as we already saw in the proof of Theorem 7.1 there must be some $\lambda\in P\sigma(A)$ such that $\mu=e^{\lambda t}$. □

The characteristic equation in situation B' is given by

$$1=\pi(\lambda)=p\cdot 2^{-\lambda}+\int_{\beta/2}^{1/2}\frac{k(\xi)}{g(\xi)}\,e^{-\lambda(G(2\xi)-G(\xi))}\,d\xi$$

(where p was given by (8.6)) and it follows that the results of Theorem 6.1 remain valid for this wider class of functions g. Hence there exists an $\varepsilon_1>0$ such that

$$\operatorname{Re}\lambda\leqslant-\varepsilon_1,\qquad \lambda\in\sigma(A)\backslash\{0\}$$

(recall that $\lambda_d=0$) and the conclusion of Theorem 7.1 remains valid if we chose $\varepsilon=\min(\varepsilon_1, q)$.

We can state our main result now

Corollary 8.6. *If B' is satisfied then $m(t,\cdot\,;\phi)=e^{\lambda_d t}(P\phi+o(1))$, $t\to+\infty$.*

Of course the conclusion of Corollary 7.3 remains valid as well, if B' is satisfied.

If $a\geqslant\frac{1}{2}$, extension to the more general case B is straightforward. In that case (8.6) should be replaced by

$$p=\int_{Q_1}\frac{k(\xi)}{g(\xi)}\,d\xi.$$

Furthermore we were able to prove that the result stated in Corollary 8.6 remains valid if the first condition in B' is replaced by $a\geqslant\frac{1}{2}\beta$. In their study of the inverse problem in [1], Anderson et al. found that the growth-rate g satisfied the condition in B'; but unfortunately Fig. 4(B) in [1] suggests that neither $a\geqslant\frac{1}{2}$ nor $a\geqslant\frac{1}{2}\beta$ is satisfied. It seems to two of us that extension to situations where $a<\frac{1}{2}\beta$ should be possible, although one probably has to deal with intransparent and troublesome technical problems which do not provide new insight; the third of us has some doubts about it.

9. Concluding remarks

It is rather difficult to make dynamic observations of individual micro-organisms and consequently the "data" b, g and μ are hard to obtain. In fact it might be easier to measure the stable distribution and one may want to derive information about b, g and μ from such measurements. We refer to Bell and Anderson [1, 2, 3] for a discussion of this inverse problem (also see [4]).

The present study can serve as a starting point for an investigation of nonlinear problems. More precisely we think of situations where the growth of the individuals depends on the availability of a certain substrate, which in turn is influenced by the consumption [6, 7, 14]. In [4] Diekmann et al. argue that there are several ways to describe reproduction by fission under changing conditions, each of them corresponding to a different intrinsic mechanism. Using the results of this paper they show that for one of these mechanisms the stable distributions in a chemostat is independent of controllable parameters like the dilution rate and the inflowing substrate concentration.

We shall deal with other generalizations such as fission into not necessarily equal parts and time-periodic (seasonal) growth, death, and fission rates in forthcoming publications. We intend to study models of size- and age-dependent population growth [2, 3, 18] in the near future.

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Appendix

Choose x_1 and x_2 with $x_1 < x_2$ and let $h > 0$ be small. Individuals which have at time $t+h$ a size between x_1 and x_2 fall into two different categories:

(i) those who had at time t a size between $x_1 - hg(x_1) + o(h)$ and $x_2 - hg(x_2) + o(h)$ and which have neither split nor died

(ii) those which were born between t and $t+h$ as daughters of mothers with a size between $2x_1 + O(h)$ and $2x_2 + O(h)$. Or, in formula

$$\int_{x_1}^{x_2} n(t+h, x)\,dx = \int_{x_1 - hg(x_1)}^{x_2 - hg(x_2)} n(t, x)[1 - h(\mu(x) + b(x))]\,dx + 2h \int_{2x_1 + O(h)}^{2x_2 + O(h)} b(x) n(t, x)\,dx + o(h).$$

Rearranging the terms and dividing by h we find

$$\frac{1}{h}\int_{x_1}^{x_2} [n(t+h, x) - n(t, x)]\,dx + \frac{1}{h}\left\{\int_{x_2 - hg(x_2)}^{x_2} n(t, x)\,dx - \int_{x_1 - hg(x_1)}^{x_1} n(t, x)\,dx\right\} + o(1)$$
$$= -\int_{x_1}^{x_2} (\mu(x) + b(x)) n(t, x)\,dx + 4\int_{x_1}^{x_2} b(2x) n(t, 2x)\,dx.$$

The right-hand side is independent of h. In the limit $h \to 0$ the left hand side yields

$$\int_{x_1}^{x_2} \frac{\partial n}{\partial t}(t, x)\,dx + g(x_2) n(t, x_2) - g(x_1) n(t, x_2).$$

If we now divide both sides by $x_2 - x_1$ and subsequently take the limit $x_2 - x_1 \downarrow 0$ we find the balance law (2.1).

Of course taking the limits $h \to 0$ and $x_2 - x_1 \downarrow 0$ is not justified a priori and, in fact, not even a posteriori (see the end of Sect. 3). Nevertheless this formal procedure is a helpful intermediate step towards the calculation of $n(t, x)$. In Sect. 3 we employ the concepts of a semigroup of bounded linear operators and its infinitesimal generator to give a precise mathematical formulation of the relation between the balance law and its solution.

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THE DYNAMICAL BEHAVIOUR OF THE AGE-SIZE-DISTRIBUTION OF A CELL POPULATION

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KEY WORDS & PHRASES: *age-size-distribution, integration along characteristics, abstract renewal equation, Laplace transform, operator-valued function, positive operator, non-supporting operator, dominant singularity, renewal theorem.*

ABSTRACT

We study the model proposed by Bell and Anderson describing the dynamics of a proliferating cell population. This model assumes that the individual's behaviour is completely determined by its age and size. By the method of integration along characteristics the problem is reduced to a renewal type integral equation. Using Laplace transform techniques and results from positive operator theory we can describe the large time behaviour of the solution, if we impose a condition on the growth rate.

Introduction

We investigate a mathematical model for cell growth and division. Our main assumption is that (chronological) age and size (by size we mean volume, length or any other quantity which is preserved at division) are the traits required to describe the cell's progress through its cycle properly. Age seems reasonable because some biochemical reactions (e.g. replication of DNA) proceed sequentially during the life time of a cell, while other reactions, such as the increase of structural materials, depend on such factors as diffusion times and surface to volume ratios, suggesting the indispensability of size as a parameter. (Bell & Anderson (1967)).

There is a vast amount of literature on cell cycle models and almost as many models have been proposed as there are papers on the subject, and the number of papers is enormous. We refer to chapter II and III of the monograph of Eisen (1979) for an overview. In this respect our paper can be seen as the umpteenth attempt to describe some features of proliferating cell populations. However, the main goal of this paper is to show how abstract results from functional analysis (in particular positive operator theory) can be exploited to "solve" a concrete problem.

This paper is subdivided into nine sections. In section 1 we present the model and we make some assumptions on the functions which describe the life of individual cells. In section 2 the problem is reduced to an integral equation (abstract renewal equation) from which the distribution of birth sizes can be calculated. Existence and uniqueness of a solution to this integral equation is proved in section 3. Then, in section 4 the abstract renewal equation is reduced to a family of operator equations by means of the Laplace transform. It turns out that the investigation of the large time behaviour of the solution of the renewal equation is very closely linked with the location of some set of singular points, in particular the position of the singular point with largest real part, the so-called dominant singularity (or, in another context, eigenvalue) which can be determined by employing methods from positive operator theory. We shall briefly discuss some results from positive operator theory in section 5, and these results are used in section 6 to prove existence of a dominant singularity under some extra condition on the growth rate (i.e. the function describing the dynamics of an individual's size). In section 7 we calculate the residue at this dominant singularity and the outcome is used in section 8, where we apply the inverse Laplace transform which gives us the large time behaviour of the birth function. Finally in section 9 we explain what this means for the solution of our original problem and why we cannot dispense with the assumptions made. In particular we will show what happens in case of exponential (individual) growth (i.e. growth of an individual is proportional to its size), and it will appear that these results reject a supposition of Bell (1968).

1. The model

Here we shall confine our attention to large populations so that fluctuations from the mean can be ignored. We assume that a cell is fully characterized by its age a and size x. Here size can mean volume, length, DNA-content or any other quantity which obeys a physical conservation law. Size increases with time and we assume that this process can be described by the ordinary differential equation

$$\frac{dx}{dt} = g(x). \tag{1.1}$$

This means in particular that the growth rate g does neither depend on age, which seems very reasonable from a biological point of view, nor on environmental factors (such as food density) which are influenced by the population itself, causing nonlinearities in the equation. Age also increases with time and obeys $\frac{da}{dt} = 1$. However our theory can be easily extended to the case where a denotes some physiological age, which does not necessarily increase linearly with time: $\frac{da}{dt} = f(a)$ where f is a bounded continuous positive function. We assume that if a cell divides, it produces two daughter cells, both having age zero and half the size of the mother. Let $n(t,a,x)$ be the cell density function, i.e. $\int_{x_1}^{x_2}\int_{a_1}^{a_2} n(t,a,x)dadx$ is the number of cells having age between a_1 and a_2, and size between x_1 and x_2. From the conservation principle it follows that the equation for the density function can be written as

$$\frac{\partial n}{\partial t} = -\nabla \cdot J - F - D, \tag{1.2}$$

where the flux $J = J(t,a,x)$ is given by $J = (n(t,a,x), g(x)n(t,a,x))$, and ∇ is the operator $(\frac{\partial}{\partial a}, \frac{\partial}{\partial x})$. The sinks F and D account for the individuals which "disappear" as a result of fission and death respectively. We refer to the forthcoming book of Metz & Diekmann (in preparation) for a more general description how to derive balance equations such as (1.2) (also see Eisen (1979)).

Let fission and death be described by the per capita probabilities per unit of time $b(a,x)$ and $\mu(a,x)$ respectively, then $F = F(t,a,x) = b(a,x)n(t,a,x)$ and $D = D(t,a,x) = \mu(a,x)n(t,a,x)$.

We shall now introduce a number of mathematical assumptions on the functions g, b and μ and discuss their biological meaning and/or mathematical motivation. With respect to the growth rate g we assume

g is a continuous function on $[0,\infty)$ *and there exist constants* $g_{\min}, g_{\max}$ $\quad (A_g)$

such that $0 < g_{\min} \leq g_{\max} < \infty$ and $g_{\min} \leq g(x) \leq g_{\max}$ *for all* $x \in [0,\infty)$.

It follows from this assumption that certain combinations of a and x are forbidden in the sense that cells with such a combination of age and size will never come into existence. More precisely there exists a (continuous) curve in the (a,x)-plane starting from $(a,x) = (0,0)$ and tending towards (∞,∞) below which no individual will ever dwell. We can compute this curve explicitly. Consider a cell whose size at birth is $x (x \geq 0)$ (assuming that such cells indeed exist). Let $X(a,x)$ be its size at age a, if it has not died or divided before reaching that age. Then X is the solution of the initial value problem $\frac{dx}{da} = g(x)$, $x(0) = x$, which has a continuous (differentiable) solution tending to ∞ if a tends to ∞ because of assumption (A_g). The curve $\{(a, X(a,x)) | a \geq 0\}$ is called the characteristic curve starting from $(0,x)$. (See figure 1) We refer to section 2 for more details.

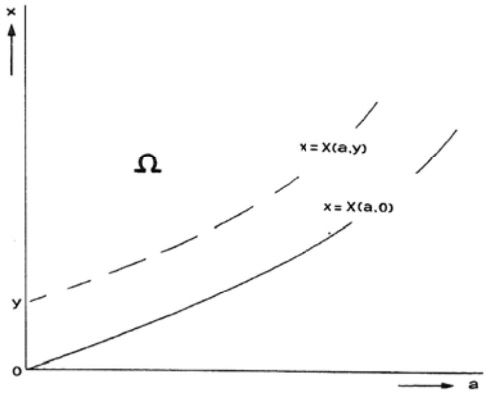

Figure 1. The set Ω. An individual with birth size y travels along the curve $\{X(a,y)|\ a \geq 0\}$ until it dies or divides. Individuals can only exist in the shaded region $\Omega = \{(a,x) \in \mathbf{R}^+ \times \mathbf{R}^+ | x \geq X(a,0)\}$. The actual state space Ω_s (i.e. the subset of $\mathbf{R}^+ \times \mathbf{R}^+$ in which indeed individuals do occur) is a subset of Ω, and in some cases Ω_s is smaller than Ω. (We refer to section 6 for an example.)

We impose the following conditions on b and μ:

$b \in L_\infty(\Omega)$ (*i.e. b is measurable and essentially bounded on* Ω)

$b(a,x) = 0,\ a \leq a_0,\ (a,x) \in \Omega,$ $\qquad (A_b)$

$b(a,x) > 0,\ a > a_0,\ (a,x) \in \Omega,$

$\liminf_{a \to \infty} b(a, X(a,x)) = \underline{b} > 0$ *uniformly in x.*

Here $a_0 > 0$ is some threshold below which cells cannot divide. The biological reason for this is that every cell has to go through a phase during which DNA is replicated, and the duration of this phase is more or less constant (see Bell & Anderson (1967), Eisen (1979)). Biologically, the last condition in (A_b) says that old individuals continue dividing at a positive rate.

$\mu \in L_\infty^{loc}(\Omega)$ (*i.e.* μ *is measurable and essentially bounded on compact subsets of* Ω), $\qquad (A_\mu)$

$\mu(a,x) \geq 0,\ (a,x) \in \Omega.$

Let

$$d(a,x) = b(a,x) + \mu(a,x). \tag{1.3}$$

We assume

There exists a constant d_∞ *with* $0 < d_\infty \leq \infty$ *such that* $\lim_{\sigma\to\infty} d(a+\sigma, X(\sigma,x)) = d_\infty$

uniformly in a *and* x. *Moreover, if* $d_\infty < \infty$, *there exists a constant* $M \geq 0$ *such that* $\qquad (A_d)$

for all a *and* x: $\int_0^\infty |d(a+\sigma, X(\sigma,x)) - d_\infty| d\sigma \leq M$.

Biologically assumption (A_d) means that the probability for a cell to reach age a without dying or dividing decreases more or less exponentially if a becomes large. In section 9 it is explained why this assumption is needed.

We can rewrite (1.2) as

$$\frac{\partial}{\partial t} n(t,a,x) + \frac{\partial}{\partial a} n(t,a,x) + \frac{\partial}{\partial x}(g(x)n(t,a,x)) = -(\mu(a,x) + b(a,x))n(t,a,x), \tag{1.4}$$

$$t \geq 0,\ (a,x) \in \Omega.$$

The fact that dividing mothers of age a and size $2x$ give birth to two daughters of age a and size x is accounted for by the boundary condition

$$n(t,0,x) = 4\int_{a_0}^{\infty} b(a,2x)n(t,a,2x)da. \tag{1.5}$$

See Bell & Anderson (1967) for an explanation of the factor 4.

Remark 1.1. In (1.5) we only have to integrate over those ages a that satisfy $X(a,0) \leq 2x$.

We specify an initial condition

$$n(0,a,x) = n_0(a,x),\ (a,x) \in \Omega. \tag{1.6}$$

Biological considerations yield that n_0 should satisfy

$$n_0(a,x) \geq 0,\ (a,x) \in \Omega \text{ and } n_0 \in L_1(\Omega). \tag{1.7}$$

2. Reduction to an abstract renewal equation

Usually age-dependent population models are reduced to a renewal equation (which is a Volterra integral equation of convolution type) for the birth function (see Hoppensteadt (1975)). Here we will show that this can also be done for our age-size-structured model (1.4)-(1.6). In this case, however, we obtain an abstract renewal equation, in the sense that solutions take values in some function space.

Let $m(t,a,x)$ be defined by

$$m(t,a,x) = g(x)n(t,a,x), \tag{2.1}$$

then m satisfies the equation

$$\frac{\partial m}{\partial t} + \frac{\partial m}{\partial a} + g(x)\frac{\partial m}{\partial x} = -(\mu(a,x) + b(a,x))m(t,a,x), \tag{2.2a}$$

$$m(t,0,x) = \frac{4g(x)}{g(2x)}\int_{a_0}^{\infty} b(a,2x)m(t,a,2x)da, \tag{2.2b}$$

$$m(0,a,x) = m_0(a,x) \stackrel{def}{=} g(x)n_0(a,x). \tag{2.2c}$$

By the method of integration along characteristics (see Courant & Hilbert (1962)) we can convert this system into an integral equation.

The characteristic curve through (t,a,x) is determined by $s \to (T(s,t),A(s,a),X(s,x))$, where s is an independent book-keeping variable and T,A,X are solutions of the ODE's $\frac{dT}{ds} = 1$, $T(0,t) = t$, $\frac{dA}{ds} = 1$, $A(0,a) = a$, $\frac{dX}{ds} = g(X)$, $X(0,x) = x$, thus $T(s,t) = s+t$, $A(s,a) = s+a$, and $X(s,x) = G^{-1}(s+G(x))$, where

$$G(x) = \int_0^x \frac{d\xi}{g(\xi)}, \quad x \geq 0, \tag{2.3}$$

can be interpreted as the time needed to grow from 0 to x and G^{-1} denotes its inverse. Observe that $G^{-1}(a) = X(a,0)$.

Now let t,a,x be fixed and let $\bar{m}(s) = m(T(s,t),A(s,a),X(s,x))$, then

$$\frac{d\bar{m}}{ds} = -d(A(s,a),X(s,x))\bar{m}(s), \tag{2.4}$$

where $d(a,x)$ is given by (1.3). Let

$$Q(s,a,x) \stackrel{def}{=} \exp\left[-\int_0^s d(A(\sigma,a),X(\sigma,x))d\sigma\right], \tag{2.5}$$

which can be interpreted as the probability that a cell with age a and size x reaches age $a+s$. From (2.4) we obtain that

$$\bar{m}(s) = \bar{m}(0)Q(s,a,x). \tag{2.6}$$

Let

$$t' = T(s,t),\ a' = A(s,a),\ x' = X(s,x). \tag{2.7}$$

(i) We choose $t = 0$. Then $a = a'-t'$, $x = X(-t',x')$. If we substitute this in (2.6) we obtain

$$m(t',a',x') = m(0,a'-t',X(-t',x'))\cdot Q(t',a'-t',X(-t',x')), \text{ if } a' > t'. \tag{2.8}$$

(ii) We choose $a = 0$. Then $t = t'-a'$, $x = X(-a',x')$, and we deduce from (2.6)

$$m(t',a',x') = m(t'-a',0,X(-a',x'))\cdot E(a',X(-a',x')), \text{if } a' < t', \tag{2.9}$$

where

$$E(a,x) \stackrel{def}{=} Q(a,0,x) = \exp\left[-\int_0^a d(\sigma,X(\sigma,x))d\sigma\right] \tag{2.10}$$

is the probability that a cell having size x at birth reaches age a.

If we drop the accents in (2.9) and (2.10), and use (2.1) and (2.2c) we find

$$n(t,a,x) = \frac{g(X(-t,x))}{g(x)} n_0(a-t,X(-t,x)) \cdot Q(t,a-t,X(-t,x)), \quad t < a, \tag{2.11}$$

$$n(t,a,x) = \frac{g(X(-a,x))}{g(x)} n(t-a,0,X(-a,x)) \cdot E(a,X(-a,x)), \quad t > a. \tag{2.12}$$

Let the birth function B be defined by

$$B(t,x) = n(t,0,x). \tag{2.13}$$

If we substitute (2.11)-(2.12) into (1.5), then we obtain the following integral equation for B:

$$B(t,x) = \Phi(t,x) + \int_{a_0}^{t} k(a,2x) B(t-a,X(-a,2x)) da, \tag{2.14}$$

where

$$\Phi(t,x) = \frac{4g(X(-t,2x))}{g(2x)} \int_{t}^{\infty} b(a,2x) Q(t,a-t,X(-t,2x)) \cdot n_0(a-t,X(-t,2x)) da, \tag{2.15}$$

and

$$k(a,x) = \frac{4g(X(-a,x))}{g(x)} b(a,x) E(a,X(-a,x)). \tag{2.16}$$

$\Phi(t,x)$ is only defined for values of x satisfying $G(2x) \geq t$, and one should read $\Phi(t,x) = 0$ if $G(2x) \leq t$. Furthermore $k(a,x) = 0$ if $a \leq a_0$ or $a \geq G(x)$, and $k(a,x) \geq 0$ if $a_0 \leq a \leq G(x)$.

The integral equation (2.14) was also found by Bell (1968) but he only solved it for the special case that all cells divide at the same age (see also Beyer (1970)).

It follows from (2.11)-(2.12) that knowledge of the solution $B(t,x)$ of (2.14) yields the solution $n(t,a,x)$ of (1.4)-(1.6). Therefore we shall concentrate on (2.14) during the rest of this chapter. In section 9 we shall interprete some result in terms of the density $n(t,a,x)$.

We can rewrite (2.14) as the abstract renewal equation

$$B(t) = \Phi(t) + \int_{0}^{t} K(a) B(t-a) da, \tag{2.17}$$

where, for fixed $t \geq 0$, $\Phi(t) \in L_1[0,\infty)$ and $K(t)$ defines a bounded operator from $L_1[0,\infty)$ into itself:

$$(K(t)\psi)(x) = k(t,2x)\psi(X(-t,2x)), \quad \psi \in L_1[0,\infty), \tag{2.18}$$

where one should read $\psi(X(-t,2x)) = 0$ if $G(2x) < t$.

Remark 2.1. Throughout this chapter we call a Banach space-valued function integrable if it is Bochner-integrable. This means the following: let E be a Banach space with norm $\|\cdot\|_E$ and let $f:(a,b) \to E$, where $-\infty \leq a < b \leq \infty$. Then $f(t)$ is Bochner-integrable if and only if f is strongly measurable and $\|f(t)\|_E$ is Lebesgue integrable (see Hille & Phillips (1957)).

We call $B(t)$ a solution of (2.17) if and only if

i) $B(t) \in L_1[0,\infty)$, $t \geq 0$,

ii) $B(\cdot)$ is integrable on $[0,t_0]$ for all $t_0 \geq 0$,

iii) $B(t)$ obeys (2.17).

3. Existence and Uniqueness of solutions

It turns out that the proof of an existence and uniqueness result for the abstract renewal equation (2.17) is rather similar to the scalar case which has been extensively treated in the book of Bellman & Cooke (1963). First we shall prove a lemma.

Lemma 3.1. (a) *Let d_∞ (of assumption (A_d)) be finite. Then there exist positive constants T_0, m_K, M_K and M_Φ such that for all $t \geq T_0$: $\|\Phi(t)\| \leq M_\Phi e^{-d_\infty t}$, and for all $\psi \in L_1[0,\infty)$: $m_K e^{-d_\infty t}\|\psi\| \leq \|K(t)\psi\| \leq M_K e^{-d_\infty t}\|\psi\|$.*
(b) *Let $d_\infty = \infty$. For all $c > 0$ there exist constants $L_K(c), L_\Phi(c) > 0$ such that for all $t \geq 0$: $\|\Phi(t)\| \leq L_\Phi(c)e^{-ct}$, $\|K(t)\psi\| \leq L_K(c)e^{-ct}\|\psi\|$, for all $\psi \in L_1[0,\infty)$.*

Proof. We shall only prove the second estimate in (a).

$$E(a,x) = \exp[-\int_0^a d(\sigma,X(\sigma,x))d\sigma] = \exp[-\int_0^a \{d(\sigma,X(\sigma,x))-d_\infty\}d\sigma]\cdot\exp[-\int_0^a d_\infty d\sigma].$$

Let M be the constant of assumption (A_d), then

$$e^{-M}e^{-d_\infty a} \leq E(a,x) \leq e^M e^{-d_\infty a}.$$

The second part of (a) now follows immediately from these estimates and the assumptions (A_g) and (A_b). In an analogous manner we can prove part (b). □

The following existence and uniqueness result can be proved.

Theorem 3.2. *Let $t_0 > 0$. There exists a unique bounded integrable solution $B(t)$ of (2.17) on $[0,t_0]$.*

The existence result can be established by the method of successive approximations. Uniqueness then follows from a Gronwall-type lemma. We refer to Bellman & Cooke (1963) where the scalar case has been worked out in great detail, and the reader will have no difficulty to see that all proofs can be carried over. Because t_0 can be chosen arbitrarily large, theorem 3.2 implies global existence of the solution $B(t)$.

Remark 3.3. Strictly speaking condition (A_b) and (A_μ) are sufficient to prove local existence and uniqueness.

In the next section we shall apply Laplace transformation to the integral equation (2.17). Therefore we need the following estimate.

Theorem 3.4. *There exists a $\beta \in \mathbf{R}$ such that $\|B(t)\| \leq M_B e^{\beta t}$, $t \geq 0$, where $M_B > 0$ is a constant.*

Proof. Let $\beta \in \mathbf{R}$ be such that $\|\Phi(t)\| \leq c_1 e^{\beta t}$ and $\int_0^\infty e^{-\beta t}\|K(t)\|dt = c_2 < 1$. From lemma 3.1 it is clear that such a β indeed exists. Then

$$\|B(t)\| \leq c_1 e^{\beta t} + \int_0^t \|K(a)\| \cdot \|B(t-a)\| da = c_1 e^{\beta t} + e^{\beta t} \int_0^t \{\|K(a)\| \cdot e^{-\beta a}\} \cdot \{\|B(t-a)\| \cdot e^{-\beta(t-a)}\} da.$$

Let $v(t) \overset{def}{=} \max_{0 \leq a \leq t} \|B(a)e^{-\beta a}\|$, then $v(t) \leq c_1 + v(t) \int_0^t e^{-\beta a} \|K(a)\| da \leq c_1 + c_2 v(t)$, hence $v(t) \leq \frac{c_1}{1-c_2}$, from which we obtain that $\|B(t)\| \leq \frac{c_1}{1-c_2} e^{\beta t}$. □

4. Laplace Transformation

A technique which turned out to be extremely useful in the study of scalar renewal equations is Laplace transformation (e.g. Bellman & Cooke (1963), Hoppensteadt (1975)). This technique can also be employed in the study of abstract renewal equations such as (2.17). First we shall introduce some notations. Let $I \subseteq \mathbf{R}$ be an interval, and E a Banach space. We define by $L_p(I,E)$, $1 \leq p \leq \infty$, the Banach space consisting of all functions $f: I \to E$ satisfying $\|f\|_p \overset{def}{=} \{\int_I \|f(t)\|^p dt\}^{\frac{1}{p}} < \infty$, if $p < \infty$ and $\|f\|_\infty \overset{def}{=} \text{ess sup} \|f(t)\| < \infty$, if $p = \infty$. If $I = [0,\infty)$ we shall write $L_p(0,\infty;E)$ instead of $L_p([0,\infty);E)$.

Remark 4.1. We have to distinguish between the norm of $f(t)$, $t \geq 0$, as an element of E and the norm of f being an element of $L_p(I;E)$. In the first case we write $\|f(t)\|$, in the second case $\|f\|_p$.

Definition. Let f be a function from $[0,\infty)$ to some Banach space E, then its Laplace transform $\hat{f}$ is defined by $\hat{f}(\lambda) = \int_0^\infty e^{-\lambda t} f(t) dt$, whenever this integral is defined with respect to the norm topology.

The following result is standard (Hille & Phillips (1957)).

Lemma 4.2. *If $f \in L_1(0,\infty;E)$ then $\hat{f}(\lambda)$ is analytic in $\text{Re}\,\lambda > 0$ and continuous in $\text{Re}\,\lambda \geq 0$ (with respect to the norm-topology).*

We shall state two results from Fourier theory which are generally known for the case that E is finite-dimensional. The first is the so-called Riemann-Lebesgue lemma (Hille & Phillips (1957), thm 6.4.2).

Lemma 4.3 (Riemann-Lebesgue). *Let $f \in L_1(0,\infty;E)$ and $\hat{f}$ its Laplace transform. Then $\lim_{|\eta| \to \infty} \hat{f}(\xi + i\eta) = 0$, uniformly for ξ in bounded closed subintervals of $(0,\infty)$.*

The second result which became known as Plancherel's theorem says that the Fourier transform of an L_2-function is again an L_2-function, and the mapping $f \to \hat{f}$ defines an isometry. We refer to Yosida (1980) for a proof in the scalar case, and the reader will have no difficulty to see that Yosida's proof can be carried through directly for Banach space-valued functions.

Lemma 4.4. *Let $f \in L_1(-\infty,\infty;E) \cap L_2(-\infty,\infty;E)$, then the function $\eta \to \hat{f}(i\eta)$ is an element of $L_2(-\infty,\infty;E)$ and $\int_{-\infty}^{\infty} \|f(t)\|^2 dt = \int_{-\infty}^{\infty} \|\hat{f}(i\eta)\|^2 d\eta$.*

This last equality is called Parseval's relation.

Let the right-half-plane Λ be defined by

$$\Lambda \stackrel{def}{=} \{\lambda \in \mathbf{C} | \text{Re}\,\lambda > -d_\infty\} \tag{4.1}$$

(where $\Lambda = \mathbf{C}$ if $d_\infty = \infty$). Then it follows from lemma 3.1 and lemma 4.2 that $\hat{K}(\lambda)$ and $\hat{\Phi}(\lambda)$ are defined and analytic in Λ. Moreover it follows from lemma 3.1 that $\hat{K}(\lambda)$ is not defined if $\text{Re}\,\lambda < -d_\infty$.

Remark 4.5. It is not a priori clear whether $\hat{K}(\lambda)$ is defined for λ on the vertical line $\text{Re}\,\lambda = -d_\infty$. As to $\hat{\Phi}(\lambda)$ it depends on the initial age - size distribution $n_0(a,x)$ whether or not it is defined for values of λ satisfying $\text{Re}\,\lambda \leqslant -d_\infty$. However this is not important for our purposes.

We define $\hat{B}(\lambda) = \int\limits_0^\infty e^{-\lambda t} B(t)dt$ for those values of λ for which the integral converges. From theorem 3.3 we conclude that $\hat{B}(\lambda)$ exists if $\text{Re}\,\lambda > \beta$. The convolution in (2.17) is converted by the Laplace transformation into a product of Laplace transforms. We wish to extend $\hat{B}(\lambda)$ to Λ minus some set Σ of singular points. More precisely

$$\hat{B}(\lambda) = \hat{\Phi}(\lambda) + \hat{K}(\lambda)\hat{B}(\lambda),\ \lambda \in \Lambda. \tag{4.2}$$

Let Σ be the set of all $\lambda \in \Lambda$ for which $I - \hat{K}(\lambda)$ is singular.

$$\Sigma = \{\lambda \in \Lambda | 1 \in \sigma(\hat{K}(\lambda))\}, \tag{4.3}$$

where $\sigma(\hat{K}(\lambda))$ denotes the spectrum of the operator $\hat{K}(\lambda)$. The condition $1 \in \sigma(\hat{K}(\lambda))$ is the usual precursor of a *characteristic equation* (Heijmans (to appear), Hoppensteadt (1975)).

For $\lambda \in \Lambda \setminus \Sigma$ we have

$$\hat{B}(\lambda) = (I - \hat{K}(\lambda))^{-1}\hat{\Phi}(\lambda). \tag{4.4}$$

In section 8 we shall prove that the element λ_d of Σ with largest real part determines the large time behaviour of the solution $B(t)$. Often λ_d turns out to be real, and the corresponding eigenvector of $\hat{K}(\lambda_d)$ to be positive. The theory of positive operators is an important instrument to prove existence of λ_d, and has been succesfully exploited in a number of problems from population dynamics (Diekmann et al. (1984), Heijmans (to appear), Heijmans (1984), Metz & Diekmann (in prep.)). As an intermezzo we shall now present some results from positive operator theory with the emphasis on the existence and uniqueness of positive eigenvectors and eigenfunctionals.

5. Positive Operators

For the basic theory of order structures in a Banach space and positive operators, we refer to Schaefer (1974).

In the sequel E is some Banach space and E^* is it's dual, i.e. the space of all linear functionals (or linear forms) on E. We denote the duality pairing of $\psi \in E$, $F \in E^*$ with $<F,\psi>$. A subset $E_+ \subseteq E$ is called a cone if the following conditions are satisfied

(i) E_+ is closed,

(ii) $\alpha\phi + \beta\psi \in E_+$ if $\phi,\psi \in E_+$ and $\alpha,\beta \geqslant 0$

(iii) $\psi \in E_+$ and $-\psi \in E_+$ implies that $\psi = 0$.

The reader can easily verify that by virtue of "$\phi \leqslant \psi$ iff $\psi - \phi \in E_+$" each cone $E_+ \subseteq E$ defines an order relation on E by which E becomes an ordered Banach space. We say that $\phi < \psi$ if $\phi \leqslant \psi$ and $\phi \neq \psi$. The cone E_+ is called total if the set $\{\psi - \phi | \psi, \phi \in E_+\}$ is dense in E. The dual set E_+^* is by definition the subset of E^* consisting of all positive functionals on E, i.e. $F \in E_+^*$ if and only if $F \in E^*$ and $<F,\psi> \geqslant 0$ for all $\psi \in E_+$. If E_+ is total then E_+^* is a cone as well. A positive functional F is said to be strictly positive if $<F,\psi> > 0$ for all $\psi \in E_+$, $\psi \neq 0$. A bounded linear operator $T: E \to E$ is called positive (with respect to the cone E_+) if $T\psi \in E_+$ for all $\psi \in E_+$. Notation $T \geqslant 0$. We denote the spectral radius of T by $r(T)$.

The first authors who systematically studied positive operators and their spectral properties were Krein and Rutman (1948). In that paper they generalized the Frobenius theorem (which states that the spectral radius of a non-negative matrix is an eigenvalue of that matrix). They proved, among others, the following result.

Theorem 5.1 (Krein & Rutman (1948)). *Let $T: E \to E$ be compact and positive with respect to the total cone $E_+ \subseteq E$, and let $r = r(T) > 0$. Then there exists a $\psi \in E_+$, $\psi \neq 0$ such that $T\psi = r\psi$.*

They also introduced the notion of strong positivity. A positive operator $T: E \to E$ is called strongly positive if for all $\psi \in E_+$, $\psi \neq 0$ there is a natural number p such that $T^p\psi \in \mathring{E}_+$, where $\mathring{E}_+$ denotes the interior of the cone E_+ (assuming that E_+ has interior points). They proved that, if the assumptions of theorem 5.1 are fulfilled and, moreover, T is strongly positive, then

(a) T has (except for a constant) one and only one eigenvector $\psi \in E_+$. Moreover $\psi \in \mathring{E}_+$ and $T\psi = r\psi$.

(b) T^* has one and only one eigenvector $F \in E_+^*$, F is strictly positive and $T^*F = rF$.

(c) All other eigenvalues λ of T satisfy $|\lambda| < r(T)$.

Many years later their study was continued by a great number of authors, extending the ideas of Krein and Rutman in several directions. Among others they weakend the condition that T has to be compact. (In many cases it is sufficient that $\lambda = r(T)$ is a pole of the resolvent $R(\lambda,T) = (\lambda I - T)^{-1}$.) Furthermore several different concepts generalizing the concept of strong positivity have been introduced. We mention three of these generalizations. Schaefer (1974) introduced in the early sixties the concept of irreducible positive operators. Krasnoselskii (1964) studied u_0-positive operators, and finally Sawashima (1964) developed the theory of non-supporting operators. (Sawashima uses the terminology "non-support".) All three concepts have the advantage that the interior of the cone E_+ may be empty. It seems to us that Sawashima's definition is the most natural for our purposes. If E is a Banach lattice then there is a close relation between the concepts of Sawashima and Schaefer.

Definition (Sawashima (1964)). A bounded, positive operator $T: E \to E$ is called non-supporting with respect to E_+ if for all $\psi \in E_+$, $\psi \neq 0$, and $F \in F_+^*$, $F \neq 0$, there exists an integer p such that for all $n \geqslant p$ we have $<F,T^n\psi> > 0$.

The following result, which was proved by Sawashima (1964) is needed in the next section. The result can also be found in paper by Marek (1970) which provides a comprehensive overview of some of the developments in positive operator theory between 1950 and 1970.

Theorem 5.2. *Let the cone E_+ be total, let $T: E \to E$ be non-supporting with respect to E_+, and suppose that $r = r(T)$ is a pole of the resolvent, then*

(a) *$r > 0$ and r is an algebraïcally simple eigenvalue of T.*

(b) *The corresponding eigenvector ψ satisfies: $\psi \in E_+$ and $<H,\psi> > 0$ for all $H \in E_+^*$, $H \neq 0$.*

(c) *The corresponding dual eigenvector is strictly positive.*

(d) *If X is a Banach lattice then all remaining elements $\lambda \in \sigma(T)$ satisfy $|\lambda| < r$.*

6. Location of the singular points

From now on we let $X = L_1[0,\infty)$. In section 4 we defined the analytic operator family $\hat{K}(\lambda)$, $\lambda \in \Lambda$, being the Laplace transform of $K(t)$. Evidently $\hat{K}(\lambda)$ defines a bounded operator on X for all $\lambda \in \Lambda$.

$$(\hat{K}(\lambda)\psi)(x) = \int_{a_0}^{G(2x)} e^{-\lambda a} k(a,2x)\psi(X(-a,2x))da\,, \quad \psi \in X. \tag{6.1}$$

In the Appendix we shall prove the following result.

Lemma 6.1. *For all $\lambda \in \Lambda$ the operator $\hat{K}(\lambda)$ is compact.*

We can now apply the following result, proved by Steinberg (1968).

Lemma 6.2. *Let E be a Banach space and Δ a subset of the complex plane which is open and connected. If $T(\lambda)$ is an analytic family of compact operators on E for $\lambda \in \Delta$, then either $(I-T(\lambda))$ is nowhere invertible in Δ or $(I-T(\lambda))^{-1}$ is meromorphic in Δ.*

(A function $\phi(\lambda)$ defined on a set $V \subseteq \mathbf{C}$ is called meromorphic if it is analytic on V except for an at most countable set of elements of V which are poles of finite order of ϕ.) It is clear that $\|\hat{K}(\lambda)\| \to 0$ if $\mathrm{Re}\,\lambda \to \infty$, implying that $I-\hat{K}(\lambda)$ is invertible if $\mathrm{Re}\,\lambda$ is large enough. Thus lemma 6.1 and lemma 6.2 yield:

Theorem 6.3. *The function $\lambda \to (I-\hat{K}(\lambda))^{-1}$ is meromorphic in Λ.*

Therefore the set Σ defined by (4.3) is a discrete set whose elements are poles of $(I-\hat{K}(\lambda))^{-1}$ of finite order.

Now we shall employ positivity arguments to determine the so-called dominant singular point, i.e. the element of Σ with the largest real part. Before doing so we make an additional assumption on the growthrate g.

Assumption 6.4. *There exists a $\delta > 0$ such that $2g(x)-g(2x) \geq \delta$, all $x \in [0,\infty)$.*

In Diekmann et al. (1984) (see also chapter two of the forthcoming book Metz & Diekmann (in prep.)) a similar assumption has been made to establish compactness of the semigroup. In section 9 we shall explain why assumption 6.4 is imposed. A consequence of this assumption is that a baby cell can not attain arbitrarily small sizes. We shall make this more explicit. If a cell is born with size x, than it can divide not earlier than a_0 time units later, and its daughers can not be smaller than

$$\gamma(x) \stackrel{def}{=} \tfrac{1}{2}X(a_0,x) = \tfrac{1}{2}G^{-1}(a_0+G(x)). \tag{6.2}$$

A straightforward calculation shows that γ has precisely one fixed point x_0 if assumption 6.1 is satisfied. The following result shows that x_0 is a globally stable fixed point of the mapping γ.

Lemma 6.5. *Let for arbitrary $x_1 \geqslant 0$ the sequence $\{x_n\}$ be defined recursively as $x_{n+1} = \gamma(x_n)$, $n \geqslant 1$ then: $x_1 < x_0$ implies $x_0 < x_n$, $n \geqslant 1$, and $x_1 > x_0$ implies $x_n > x_0$, $n \geqslant 1$. Moreover $\lim_{n\to\infty} x_n = x_0$.*

Proof. Since $\gamma(0) > 0$, γ is continuous and x_0 is the unique solution of $\gamma(x) > x$ if $0 \leqslant x < x_0$. From assumption 6.4 we conclude that $\gamma'(x_0) = \dfrac{g(2x_0)}{2g(x_0)} < 1$, and this yields that $\gamma(x) < x$ if $x > x_0$. Since γ is increasing we have $x_n < x_0$ if $x_1 < x_0$ and $x_n > x_0$ if $x_1 > x_0$. Moreover $\lim_{n\to\infty} x_n$ exists and is a fixed point of γ. This yields the result. □

From this lemma and the observation that a baby cell attains the minimum birth size if all its ancestors have divided at age a_0, it follows that this minimum birth size is x_0 (which is positive if a_0 is positive), provided that there are infinitely many ancestors who all lived under the same growth regime.

Remark 6.6. The state space Ω_s indicated in section 1 is given by $\Omega_s = \{(a,x) \in \mathbf{R}^+ \times \mathbf{R}^+ | x \geqslant X(a,x_0)\}$.

However, we do not want to restrict ourselves à priori to initial data defined on Ω_s only, but admit that $n_0(a,x)$ defined in (1.6) is positive on $\Omega \setminus \Omega_s$. We can prove the following result.

Lemma 6.7. *If ψ is an eigenvector of $\hat{K}(\lambda)$, then $\psi(x) = 0$, $x < x_0$.*

Proof. Let $\psi \in X$. It follows from (6.1) that $(\hat{K}(\lambda)^n\psi)(x) = 0$ if $x \leqslant x_n$, where $x_1 = \gamma(0)$ and $x_{n+1} = \gamma(x_n)$, $n \geqslant 1$. If ψ is an eigenvector of $\hat{K}(\lambda)$ then ψ is an eigenvector of $\hat{K}(\lambda)^n$ for every positive integer n. As a consequence $\psi(x) = 0$ if $x \leqslant x_n$, and now the result follows from lemma 6.5. □

We denote with Y the subspace of X containing all $\psi \in L_1[0,\infty)$ which are identically zero on $[0,x_0)$. Obviously $\hat{K}(\lambda)Y \subseteq Y$. We let $\hat{K}_0(\lambda)$ be the restriction of $\hat{K}(\lambda)$ to Y. It is clear immediately that lemma 6.1 and theorem 6.3 remain valid if $\hat{K}(\lambda)$ is replaced by $\hat{K}_0(\lambda)$. Moreover (4.3) can be replaced by $\Sigma = \{\lambda \in \Lambda | 1 \in \sigma(\hat{K}_0(\lambda))\}$. Let Y_+ be the subset of Y containing all elements which are non-negative a.e. (almost everywhere). The following result is straightforward.

Theorem 6.8. *Y_+ defines a cone in Y which is total. Moreover $\hat{K}_0(\lambda)$ is positive with respect to Y_+ for all $\lambda \in \Lambda \cap \mathbf{R}$.*

We let Y_+^* be the dual of Y_+ and this defines a cone in Y^* because Y_+ is total. Clearly Y_+^* can be identified with $L_\infty^+[x_0,\infty)$, i.e. all measurable function on $[x_0,\infty)$ which are non-negative and essentially bounded.

The following lemma provides a useful characterization of the non-zero elements of Y_+^*.

Lemma 6.9. *If $F \in Y_+^*$, $F \neq 0$, then there exists an $\epsilon > 0$ such that for all $f \in Y_+$ satisfying $f(x) > 0$ for almost every $x \in [x_0+\epsilon,\infty)$ the relation $\langle F,f \rangle > 0$ holds.*

Proof. $F \in Y_+^*$, $F \neq 0$ implies that there exists a measurable set $V \subset [x_0,\infty)$ with measure $\mu > 0$ such that $F(x) > 0$, $x \in V$. If we choose $\epsilon < \mu$, then the intersection $V \cap [x_0+\epsilon,\infty)$ has a measure which is greater than $\mu-\epsilon > 0$, and this yields the result. □

Now we can prove the following strong positivity result with respect to $\hat{K}_0(\lambda)$.

Theorem 6.10. *For all $\lambda \in \Lambda \cap \mathbf{R}$ the operator $\hat{K}_0(\lambda)$ is non-supporting with respect to Y_+.*

Proof. Let $\psi \in Y_+, \psi \neq 0$ and $\lambda \in \Lambda \cap \mathbf{R}$. If we substitute $z = X(-a,2x)$ in (6.1) we obtain

$$(\hat{K}_0(\lambda)\psi)(x) = \int_{x_0}^{X(-a_0,2x)} e^{-\lambda(G(2x)-G(z))} \cdot k(G(2x)-G(z),2x) \frac{\psi(z)}{g(z)}\, dz.$$

Let $F \in Y_+^*$, $F \neq 0$ and let $\epsilon > 0$ be given by lemma 6.9. There exists a $x_1 > x_0$ such that $\int_{x_0}^{X(-a_0,2x_1)} \psi(z)dz > 0$. This yields that $(\hat{K}_0(\lambda)\psi)(x) > 0$ if $x \geq x_1$. Let $x_2 = \gamma(x_1)$, where γ is defined by (6.2). Then $(\hat{K}_0(\lambda)^2\psi(x) > 0$, $x \geq x_2$. Recursively we find $(\hat{K}_0(\lambda)^n\psi)(x) > 0$, $x \geq x_n$, where $x_n = \gamma(x_{n-1})$, $n \geq 2$. We conclude from lemma 6.5 that there exists a $p \in \mathbf{N}$ such that $x_n < x_0 + \epsilon$ if $n \geq p$. Now we can apply lemma 6.9 which says that $<F,\hat{K}_0(\lambda)^n\psi > 0$ if $n \geq p$, and this proves the result. □

We can draw the following conclusions from theorem 5.2.

Let $r_\lambda = r(\hat{K}_0(\lambda))$, $\lambda \in \Lambda$. If $\lambda \in \Lambda \cap \mathbf{R}$, then

(a) r_λ is an algebraïcally simple eigenvalue of $\hat{K}_0(\lambda)$.

(b) The corresponding eigenvector $\psi_\lambda \in Y_+$ satisfies $\psi_\lambda(x) > 0$, $x \in [x_0,\infty)$ a.e. (We fix ψ_λ by the normalization $\|\psi_\lambda\| = 1$.)

(c) The corresponding eigenfunctional $F_\lambda \in Y_+^*$ satisfies $F_\lambda(x) > 0$, $x \in [x_0,\infty)$ a.e. (i.e. F_λ is strictly positive).

Hence, if $\lambda \in \Lambda$ is real and $r_\lambda = 1$, then $\lambda \in \Sigma$.

Lemma 6.11. *There exists a unique $\lambda \in \Lambda \cap \mathbf{R}$ such that $r(\hat{K}_0(\lambda)) = 1$.*

Proof. Let $\lambda,\mu \in \Lambda \cap \mathbf{R}$, $\lambda > \mu$ and $\psi \in Y_+$.

$$(\hat{K}_0(\mu)\psi)(x) = \int_{a_0}^{G(2x)} e^{-\mu a} k(a,2x)\psi(X(-a,2x))da$$

$$\geq e^{(\lambda-\mu)a_0} \int_{a_0}^{G(2x)} e^{-\lambda a} k(a,2x)\psi(X(-a,2x))da = e^{(\lambda-\mu)a_0}(\hat{K}_0(\lambda)\psi)(x).$$

If we substitute $\psi = \psi_\lambda$, then we obtain $\hat{K}_0(\mu)\psi_\lambda \geq e^{(\lambda-\mu)a_0} r_\lambda \psi_\lambda$. Taking duality pairings with F_μ on both sides yields

$$r_\mu \geq e^{(\lambda-\mu)a_0} \cdot r_\lambda \tag{6.3}$$

where we have used that $<F_\mu,\psi_\lambda>>0$. Thus $\lambda \to r(\hat{K}_0(\lambda))$ is strictly decreasing in $\Lambda \cap \mathbf{R}$. Moreover this function is continuous. It follows easily that $\lim_{\lambda\to\infty} r(\hat{K}_0(\lambda)) = 0$. If we can prove that $\lim_{\lambda\downarrow -d_\infty} r(\hat{K}_0(\lambda)) = \infty$ then the conclusion of the lemma follows. We have to distinguish between two cases.

(a) $d_\infty = \infty$. Then (6.3) implies that $\lim_{\lambda\to-\infty} r(\hat{K}_0(\lambda)) = \infty$.

(b) $d_\infty < \infty$. Since $\|\psi_\lambda\| = 1$,

$$r(\hat{K}_0(\lambda)) = \|\hat{K}_0(\lambda)\psi_\lambda\| = \int_{x_0}^{\infty} \{\int_0^{\infty} e^{-\lambda t}(K(t)\psi_\lambda)(x)dt\}dx = \int_0^{\infty} e^{-\lambda t}\{\int_{x_0}^{\infty} (K(t)\psi_\lambda)(x)dx\}dt$$

$$= \int_0^\infty e^{-\lambda t}\|K(t)\psi_\lambda\|dt \geqslant \int_{T_0}^\infty e^{-\lambda t}\|K(t)\psi_\lambda\|dt \geqslant \int_{T_0}^\infty m_K e^{-d_\infty t} e^{-\lambda t}\, dt = \frac{m_K}{\lambda+d_\infty} e^{-(\lambda+d_\infty)T_0},$$

where we have used lemma 3.1. The change of order of integration was permitted because of Fubini's theorem (Dunford & Schwartz (1958)). It follows that $\lim_{\lambda \downarrow -d_\infty} r(\hat{K}_0(\lambda)) = \infty$. □

We denote the unique solution of $r(\hat{K}_0(\lambda)) = 1$ by λ_d, and we shall write ψ_d and F_d in stead of ψ_{λ_d} and F_{λ_d} respectively. We assume that ψ_d and F_d are normalized by

$$\|\psi_d\| = 1, \ <F_d,\psi_d> = 1. \tag{6.4}$$

In order to prove that indeed λ_d is indeed the element of Σ with the largest real part, we need the following lemma.

Lemma 6.12. *Let $f \in L_1[0,\infty)$ be a complex-valued function. Then $|\int_0^\infty f(x)dx| = \int_0^\infty |f(x)|dx$ if and only if there exists a constant $\alpha \in \mathbb{C}$, $|\alpha| = 1$ such that $|f(x)| = \alpha f(x)$ a.e. on $[0,\infty)$.*

This result has been proved in Heijmans (to appear).

Theorem 6.13. *If $\lambda \in \Sigma$, $\lambda \neq \lambda_d$, then* $\mathrm{Re}\,\lambda < \lambda_d$.

Proof. Suppose $\lambda \in \Sigma$ and $\hat{K}_0(\lambda)\psi = \psi$. Hence $|\hat{K}_0(\lambda)\psi| = |\psi|$, where $|\psi|(x) \overset{def}{=} |\psi(x)|$. This yields $\hat{K}_0(\lambda_R)|\psi| \geqslant |\psi|$, where $\lambda_R = \mathrm{Re}\,\lambda$. Taking duality pairings with F_{λ_R} on both sides yields $r_{\lambda_R} <F_{\lambda_R},|\psi|> \geqslant <F_{\lambda_R},|\psi|>$, from which we conclude that $r_{\lambda_R} \geqslant 1$. In the proof of lemma 6.11 we have shown that $\lambda \to r_\lambda$ is decreasing in $\lambda \in \Lambda \cap \mathbf{R}$, and this implies that $\lambda_R = \mathrm{Re}\,\lambda_d$. Now suppose that $\mathrm{Re}\,\lambda = \lambda_d$ and $\mathrm{Im}\,\lambda = \eta$. Thus $\hat{K}_0(\lambda_d)|\psi| \geqslant |\psi|$. Suppose that $\hat{K}_0(\lambda_d)|\psi| > |\psi|$. Taking duality pairings with F_d on both sides yields $<F_d,|\psi|> \; > \; <F_d,|\psi|>$ which is a contradiction. As a consequence $\hat{K}_0(\lambda_d)|\psi| = |\psi|$, from which we deduce that $|\psi| = c \cdot \psi_d$ for some constant c which we may assume to be one. Therefore $\psi(x) = \psi_d(x)e^{i\alpha(x)}$ for some real-valued function α. If we substitute this in $\hat{K}_0(\lambda_d)\psi_d = |\hat{K}_0(\lambda)\psi|$ we obtain

$$\int_{a_0}^\infty e^{-\lambda_d a} k(a,2x)\psi_d(X(-a,2x))da = \left|\int_{a_0}^\infty e^{-\lambda_d a - i\eta a} k(a,2x)\psi_d(X(-a,2x))e^{i\alpha(X(-a,2x))}da\right|.$$

From lemma 6.12 we conclude that $\alpha(X(-a,2x)) - \eta a = \beta$, for some constant β. If we substitute this in $\hat{K}_0(\lambda)\psi = \psi$ we obtain $e^{i\beta}\int_0^\infty e^{-\lambda_d a} k(a,2x))da = \psi_d(x)e^{i\alpha(x)}$, thus $\alpha(x) = \beta$ from which we conclude that $\eta = \mathrm{Im}\,\lambda = 0$. □

This result, combined with the Riemann-Lebesgue lemma (lemma 4.3) and theorem 6.3, implies among others that there exists a positive horizontal distance between λ_d and the other points in Σ.

Corollary 6.14. *There exists an $\epsilon > 0$ such that $\lambda_d - \epsilon > -d_\infty$ and $\mathrm{Re}\,\lambda \leqslant \lambda_d - \epsilon$ if $\lambda \in \Sigma$, $\lambda \neq \lambda_d$.*

Clearly $\hat{K}_0(\lambda)$ and $\hat{K}(\lambda)$ have the same eigenvectors (lemma 6.7). However $\hat{K}_0(\lambda)^*$ and $\hat{K}(\lambda)^*$ do not have the same eigenvectors. Let F_d' be the eigenvector of $\hat{K}(\lambda_d)^*$ corresponding to the eigenvalue one. Obviously, F_d' defines a positive functional on X. We can prove the following relation between F_d and F_d'. Let $<F_d',\psi_d> = 1$.

Theorem 6.15. *For all $\psi \in Y$, the equality $<F_d,\psi> = <F_d',\psi>$ holds.*

Proof. Let $\psi \in Y$, then $\psi = <F_d,\psi> \cdot \psi_d + \rho$, where $\rho \in \Re(\hat{K}_0(\lambda_d)-I) \overset{def}{=} Z$, i.e. the range of $\hat{K}_0(\lambda_d)-I$. Since the spectral radius of the restriction of $\hat{K}_0(\lambda_d)$ to the subspace Z is strictly less than one (theorem 5.2d) it follows that $\|\hat{K}_0(\lambda_d)^n \rho\| < \theta^n \|\rho\|$ for all $\rho \in Z$, where θ is some constant strictly less than one. Since $\hat{K}(\lambda_d)\psi = \hat{K}_0(\lambda_d)\psi$ we have $<F_d',\psi> = <\hat{K}(\lambda_d)^{*n} F_d',\psi> = <F_d',\hat{K}_0(\lambda_d)^n(<F_d,\psi>\psi_d + \rho)> = <F_d,\psi> + <F_d',\hat{K}_0(\lambda_d)^n \rho>$. If we let $n \to \infty$ then the second term at the right-hand-side tends to zero yielding that $<F_d',\psi> = <F_d,\psi>$. □

7. Computation of the residue in λ_d.

Here we shall concentrate on the behaviour of $(I-\hat{K}(\lambda))^{-1}$ in a neighbourhood of $\lambda = \lambda_d$, which is a pole of finite order (cf. theorem 6.3). The techniques exploited in this section are very similar to those in a paper by Schumitzky & Wenska (1975). We define

$$R(\lambda) = (I-\hat{K}(\lambda))^{-1}, \ \lambda \in \Lambda \setminus \Sigma. \tag{7.1}$$

Since $\hat{K}(\lambda)$ is analytic in a neighbourhood of λ_d we can write down its Taylor expansion.

$$\hat{K}(\lambda) = \sum_{n=0}^{\infty} (\lambda-\lambda_d)^n K_n, \tag{7.2}$$

where the series converges in the norm topology. Let $p \geqslant 1$ be the order of the pole of $R(\lambda)$ in $\lambda = \lambda_d$. In a neighbourhood of λ_d, $R(\lambda)$ can be represented by a Laurent series:

$$R(\lambda) = \sum_{n=-p}^{\infty} (\lambda-\lambda_d)^n R_n, \tag{7.3}$$

where by definition $R_{-p} \neq 0$. From

$$R(\lambda)(I-\hat{K}(\lambda)) = (I-\hat{K}(\lambda))R(\lambda) = I \tag{7.4}$$

if follows immediately that

$$R_{-p}(I-K_0) = (I-K_0)R_{-p} = 0. \tag{7.5}$$

From this relation and $K_0 = \hat{K}(\lambda_d)$ we obtain

$$\Re(R_{-p}) = \{\psi_d\}, \tag{7.6}$$

where $\Re(R_{-p})$ denotes the range of the operator R_{-p}, and $\{\psi_d\}$ stands for the span of the positive eigenvector ψ_d, i.e. $\{\psi_d\} = \{\gamma \cdot \psi_d | \gamma \in \mathbf{C}\}$. A relation similar to (7.4) is valid for the dual operators $K_0^* = \hat{K}(\lambda_d)^*$ and R_{-p}^*. Therefore

$$\Re(R_{-p}^*) = \{F_d\}. \tag{7.7}$$

From (7.4) we also deduce that

$$-R_{-p}K_1 + R_{-p+1}(I-K_0) = 0, \ \text{if } p > 1, \tag{7.8a}$$

$$-R_{-1}K_1 + R_0(I-K_0) = I, \ \text{if } p = 1. \tag{7.8b}$$

Together with (7.5) this implies

$$R_{-p}K_1R_{-p} = 0, \ \text{if } p > 1, \tag{7.9a}$$

$$R_{-1}K_1R_{-1} = -R_{-1}, \text{ if } p = 1. \tag{7.9b}$$

We can state our main result now.

Theorem 7.1. *$R(\lambda)$ has a pole of order one in $\lambda = \lambda_d$ and the residue R_{-1} is given by*

$$R_{-1}\psi = \frac{<F_d',\psi>}{<F_d',-K_1\psi_d>} \cdot \psi_d, \ \psi \in X. \tag{7.10}$$

Observe that $-K_1 = [-\frac{d}{d\lambda}\hat{K}(\lambda)]_{\lambda=\lambda_d}$ defines a positive non-supporting operator on Y and thus it follows from theorem 6.15 that $<F_d',-K_1\psi_d> = <F_d,-K_1\psi_d> > 0$.

Proof of theorem 7.1. Let ϕ_d and H_d be solutions of $R_{-p}\phi = \psi_d$ and $R_{-p}^*H = F_d$ respectively. On account of (7.6) and (7.7) such solutions indeed exist. If $p > 1$ then (7.9a) yields $0 = <H_d, R_{-p}K_1R_{-p}\phi_d> = <F_d,K_1\psi_d>$ which is a contradiction since F_d is strictly positive and $-K_1\psi_d$ is positive and nonzero. Therefore $p = 1$, and $\mathcal{R}(R_{-1}) = \{\psi_d\}$. Now let $R_{-1}\psi = f(\psi)\cdot\psi_d$ for some linear functional f. Then $<H_d,R_{-1}\psi> = <R_{-1}^*H_d,\psi> = <F_d,\psi> = <H_d,-R_{-1}KR_{-1}\psi> = <R_{-1}^*H_d, -K_1(f(\psi)\cdot\psi_d)> = f(\psi)\cdot<F_d,-K_1\psi_d>$, thus $f(\psi) = <F_d,\psi> / <F_d,-K_1\psi_d>$ which proves the result. □

It is not à priori clear whether or not $<F_d',\psi> > 0$ if $\psi \in X_+, \psi \neq 0$. This, however, is proved in the following lemma.

Lemma 7.2. *If $\psi \in X_+, \psi \neq 0$ then $<F_d',\psi > 0$.*

Proof. If the restriction of ψ to $[x_0,\infty)$ is not identically zero, then the result follows from theorem 6.15. Now suppose that ψ is positive on a subset of $[0,x_0]$ with positive measure. Thus

$$(\hat{K}(\lambda_d)\psi)(x) \geq \int_{G(2x)-G(x_0)}^{G(2x)} e^{-\lambda_d a}k(a,2x)\psi(X(-a,2x))da$$

$$= \int_0^{x_0} e^{-\lambda_d(G(2x)-G(z))}\cdot k(G(2x)-G(z),2x)\,\frac{\psi(z)}{g(z)}\,dz > 0$$

for all $x \geq x_0$. Therefore $<F_d',\psi> = <\hat{K}(\lambda_d)^*F_d',\psi> = <F_d',\hat{K}(\lambda_d)\psi> > 0$. □

8. The inverse Laplace transform

Let E be a Banach space. The Hardy-Lebesgue class $H_p(\alpha;E)$ is the class of functions $g(\lambda)$ with values in E, which are analytic in $\mathrm{Re}\,\lambda > \alpha$ and satisfy the following conditions (cf. Friedman & Shinbrot (1967), Hille & Phillips (1957)).

$$\sup_{\zeta>\alpha}\left\{\int_{-\infty}^{\infty}\|g(\zeta+i\eta)\|^p\,d\eta\right\}^{\frac{1}{p}} < \infty, \tag{8.1a}$$

$$g(\alpha+i\eta) = \lim_{\zeta\downarrow\alpha} g(\zeta+i\eta) \textit{ exists a.e. and is an element of } L_p(-\infty,\infty;E). \tag{8.1b}$$

The following inverse Laplace transform formula can be found in Friedman & Shinbrot (1967).

Lemma 8.1. *Let* $g(\lambda) \in H_1(\alpha;E)$, *then the function*

$$f(t) = \frac{1}{2\pi i}\int_{\gamma-i\infty}^{\gamma+i\infty} e^{\lambda t} g(\lambda) d\lambda, \quad (\gamma \geq \alpha) \tag{8.2}$$

is defined and independent of γ, *for all* $t \in (-\infty,\infty) \cdot f(t) = 0$, $t < 0$, $f(t)$ *is continuous and* $\hat{f}(\lambda) = g(\lambda)$.

We rewrite the abstract renewal equation (2.17) as

$$B = \Phi + K * B, \tag{8.3}$$

where $K*B$ denotes the convolution product, i.e. $(K*B)(t) = \int_0^t K(a)B(t-a)da$. If we substitute

$$B = \Phi + v, \tag{8.4}$$

we obtain

$$v = \Psi + K*v, \tag{8.5}$$

where

$$\Psi = K*\Phi. \tag{8.6}$$

Taking Laplace transforms on both sides of (8.5) gives us

$$\hat{v}(\lambda) = (I - \hat{K}(\lambda))^{-1}\hat{\Psi}(\lambda). \tag{8.7}$$

We can prove the following result.

Lemma 8.2. $\hat{v}(\lambda) \in H_1(\alpha;X)$, *if* $\alpha > \lambda_d$.

Proof. Let $\lambda \in \mathbf{C}$ be such that $\text{Re}\,\lambda \geq \alpha$. It follows from lemma 3.1 and lemma 4.4 that the functions $\eta \to \hat{\Phi}(\zeta+i\eta)$ and $\eta \to \hat{K}(\zeta+i\eta)$ are element of $L_2(-\infty,\infty;X)$ and $L_2(-\infty,\infty;\mathcal{B}(X))$ respectively, if $\zeta > -d_\infty$, where $\mathcal{B}(X)$ is the space of bounded linear operators on X. Therefore the function $\eta \to \hat{\Psi}(\zeta+i\eta)$ is an element of $L_1(-\infty,\infty;X)$ if $\zeta > -d_\infty$. Moreover we know from the Riemann-Lebesgue lemma (lemma 4.3) that $\|(I-\hat{K}(\zeta+i\eta))^{-1}\| \leq 2$ if $|\eta|$ is large enough, say $|\eta| \geq \eta_0$. From the continuity of the function $\eta \to (I-\hat{K}(\zeta+i\eta))^{-1}$ on $[-\eta_0,\eta_0]$ (if $\zeta \geq \alpha$) we conclude that there exists a constant $C > 0$ such that $\|(I-\hat{K}(\zeta+i\eta))^{-1}\| < C$ for all $\eta \in (-\infty,\infty)$. Thus $\|\hat{v}(\zeta+i\eta)\| \leq C\|\hat{\Psi}(\zeta+i\eta)\|$ where we have used (8.7). The positivity of $K(t)$ and $\Psi(t)$ yields that

$$\|\hat{\Psi}(\zeta+i\eta)\| \leq \|\hat{\Psi}(\alpha+i\eta)\|, \; \zeta \geq \alpha,$$

and we conclude that condition (8.1a) is satisfied. The validity of condition (8.1b) follows from the analyticity of $(I-\hat{K}(\lambda))^{-1}$, $\hat{\Phi}(\lambda)$ and $\hat{K}(\lambda)$ on the region $\text{Re}\,\lambda > \lambda_d$ and the fact that $\alpha > \lambda_d$. □

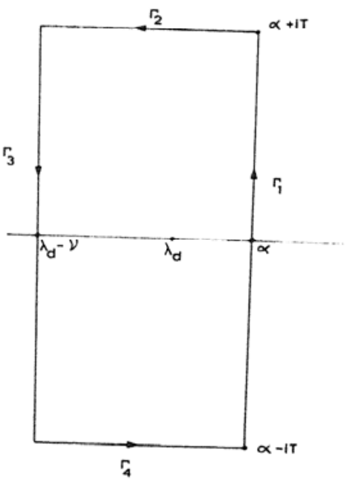

Figure 2. $\Gamma = \bigcup_{i=1}^{4} \Gamma_i$

Now let $\alpha > \lambda_d$, then lemma 8.1 yields that

$$v(t) = \frac{1}{2\pi i} \int_{\alpha - i\infty}^{\alpha + i\infty} e^{\lambda t} \hat{v}(\lambda) d\lambda \tag{8.8}$$

is well-defined. Some contributions to this integral can be evaluated by the method of residues. Therefore we shift the vertical integration curve Re $\lambda = \alpha$ to the left across the singularity $\lambda = \lambda_d$, such that it crosses no other elements of Σ (see fig. 2). Let $\epsilon > 0$ be given by corollary 6.14, and let $0 < \nu < \epsilon$. Let Γ be the rectangular contour in fig. 2. It follows immediately from the Riemann-Lebesgue lemma (lemma 4.3) that

$$\lim_{T \to \infty} \int_{\Gamma_i} e^{\lambda t} \hat{v}(\lambda) d\lambda = 0, \; i = 2,4.$$

Now it follows from Cauchy's theorem (which is also valid for vector-valued functions: see Hille & Phillips (1957)) that

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

where we have used that the first integral does not depend on T. The residue theorem gives:

$$\frac{1}{2\pi i}\oint_{\Gamma} e^{\lambda t}\hat{\nu}(\lambda)d\lambda = \underset{\lambda=\lambda_d}{Res}\{e^{\lambda t}\hat{\nu}(\lambda)\} = e^{\lambda_d t}R_{-1}\hat{\Psi}(\lambda_d)$$

$$= e^{\lambda_d t}R_{-1}\hat{K}(\lambda_d)\hat{\Phi}(\lambda_d) = e^{\lambda_d t}\cdot\frac{<F_d',\hat{K}(\lambda_d)\hat{\Phi}(\lambda_d)>}{<F_d',-K_1\psi_d>}\cdot\psi_d$$

$$= e^{\lambda_d t}\frac{<F_d',-K_1\hat{\Phi}(\lambda_d)>}{<F_d',-K_1\psi_d>}\cdot\psi_d,$$

where we have used theorem 7.1, (8.6) and (8.7). As in the proof of lemma 8.2 we have that the function $\eta \to \hat{\nu}(\lambda_d-\nu+i\eta)$ is an element of $L_1(-\infty,\infty;X)$. Now

$$\|\frac{1}{2\pi i}\int_{\lambda_d-\nu-i\infty}^{\lambda_d-\nu+i\infty} e^{\lambda t}\hat{\nu}(\lambda)d\lambda\| \leqslant M\cdot e^{(\lambda_d-\nu)t},$$

where

$$M \overset{def}{=} \frac{1}{2\pi}\int_{-\infty}^{\infty}\|\hat{\nu}(\lambda_d-\nu+i\eta)\|d\eta \text{ depends on } \nu \text{ and } \Phi.$$

Remark 8.3. It follows from the boundedness of $(I-\hat{K}(\lambda))^{-1}$ on the vertical line $\mathrm{Re}\,\lambda = \lambda_d-\nu$, the Schwarz inequality and Parseval's relation (section 3) that

$$M \leqslant M_1\cdot\{\int_0^{\infty} e^{-2(\lambda_d-\nu)t}\|K(t)\|^2dt\}^{\frac{1}{2}}\cdot\{\int_0^{\infty} e^{-2(\lambda_d-\nu)t}\|\Phi(t)\|^2dt\}^{\frac{1}{2}},$$

where M_1 only depends on ν.

We can state our main result now.

Corollary 8.4. *Let $\epsilon > 0$ be given by corollary 6.12, and let $0 < \nu < \epsilon$, then $\|e^{-\lambda_d t}B(t)-c\cdot\psi_d\| \leqslant Le^{-\nu t}$, $t \geqslant 0$, for some constant L, where $c = \dfrac{<F_d',\hat{\Phi}(\lambda_d)>}{<F_d',-K_1\psi_d>}$ is a constant depending linearly on Φ.*

Proof. We have $B(t) = \Phi(t) + \nu(t)$, and $\nu(t) = e^{\lambda_d t}(c\cdot\psi_d+O(e^{-\nu t}))$. Now the result follows from lemma 3.1. □

Remark 8.5. Observe from corollary 8.4 that if t has become infinite, no cells with size less than x_0 are born, although such cells may be present at time zero.

9. Interpretation, conclusions and final remarks

For the sake of converience we repeat (2.11) and (2.12)

$$n(t,a,x) = \frac{g(X(-t,x))}{g(x)}\,Q(t,a-t,X(-t,x))n_0(a-t,X(-t,x)),\ t \leqslant a,$$

$$n(t,a,x) = \frac{g(X(-a,x))}{g(x)}\,E(a,X(-a,x))B(t-a,X(-a,x)),\ t > a.$$

This does not define a classical solution of (1.4)-(1.6). However it can be proved that n is differentiable along the characteristics of the partial differential operator $D = \frac{\partial}{\partial t} + \frac{\partial}{\partial a} + g(x)\frac{\partial}{\partial x}$, and in this sense indeed is a solution of (1.4)-(1.6).

Let

$$n_d(a,x) = e^{-\lambda_d a} \cdot \frac{g(X(-a,x))}{g(x)} E(a,X(-a,x))\psi_d(X(-a,x)). \tag{9.1}$$

Now we can restrate corollary 8.4 in terms of the solution n of (1.5)-(1.6).

Corollary 9.1. *Let $\epsilon > 0$ be given by corollary 6.14 and let $0 < \nu < \epsilon$, then the solution $n(t,a,x)$ of (1.4)-(1.6) satisfies $\|e^{-\lambda_d t}n(t,\cdot,\cdot)-h(n_0)n_d\| \leq L'e^{-\nu t}\|n_0\|$, $t \geq 0$, where $\|\cdot\|$ stands for the $L_1(\Omega)$-norm, L' is a positive constant, and h is a strictly positive linear functional on $L_1(\Omega)$.*

Remark 9.2. h can be computed from $h(n_0) = \dfrac{<F_d', \Phi(\lambda_d)>}{<F_d', -K_1\psi_d>}$.

Corollary 9.1 is a typical renewal result. The population grows (or decays) exponentially with exponent λ_d (which is sometimes called the Malthusian parameter). As time increases an asymptotically stable age-size distribution is reached. If $t = \infty$ the dependence on the initial condition is only reflected by the scalar $h(n_0)$.

If in our model the rates b and μ depend on age only then we can integrate (1.4)-(1.6) over all sizes x and we find the age-dependent problem

$$\frac{\partial N}{\partial t} + \frac{\partial N}{\partial a} = -(\mu(a)+b(a))N(t,a), \tag{9.2a}$$

$$N(t,0) = 2\int_0^\infty b(a)N(t,a)da, \tag{9.2b}$$

$$N(0,a) = N_0(a), \tag{9.2c}$$

where $N(t,a) \overset{def}{=} \int_0^\infty n(t,a,x)dx$. If the assumptions (A_b), (A_μ) and (A_d) of section 1 are satisfied then a stable age-distribution is reached as $t \to \infty$:

$$N(t,a) \sim e^{\lambda_d t}N_d(a),\ t \to \infty,$$

(this result can also be found in Eisen (1979)) and the growthrate $g(x)$ has no effect on this stable age-distribution. More details can be found in Hannsgen et al. (1984).

Now we shall explain what can happen if assumption 6.4 is not fulfilled.

I. We expect that most of our result remain valid if $g(2x) < 2g(x)$, all x (but not necessarily $2g(x)-g(2x) > \delta$, for some $\delta > 0$). But probably one gets mixed up with great technical difficulties, which, however, do not provide additional insight.

II. If $g(2x) > 2g(x)$, for all x, then some sort of instability comes into the problem. Although γ defined by (6.3) again has a unique fixed point x_0, in this case it is unstable:

$$\frac{d\gamma}{dx}\Big|_{x=x_0} = \frac{g(2x_0)}{2g(x_0)} > 1.$$

For the sequence $\{x_n\}$ of lemma 6.4 this result in

$$x_n \to 0, \text{ if } x_1 < x_0,$$

$$x_n \to \infty, \text{ if } x_1 > x_0.$$

If we start with a population all of whose members have size $> \bar{x}(0)$, where $\bar{x}(0) > x_0$, then at time t all individuals have size $> \bar{x}(t)$, where $\bar{x}(t) \to \infty$. As a consequence there cannot exist a stable age-size distribution. A second problem arising in this case is caused by the fact that growth becomes very small if x tends to zero. As a consequence individuals can not grow away from zero.

III. Suppose that $g(2x) = 2g(x)$, all x. (Notice that this and also former case is actually excluded by the boundedness condition on g: however the same integral equation for the birth function $B(t)$ still holds.) Biologically this condition means that the time T needed to grow from x to $2x$ does not depend on x. We can prove that in this case the set of singular points Σ is periodic, i.e. there exists a $p > 0$ such that $\lambda \in \Sigma \Rightarrow \lambda + ikp \in \Sigma$, $k \in \mathbf{Z}$.

Lemma 9.3. *Let $g(2x) = 2g(x)$, for all x and let $T = G(2x) - G(x)$ (which does not depend on x), then Σ is periodic with period $p = \frac{2\pi}{T}$.*

Proof. Suppose $\lambda \in \Sigma$ and let $\psi \in X$ be determined by $\hat{K}(\lambda)\psi = \psi$:

$$\psi(x) = \int_{a_0}^{\infty} e^{-\lambda a} k(a,2x)\psi(X(-a,2x))da.$$

Let $T = G(2x) - G(x)$ and $p = \frac{2\pi}{T}$. Let $\psi_k(x) = e^{-ikpG(x)} \cdot \psi(x)$, then

$$(\hat{K}(\lambda + ikp)\psi_k)(x) = \int_{a_0}^{\infty} e^{-\lambda a} e^{-ikpa} k(a,2x)\psi(X(-a,2x))e^{-ikp(G(2x)-a)}da$$

$$= e^{-ikpG(2x)} \int_{a_0}^{\infty} e^{-\lambda a} k(a,2x)\psi(X(-a,2x))da =$$

$$= e^{-ikp(T+G(x))}\cdot\psi(x) = \psi_k(x), \text{ hence } \lambda + ikp \in \Sigma. \quad \square$$

Now let $\psi_k(x) = e^{-ikpG(x)}\cdot\psi_d(x)$, where ψ_d is the positive eigenvector of $\hat{K}(\lambda_d)$ (assumed that a solution λ_d of $r(\hat{K}(\lambda)) = 1$ exists). Let

$$n_0^k(a,x) = e^{-\lambda_k a} \frac{g(X(-a,x))}{g(x)} E(a,X(-a,x))\psi_k(X(-a,x)), \quad k \in \mathbf{Z},$$

where $\lambda_k = \lambda_d + ikp$ (see (9.1)). Choose $\gamma_k \in \mathbf{C}$, $k \in \mathbf{Z}$ such that $\Sigma_{k=1}^{\infty} |\gamma_k| < \frac{1}{2}$, $\gamma_{-k} = \bar{\gamma}_k$, and define the initial age-size-distribution $n_0(a,x)$ by

$$n_0(a,x) \overset{def}{=} n_0^0(a,x) + \sum_{\substack{k=-\infty \\ k\neq 0}}^{\infty} \gamma_k n_0^k(a,x),$$

$$= (1 + 2Re \sum_{k=1}^{\infty} \gamma_k e^{-ikpG(x)})n_0^0(a,x),$$

then $n_0(a,x) \geq 0$, $(a,x) \in \Omega$ and the solution $B(t,x)$ of the associated integral equation (2.14) is given by

$$B(t,x) = e^{\lambda_d t} \cdot \psi_d(x) \cdot \{1 + 2\,\mathrm{Re} \sum_{k=1}^{\infty} \gamma_k e^{ikp(t-G(x))}\} = e^{\lambda_d t} \cdot \psi_d(x) \cdot h(t,x)$$

where

$$h(t,x) \overset{def}{=} 1 + 2\,\mathrm{Re} \sum_{k=1}^{\infty} \gamma_k e^{ikp(t-G(x))}$$

satisfies

$$h(t+T,x) = h(t,x),$$

$$h(t,2x) = h(t,x).$$

This proves that there does not exist a stable age-size-distribution in this case.

This result disproves a remark of Bell (1968) which says that in case of exponential growth ($g(x) = c \cdot x$) there can exist a stable age-size-distribution if b depends in an appropriate manner on x and a. Trucco & Bell (1970) showed that in the case of dispersionless growth (i.e. $\frac{1}{x} X(a,x)$ depends on a only: this is satisfied if $g(x) = c \cdot x$) it is not possible that the first and second moments of the distribution of birth sizes both approach finite non-zero limits as $t \to \infty$, yielding that there does not exist a stable age-size distribution (see also Trucco (1970)). Hannsgen, Tyson & Watson (1984) proved that in case of exponential growth and under the assumption that the generation time (= age at which a cell divides) is a random variable with a given probability density function there cannot exist a stable, time-independent size distribution for the birth function.

IV. If $[0,\infty) = I_1 \cup I_2 \cup I_3$ such that $g(2x) < 2g(x)$, $x \in I_1$, $g(2x) = 2g(x)$, $x \in I_2$, $g(2x) > 2g(x)$, $x \in I_3$, then the question of existence of a stable distribution is a very hard one, but also a very interesting and exciting one from the mathematical point of view.

The reason for making assumption (A_d) is a technical one. It guarantees the existence of a dominant element λ_d of Σ (see lemma 6.11).

Undoubtedly our theory is also valid if a less restrictive condition than (A_g) is imposed. However, our main purpose is not generality but to give an idea how abstract results from functional analysis can be used in the study of concrete structured population models. The results that we obtained here can also be found using semigroup methods, and readers who are trying to do so, will find out that the two approaches are more closely linked then it seems at first sight.

Appendix

Here we shall prove that for all $\lambda \in \Lambda$ the operator $\hat{K}(\lambda)$ is compact. We need the following result of Krasnoselskii et al. (1976, chapter 2, § 5. 6). They proved that a linear integral operator which has a compact majorant is compact itself. We shall make this more precise. Let $\Omega \subseteq \mathbf{R}$ be a measurable set and let the linear integral operator $T: L_1(\Omega) \to L_1(\Omega)$ be given by

$$(T\phi)(x) = \int_{\Omega} h(x,y)\phi(y)dy.$$

Suppose that

$$|h(x,y)| \leq h^+(x,y),\ x,y \in \Omega,$$

and let the operator T^+ be given by

$$(T^+\phi)(x) = \int_\Omega h^+(x,y)\phi(y)dy.$$

Then the following result holds (Krasnoselskii et al. (1976)):

Lemma 1. *If T^+ is a bounded, compact operator from $L_1(\Omega)$ into itself then T is also compact.*

Now let $\lambda \in \Omega$, then

$$(\hat{K}(\lambda)\psi)(x) = \int_0^{X(-a_0,2x)} e^{-\lambda(G(2x)-G(z))} k(G(2x)-G(z),2x)\frac{\psi(z)}{g(z)}dz.$$

With (2.16), (A_g) and lemma 3.1 this yields

$$|e^{-\lambda(G(2x)-G(z))}.k(G(2x)-G(z),2x).\frac{1}{g(z)}| < e^{-(Re\,\lambda+d_\infty)(G(2x)-G(z))}.\frac{4}{g_{\min}}\|b\|_\infty \cdot e^M.$$

Let $p = \mathrm{Re}\lambda + d_\infty$, then $p>0$, since $\lambda \in \Lambda$. Let the operator $K^+(p)$ be defined as

$$(K^+(p)\psi)(x) = \int_0^{X(-a_0,2x)} e^{-p(G(2x)-G(z))}.\psi(z)dz.$$

If we can prove that $K^+(p)$ is compact for all $p>0$ then it follows from Lemma 1 that $\hat{K}(\lambda)$ is compact for all $\lambda \in \Lambda$.

The following compactness criterium can be found in Kufner et al. (1977).

Lemma 2. *The bounded linear operator $T: L_1(\Omega) \to L_1(\Omega)$ is compact if for every $\epsilon>0$ there exists a $\delta>0$ such that $\int_\Omega |(T\phi)(x+h)-(T\phi)(x)|dx < \epsilon\|\phi\|$ for all $\phi \in L_1(\Omega)$ and $|h|<\delta$.*

We shall use this criterium to prove that $K^+(p)$ is compact for all $p>0$. For simplicity we assume that $g(x)=1$, for all x. The reader will have no difficulty to see that the proof can be carried through for more general g. Let $\psi \in L_1[0,\infty)$ and let $h>0$. Then

$$|(K^+(p)\psi)(x+h)-(K^+(p)\psi)(x)| =$$

$$|e^{-2p(x+h)} \int_0^{2(x+h)-a_0} e^{pz}\psi(z)dz - e^{-2px}\int_0^{2x-a_0} e^{pz}\psi(z)dz|$$

$$\leq |e^{-2p(x+h)} - e^{-2px}| \cdot \int_0^{2x-a_0} e^{pz}|\psi(z)|dz + e^{-2p(x+h)}\int_{2x-a_0}^{2(x+h)-a_0} e^{pz}|\psi(z)|dz \stackrel{def}{=} f_1(x)+f_2(x),$$

where $f_1(x) = (1-e^{-2ph})(K^+(p)|\psi|)(x)$, $f_2(x) = e^{-2p(x+h)}\int_{2x-a_0}^{2(x+h)-a_0} e^{pz}|\psi(z)|dz$, and $|\psi|(x) \stackrel{def}{=} |\psi(x)|$. Thus

$$\|f_2\| = \int_0^\infty f_2(x)dx = \int_{\frac{1}{2}a_0}^\infty e^{-2p(x+h)}.\{\int_{2x-a_0}^{2(x+h)-a_0} e^{pz}|\psi(z)|dz\}dx$$

$$= \int_0^\infty e^{pz} |\psi(z)| \cdot \{ \int_{\frac{1}{2}(z+a_0)-h}^{\frac{1}{2}(z+a_0)} e^{-2p(x+h)} dx \} dx = \frac{1-e^{-2ph}}{2p} e^{-pa_0} \|\psi\|.$$

From these two estimates and Lemma 2, the compactness of $K^+(p)$ and thus $\hat{K}(\lambda)$ follows immediately.

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Holling's "hungry mantid" model for the invertebrate functional response considered as a Markov process. III. Stable satiation distribution

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Abstract. In this paper, we study an analytical model describing predatory behaviour. It is assumed that the parameter describing the predator's behaviour is its satiation. Using semigroup methods and compactness arguments we prove that a stable satiation distribution is reached if $t \to \infty$. Furthermore, using a Trotter-Kato theorem we justify the transition to the much simpler problem that is obtained if the prey biomass tends to zero.

Key words: Satiation — functional response — forward equation — backward equation — positive operator — semigroup — trotter-Kato theorem

Introduction

In his famous paper [9], Holling described a detailed simulation model for the prey-catching behaviour of the praying mantid *Hierodula crassa*. One of his main purposes was to gain information about the qualitative and quantitative behaviour of the functional response of an invertebrate predator. (The functional response can be defined as the number (or total weight) of prey eaten per unit of time per predator as a function of the prey (prey biomass) density.)

In a series of papers [13, 14, 15] Metz and van Batenburg presented an analytic reformulation of the theory of predation as propounded by Holling. They started by showing that Holling's assumptions implied that the predator's minimal state space is two-dimensional. More precisely: at every instant the state of the predator can be described by two parameters, its satiation (or gut content) S, and the maximum time T still to be spent handling the prey. By the phrase "handling the prey" is meant pursuing it and (in case of a successful strike) eating it. As long as the predator is searching for his meal, $T = 0$. A complete description of the predator's behaviour as a journey through this two-dimensional state space, can be found in [14].

Metz and van Batenburg also described several ways to simplify this rather complicated model. One possibility is to neglect handling time. The resulting "gobbler" model is just simple enough to be amenable to detailed analytical treatment and yet retains the essential stochastic features of the full model. The simplification can be justified if the handling time is relatively small in comparison with the searching time. In this paper we shall restrict ourselves to the gobbler model.

One of the main features of the gobbler model is that its state space is one-dimensional, the relevant parameter being the satiation S. Between two captures S decreases continuously according to some ordinary differential equation $dS/dt = f(S)$ describing digestion, where we shall assume that $f(s) = -as$, as this seems a realistic assumption from a biological point of view. (See [6, 14]).

Prey capture is a random event resulting in an instantaneous transition $S \to S + w$, where w denotes prey weight (which is assumed to be constant). This jump causes a term with non-local argument in the balance equation for the S-distribution. (See Sect. 1.) The rate of prey capture depends (in a decreasing manner) on the satiation. (In the case of Holling's praying mantid this is due to the fact that its search field decreases with increasing satiation.)

This paper, which is self-contained, deals with a number of mathematical questions raised in the papers of Metz and van Batenburg [13, 14, 15]. These questions are formulated in the first section.

Our starting point is the so-called *backward equation* which is the adjoint of the balance equation for the probability density, or *forward equation*. This backward equation happens to be more tractable from a mathematical point of view, and it has a straightforward interpretation. In this manner we are able to prove that a stable satiation distribution is reached in the course of time.

Finally we refer to [4] where one uses techniques very similar to ours, to analyse a problem which is completely different from a biological point of view.

1. The equations and their interpretation

One of the equations proposed by Metz and van Batenburg [13, 14, 15], as part of their model for predatory behaviour is:

$$\frac{\partial p(s,t)}{\partial t} = -\frac{\partial}{\partial s}(f(s)p(s,t)) - xg(s)p(s,t) + xg(s-w)p(s-w,t), \quad (1.1a)$$

where one should read $xg(s-w)p(s-w,t) = 0$ if $s - w \leq 0$. Here t denotes time, s the predator's satiation, and $p(s,t)$ is the (unknown) probability density of S, i.e.

$$\int_{s_1}^{s_2} p(s,t)\, ds = P\{s_1 < S(t) \leq s_2\}$$

is the probability that S at time t is between s_1 and s_2. w is the weight (of the edible portion) of a prey, which is assumed to be constant for all prey. $f(s)$ is the digestion rate, which has been discussed in the Introduction and there it was assumed that $f(s) = -as$. By a scaling of the time we may set $a = 1$. x is the effective prey density and $x \cdot g(s)$ stands for the rate of prey capture, if the predator's satiation is s. It is assumed that there exists a value $c > 0$ such that

$g(s)=0$ if $s \geqslant c$. c is called the satiation threshold. Accordingly we impose the boundary condition

$$p(s, t)=0, \qquad s \geqslant c+w. \tag{1.1b}$$

Furthermore we supplement (1.1a) with the initial condition

$$p(s, 0)=p_0(s). \tag{1.1c}$$

Because of the fact that (1.1a) describes the state of one single predator, we should have

$$1=\int_0^{c+w} p_0(s)\, ds=\int_0^{c+w} p(s, t)\, ds, \qquad t>0. \tag{1.2}$$

The second of these identities can be verified by integration of (1.1a) along the s-interval $[0, c+w]$.

In this paper we shall make the following assumption on g:

(A) g is a Lipschitz-continuous function on $[0, c+w]$, g is non-increasing and $g(s)=0$, if $s \geqslant c$.

Metz and van Batenburg [14] showed that for Holling's mantid model

$$g(s)=\alpha\left(1-\frac{s}{c}\right)^{+} \cdot \exp\left(-b'\left(1-\frac{s}{c'}\right)^{+}\right), \tag{1.3}$$

where $c'<c$ and α, b' are positive constants. The superscript $^+$ means that negative values are to be replaced by zero.

Remark 1.1: If (1.1a) is formally integrated from s to $c+w$, one obtains a partial differential equation for the distribution function of S which necessarily is of bounded variation. This feature will be exploited in Sect. 5.

In the literature (1.1) is called the *forward equation.* (See e.g. [2, 5].) The associated *backward equation* (or adjoint equation) is given by

$$\frac{\partial n(s, t)}{\partial t}=-s \frac{\partial n(s, t)}{\partial s}-x g(s) n(s, t)+x g(s) n(s+w, t), \tag{1.4}$$

where $xg(s)n(s+w, t)=0$ if $s>c$, and where we have substituted $f(s)=-s$. The backward equation is easier to derive in a rigorous manner directly from the constructive specification of the stochastic process and it is easier to handle as well. The main reason for this is that the backward equation has to be solved in the space of continuous functions, and the forward equation in the space of Borel measures. Below we shall briefly describe the duality relation between solutions of the forward and the backward equation.

Let $p(s, t; p_0)$ be the solution of (1.1), and let $n(s, t; \phi)$ be the solution of (1.4), obeying the initial condition

$$n(s, 0)=\phi(s), \tag{1.5}$$

where ϕ is some continuous function on the interval $[0, c+w]$. (Here we have tacitly assumed that these solutions do exist. This is proved in Sect. 3.) Then

$$\int_0^{c+w} p(s, t; p_0) \phi(s)\, ds=\int_0^{c+w} p_0(s) n(s, t; \phi)\, ds, \qquad t \geqslant 0. \tag{1.6}$$

As a matter of fact this relation defines the solution of the forward equation, if the solution of the backward equation can be found for all continuous initial functions ϕ.

Our starting point will be the backward equation. We shall prove existence and uniqueness of solutions of (1.4)-(1.5), and study the large-time behaviour of these solutions. Subsequently we shall interpret the results in terms of the forward equation.

Let $X = C[0, c+w]$ be the space of continuous functions on $[0, c+w]$ endowed with the usual sup-norm. We can rewrite (1.4)-(1.5) as an abstract Cauchy problem:

$$\frac{dn}{dt} = A_w n, \qquad n(0) = \phi \in X, \tag{1.7}$$

where the closed operator A_w on X is defined by

$$(A_w\psi)(s) = -s\frac{d\psi}{ds} - xg(s)\psi(s) + xg(s)\psi(s+w), \tag{1.8}$$

for all ψ in the domain of definition $\mathscr{D}(A_w)$ of A_w, which is given by

$$\mathscr{D}(A_w) = \{\psi \in X \mid \psi \text{ is absolutely continuous and the function } s \to -s\, d\psi/ds\,(s) \text{ defines an element of } X\}. \tag{1.9}$$

Remark 1.2: The subscript w accounts for the dependence of A_w on the prey weight w. As a matter of fact, the operator A_w also depends on the prey density x, but this is not expressed explicitly in our notation.

In Sect. 2 we shall investigate the spectrum of A_w, and in Sect. 3 we shall concentrate on the Cauchy problem (1.7).

In order to obtain more explicit results, Metz and van Batenburg [13, 14, 15] formally took the limit $w \to 0$, $x \to \infty$, $\xi = xw$ remaining constant. It appears that in the limit the mantid's catching behaviour becomes deterministic. Moreover, the limiting equation can be solved explicitly. One of the questions that one should answer is whether solutions of the original equation $(w > 0)$ converge to solutions of the limiting equation $(w = 0)$ if $w \to 0$. In Sect. 4, we shall deal with this question. In Sect. 5 we shall give a rather detailed description of the relation between solutions of the forward and the backward equation.

An important biological quantity to be derived from the model is W, i.e. the total weight of prey caught per unit of time. The expectation $\mathscr{E}W$ of W obeys the ordinary differential equation

$$\frac{d\mathscr{E}W}{dt} = xw \int_0^{c+w} g(s)p(s, t)\, ds. \tag{1.10}$$

Remark 1.3: In [14, 15] where one discusses the full stochastic model it is shown that

$$\frac{d\mathscr{E}N}{dt} = x \int_0^{c+w} g(s)p(s, t)\, ds,$$

where N is the number of prey caught per unit of time. This is equivalent to (1.10) because $W = wN$.

Metz and van Batenburg [13, 14, 15] also derived an inhomogeneous partial differential equation from which the variance of W can be obtained:

$$\frac{\partial z(s,t)}{\partial t}=\frac{\partial}{\partial s}(sz(s,t))-xg(s)z(s,t)+xg(s-w)z(s-w,t)$$

$$+xg(s-w)p(s-w,t)-xp(s,t)\int_0^{c+w} g(s)p(s,t)\,ds. \qquad (1.11a)$$

This equation must be supplemented with boundary and initial conditions:

$$z(s,t)=0, \qquad s\geqslant c+w, \qquad (1.11b)$$

$$z(s,0)=0. \qquad (1.11c)$$

Remark 1.4: It was explained in [13, 15] how var(N) can be computed from $z(s,t)$. A straightforward computation using the results of [13, 15] shows that

$$\frac{d}{dt}\mathrm{var}(W)=2xw\cdot\mathrm{cov}[W,g(S)]+w\mathscr{E}g(S)$$

$$=2xw\cdot\mathrm{cov}[W,g(S)]+w\frac{d\mathscr{E}W}{dt},$$

and

$$\mathrm{cov}[W,g(S)]=w\int_0^\infty g(s)z(s,t)\,ds.$$

In Sect. 6, we shall study (1.11).

If we let $t\to\infty$ in (1.10), we find an expression for the functional response $\Phi_w(\xi)$ (if we can prove convergence of the S-distribution towards a stationary state) which is the total biomass of prey caught per unit of time per predator in the stationary situation. Here $\xi=xw$, i.e. the density of prey biomass. It seems hard to obtain analytic results on the qualitative behaviour of $\Phi_w(\xi)$ in the most general case. However, it can be proved that for all $\xi>0$, $\lim_{w\downarrow 0}\Phi_w(\xi)=\Phi_0(\xi)$, where Φ_0 can be obtained explicitly from the limiting equation studied in Sect. 4. Furthermore we are able to compute $\Phi_w(\xi)$ explicitly in the rather unrealistic special case that $c\leqslant w$. These results are given in Sect. 7.

2. The eigenvalue problem

In this section we shall investigate the spectrum of the operator A_w defined by (1.8)–(1.9). It appears that the techniques which we shall use are in many regards similar to those in [8], where we studied the eigenvalue problem associated with a model for cell growth.

We use the following notation. For an operator L we denote by $\sigma(L)$ and $P\sigma(L)$ the spectrum and point spectrum of L respectively. $\rho(L)$ is the resolvent set, and $r(L)$ the spectral radius. $N(L)$ and $R(L)$ are the nullspace and range of L, and $\mathrm{ind}(L)=\dim N(L)-\mathrm{codim}\,R(L)$ is called the Fredholm index of L. (cf. [12, 18]).

Let $h \in X$. The inhomogeneous equation $\lambda\psi - A_w\psi = h$ can be rewritten as

$$\lambda\psi(s) + s\frac{d\psi}{ds} + xg(s)\psi(s) - xg(s)\psi(s+w) = h(s). \tag{2.1}$$

Let

$$E(s) = \exp\left(\int_w^s \frac{xg(\sigma)}{\sigma}\, d\sigma\right). \tag{2.2}$$

It is obvious that

$$E(s) = s^{\gamma x}\tilde{E}(s), \tag{2.3}$$

where $\tilde{E}(s)$ is continuous on $[0, c+w]$, and satisfies $\tilde{E}(0) > 0$. Here

$$\gamma = g(0). \tag{2.4}$$

Let

$$\Omega = \{\lambda \in \mathbb{C} \mid \gamma x + \operatorname{Re}\lambda > 0\}. \tag{2.5}$$

Suppose that $\lambda \in \Omega$. Substitution of

$$\phi(s) = s^{\lambda}E(s)\psi(s) \tag{2.6}$$

in (2.1) yields

$$\frac{1}{s^{\lambda-1}E(s)}\frac{d\phi}{ds} - xg(s)\psi(s+w) = h(s),$$

or equivalently,

$$\frac{d\phi}{ds} - xg(s)s^{\lambda-1}E(s)\psi(s+w) = h(s)s^{\lambda-1}E(s). \tag{2.7}$$

It follows from (2.6) and (2.3) that $\phi(s) = s^{\lambda}E(s)\psi(s) = s^{\lambda+\gamma x}\tilde{E}(s)\psi(s)$. Now $\lambda \in \Omega$ and the continuity of ψ imply that $\phi(0) = 0$. Integrating (2.7) from 0 to s and plugging (2.6) back into the result yields:

$$\psi(s) - \frac{x}{s^{\lambda}E(s)}\int_0^s g(\sigma)\sigma^{\lambda-1}E(\sigma)\psi(\sigma+w)\, d\sigma = \frac{1}{s^{\lambda}E(s)}\int_0^s h(\sigma)\sigma^{\lambda-1}E(\sigma)\, d\sigma. \tag{2.8}$$

Let the linear operators $\hat{T}_\lambda$ and U_λ on X be defined by

$$(\hat{T}_\lambda\rho)(s) = \frac{x}{s^{\lambda}E(s)}\int_0^s g(\sigma)\sigma^{\lambda-1}E(\sigma)\rho(\sigma+w)\, d\sigma, \tag{2.9}$$

$$(U_\lambda\rho)(s) = \frac{1}{s^{\lambda}E(s)}\int_0^s \sigma^{\lambda-1}E(\sigma)\rho(\sigma)\, d\sigma, \tag{2.10}$$

for all $\rho \in X$.

It is obvious that $\hat{T}_\lambda$ and U_λ are bounded. Now (2.8) can be rewritten as

$$\psi - \hat{T}_\lambda\psi = U_\lambda h. \tag{2.11}$$

The following result is straightforward.

Lemma 2.1. *Let* $\lambda \in \Omega$ *and* $h \in X$. *Then* $\psi \in X$ *is a solution of the inhomogeneous equation* $\lambda\psi - A_w\psi = h$ *if and only if* $\psi - \hat{T}_\lambda\psi = U_\lambda h$.

Thus the inhomogeneous equation (2.1) involving the unbounded operator A_w can be reformulated in terms of the bounded operators $\hat{T}_\lambda$ and U_λ. A closer look on (2.8) makes clear that it suffices to study this equation on the subinterval $[w, c+w]$, because knowledge of ψ on this subinterval would enable us to compute $(\hat{T}_\lambda\psi)(s)$ for all $s \in [0, c+w]$. Let

$$X_1 = C[w, c+w] \tag{2.12}$$

with the supnorm. For $\psi \in X_1$ we define $T_\lambda\psi$ in the following way. Let $\hat{\psi} \in X$ such that $\hat{\psi}(s) = \psi(s)$, $s \in [w, c+w]$, then $(T_\lambda\psi)(s) := (\hat{T}_\lambda\hat{\psi})(s)$, $s \in [w, c+w]$. Observe that $T_\lambda : X_1 \to X_1$ is well-defined, i.e. $T_\lambda\psi$ does not depend on the choice of $\hat{\psi}$.

The following result can be established using the Arzelà–Ascoli theorem (cf. [18]).

Lemma 2.2. $T_\lambda : X_1 \to X_1$ *is compact.*

Let

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

Theorem 2.3. $\sigma(A_w) \cap \Omega = P\sigma(A_w) \cap \Omega = \Sigma$.

Proof: Let $\lambda \in \Omega$. The homogeneous equation $A_w\psi = \lambda\psi$ can be rewritten as $\hat{T}_\lambda\psi = \psi$. Let $\tilde{\psi}$ be the restriction of ψ to $[w, c+w]$, then $T_\lambda\tilde{\psi} = \tilde{\psi}$. $\tilde{\psi} = 0$ would imply $\hat{T}_\lambda\psi = \psi = 0$. As a consequence, if $\lambda \in P\sigma(A_w)$, then $\lambda \in \Sigma$. Similar arguments yield that $\lambda \in \Sigma$ implies that $\lambda \in P\sigma(A_w)$. Now suppose that $\lambda \in \Omega \cap \sigma(A_w)$. The inhomogeneous equation $\lambda\psi - A_w\psi = h$, where $h \in X$, is equivalent to $\psi - \hat{T}_\lambda\psi = U_\lambda h$. Suppose that $\lambda \notin P\sigma(A_w)$, then we have $1 \notin P\sigma(T_\lambda)$ yielding that the equation $\psi - \hat{T}_\lambda\psi = U_\lambda h$ can be solved on the interval $[w, c+w]$. Its solution is $\psi(s) = ((I - T_\lambda)^{-1}U_\lambda h)(s)$, $s \in [w, c+w]$. For $s \in [0, w]$ we find $\psi(s) = (\hat{T}_\lambda\psi)(s) + (U_\lambda h)(s)$ where we have exploited the fact that $(\hat{T}_\lambda\psi)(s)$ can be computed on $[0, w]$ if $\psi(s)$ is known on $[w, c+w]$. This proves the result.

We shall need the following lemma in the proof of Theorem 2.11.

Lemma 2.4. $R(\lambda I - A_w)$ *is closed if* $\lambda \in \Omega$.

Proof: Suppose $h_n \in R(\lambda I - A_w)$ and $h_n \to h$, $n \to \infty$. Let ψ_n be such that $\lambda\psi_n - A_w\psi_n = h_n$. Lemma 2.1 yields that $\psi_n - \hat{T}_\lambda\psi_n = h_n$. Let $\tilde{\psi}_n$ and $\tilde{h}_n$ be the restriction of ψ_n respectively h_n to $[w, c+w]$. Thus $\tilde{\psi}_n - T_\lambda\tilde{\psi}_n = \tilde{h}_n$. Hence $\tilde{h}_n \in R(I - T_\lambda)$ and $\tilde{h}_n \to \tilde{h}$, $n \to \infty$ where $\tilde{h}$ denotes the restriction of h to $[w, c+w]$. From the compactness of T_λ we conclude that $R(I - T_\lambda)$ is closed. Therefore $\tilde{h} \in R(I - T_\lambda)$. Let $\tilde{\psi} \in X_1$ be such that $\tilde{\psi} - T_\lambda\tilde{\psi} = \tilde{h}$. We define ψ by:

$$\psi(s) = \tilde{\psi}(s),\ s \in [w, c+w],$$

$$\psi(s) = \frac{x}{s^\lambda E(s)} \int_0^s g(\sigma)\sigma^{\lambda-1}E(\sigma)\tilde{\psi}(\sigma + w)\, d\sigma + (U_\lambda h)(s),\ s \in [0, w].$$

It is clear that ψ is a solution of $\psi - \hat{T}_\lambda\psi = h$, hence $\lambda\psi - A_w\psi = h$.

The following result is stated for the sake of completeness. We do not need it in our calculations.

Theorem 2.5. $\mathbb{C}/\Omega \subset \sigma(A_w)$.

Proof: Let λ be such that $\gamma x + \operatorname{Re} \lambda < 0$. Without loss of generality we may assume that $\lambda \in \mathbb{R}$. Let $p = -\gamma x - \lambda > 0$. The homogeneous equation $A_w\psi = \lambda\psi$ can be solved on $[w, c+w]$ within a finite number of steps. Let $\bar{\psi}(s)$ be the solution on $[w, c+w]$. For $s \in [0, w]$ we must solve

$$\frac{d\psi}{ds} + \frac{xg(s)+\lambda}{s}\psi(s) = \frac{xg(s)\bar{\psi}(s+w)}{s}, \qquad \psi(w) = \bar{\psi}(w).$$

We obtain

$$\psi(s) = \bar{\psi}(w) \cdot \frac{1}{s^\lambda E(s)} - \frac{x}{s^\lambda E(s)} \int_s^w g(\sigma)\sigma^{\lambda-1}E(\sigma)\bar{\psi}(\sigma+w)\, d\sigma$$

$$= \frac{1}{\tilde{E}(s)}\left[s^p\bar{\psi}(w) - s^p \int_s^w g(\sigma)\sigma^{-p-1}\tilde{E}(\sigma)\bar{\psi}(\sigma+w)\, d\sigma\right],$$

and it can be easily checked that this expression defines a continuous function if $p > 0$. Therefore $\lambda \in P\sigma(A_w)$ if $\operatorname{Re} \lambda + \gamma x < 0$. This, and the closedness of the spectrum, yields the result.

The asymptotic behaviour of solutions of (1.4) for $t \to \infty$ appears to be determined by the dominant eigenvalue of A_w, i.e. the eigenvalue with the largest real part. As we did in [8], we use positive operator theory to characterize this dominant eigenvalue. We refer to the famous paper of Krein and Rutman [11], and the monograph of Schaefer [17]. See also [10]. Let

$$X_1^+ = \{\psi \in X_1 | \psi(s) \geq 0,\ w \leq s \leq c+w\}, \tag{2.14}$$

$$\Omega_R = \Omega \cap \mathbb{R}. \tag{2.15}$$

Then X_1^+ defines a closed, convex cone in X_1, and for all $\lambda \in \Omega_R$ we have that T_λ is positive with respect to X_1^+, i.e.

$$T_\lambda\psi \in X_1^+ \quad \text{if } \psi \in X_1^+.$$

In the sequel we need a stronger notion of positivity.

Definition [11]. An operator is called strongly positive if each nonzero element within the cone is mapped into the interior of that cone by some power of the operator.

Theorem 2.6. *For all $\lambda \in \Omega_R$, T_λ is strongly positive with respect to X_1^+.*

Proof: Let $\lambda \in \Omega_R$ and $\psi \in X_1^+$, $\psi \neq 0$. There exists an $\bar{s} \in (w, c+w)$ and an $\varepsilon > 0$ such that $\psi(s) > 0$, $s \in (\bar{s}-\varepsilon, \bar{s}+\varepsilon)$. Now suppose that $s \geq \bar{s} - w$ and $s \in [w, c+w]$, then we have

$$(T_\lambda\psi)(s) \geq \frac{x}{s^\lambda E(s)} \int_{s-w-\varepsilon}^{s} g(\sigma)\sigma^{\lambda-1}E(\sigma)\psi(\sigma+w)\, d\sigma > 0.$$

Applying T_λ once more yields

$$(T_\lambda^2\psi)(s) > 0, \qquad s \geq \bar{s} - 2w.$$

Hence if p is the smallest integer satisfying $p \geq (c+w)/w$, then we have $(T_\lambda^p\psi)(s) > 0$, $s \in [w, c+w]$, yielding that $T_\lambda^p\psi \in \mathring{X}_1$.

Now we can apply Theorem 6.3 of [11], and we obtain the following result. Let X_1^* be the adjoint space of X_1, and let $(X_1^+)^*$ be the adjoint cone of X_1^+. (See e.g. [11].) With T_λ^* we denote the adjoint operator of T_λ.

Lemma 2.7. *For all $\lambda \in \Omega_R$, $r_\lambda = r(T_\lambda)$ is an algebraically simple eigenvalue of both T_λ and T_λ^*. Furthermore there exist a $\psi_\lambda \in \mathring{X}_1^+$ and $F_\lambda \in (X_1^+)^*$ such that*

$$T_\lambda\psi_\lambda = r_\lambda\psi_\lambda \tag{2.16a}$$

$$T_\lambda^* F_\lambda = r_\lambda F_\lambda \tag{2.16b}$$

and ψ_λ is the only positive eigenvector of T_λ. Moreover, F_λ is strictly positive, i.e. $F_\lambda(\psi) > 0$ for all $\psi \in X_1^+\backslash\{0\}$.

Now ψ_λ is an eigenvector of A_w if and only if $r_\lambda = 1$. We shall prove that $\lambda \in \Omega_R$ is uniquely determined by this condition. Obviously

$$T_0 I = I, \tag{2.17}$$

where the function $I \in X_1$ is defined by $I(s) = 1$, $s \in [w, c+w]$. Clearly $I \in X_1^+$ and we conclude from Lemma 2.7 that $r(T_0) = 1$.

Lemma 2.8. *$r(T_\lambda)$ is strictly decreasing in $\lambda \in \Omega_R$.*

Proof: Suppose $\lambda, \mu \in \Omega_R$ and $\lambda > \mu$. A straightforward computation shows that

$$(T_\mu - T_\lambda)\mathring{X}_1^+ \subseteq \mathring{X}_1^+.$$

In particular $(T_\mu - T_\lambda)\psi_\lambda \in \mathring{X}_1^+$. From the strict positivity of F_μ we conclude that $\langle F_\mu, (T_\mu - T_\lambda)\psi_\lambda\rangle > 0$, or equivalently

$$r_\mu\langle F_\mu, \psi_\lambda\rangle > r_\lambda\langle F_\mu, \psi_\lambda\rangle.$$

Therefore $r_\mu > r_\lambda$, and this proves the lemma.

Now we shall interpret the results in terms of A_w.

Theorem 2.9. *$\lambda = 0$ is an algebraically simple eigenvalue of A_w with positive eigenvector I. A_w has no other positive eigenvectors. The eigenvalue $\lambda = 0$ is strictly dominant, i.e. $\lambda \in \sigma(A_w)$, $\lambda \neq 0 \Rightarrow \operatorname{Re}\lambda < 0$.*

Proof: From the geometric simplicity of the eigenvalue 1 of T_0 we conclude that $\lambda = 0$ is a geometric simple eigenvalue of A_w. Now suppose that $A_w\psi = I$ for some $\psi \in X$. Then Lemma 2.1 yields that $\hat{T}_0\psi - \psi = U_0 I$. Hence $T_0\tilde{\psi} - \tilde{\psi} = \phi$ where $\tilde{\psi}$ and ϕ are the restrictions of ψ respectively $U_0 I$ to the interval $[w, c+w]$. We observe that $\phi \in \mathring{X}_1^+$. The Fredholm alternative states that $F_0(\phi) = 0$, where F_0 is given by (2.16b) for $\lambda = 0$. However $F_0(\phi) > 0$, which is a contradiction. Therefore 0 is an algebraically simple eigenvalue of A_w. The proof of strict dominance of the eigenvalue $\lambda = 0$ is similar to the proof of Theorem 6.2 in [8].

The following result, stated in [12], enables us to give a more complete description of $\sigma(A_w)\cap\Omega$.

Lemma 2.10 [12]. *Suppose L is a closed linear operator on a Banach space E having a dense domain. For all* $\lambda\in\mathbb{C}$ *satisfying the following conditions*

(i) λ *is on the boundary of* $\sigma(L)$,

(ii) $R(\lambda I-L)$ *is closed*,

(iii) $N(\lambda I-L)$ *has a finite dimension*,

we have $\mathrm{ind}(\lambda I-L)=0$ *and* λ *is a pole of the resolvent.*

Now we can prove:

Theorem 2.11. $\sigma(A_w)\cap\Omega$ *consists entirely of eigenvalues* λ *satisfying*

(i) λ *is a pole of the resolvent*,

(ii) $\mathrm{ind}(\lambda I-A_w)=0$.

Proof: Suppose that $\lambda\in\sigma(A_w)\cap\Omega$ is on the boundary of $\sigma(A_w)$. Lemma 2.4 states that $R(\lambda I-A_w)$ is closed. From $\dim N(\lambda I-A_w)=\dim(I-T_\lambda)$ and the compactness of T_λ we conclude that $\dim N(\lambda I-A_w)<\infty$. Now Lemma 2.10 states that λ is an isolated eigenvalue of A_w. Hence every boundary point of $\sigma(A_w)\cap\Omega$ is isolated. As a consequence there are two possibilities:

1) $\sigma(A_w)\cap\Omega=\Omega$,

2) $\sigma(A_w)\cap\Omega$ contains only isolated eigenvalues.

However, the existence of the dominant eigenvalue $\lambda=0$ excludes the first possibility. This proves the result.

Remark 2.1: We can also state our results in terms of *normal eigenvalues* and *essential spectrum* (in the sense of Browder) (See e.g. [4, 19].) Let L be a closed linear operator on a Banach space. $\lambda\in\sigma(L)$ is called a normal eigenvalue of L if

(a) λ is an isolated element of $\sigma(L)$,

(b) $\mathrm{Ran}(\lambda I-L)$ is closed,

(c) The generalized eigenspace corresponding to λ is finite-dimensional, i.e.

$$\dim\left(\bigcup_{k=1}^{\infty} N(\lambda I-L)^k\right)<\infty.$$

It can be proved that every normal eigenvalue is an isolated pole of the resolvent of finite order. We denote the set of normal eigenvalues with $\sigma_n(L)$. The essential spectrum $\sigma_e(L)$ of L is defined by $\sigma_e(L)=\sigma(L)\backslash\sigma_n(L)$. Now, our results can be reformulated as

$$\sigma(A)\cap\Omega=\sigma_n(A),\qquad \mathbb{C}\backslash\Omega=\sigma_e(A).$$

Our next step is the derivation of the so called characteristic equation which provides us with a tool to compute all eigenvalues of A which are elements of Ω. We shall not go into detail. The interested reader is referred to [8].

For all $\lambda\in\Omega$, the operator T_λ can be decomposed in the following way.

$$(T_\lambda\psi)(s)=\frac{x}{s^\lambda E(s)}\int_0^c g(\sigma)\sigma^{\lambda-1}E(\sigma)\psi(\sigma+w)\,d\sigma$$
$$-\frac{x}{s^\lambda E(s)}\int_s^c g(\sigma)\sigma^{\lambda-1}E(\sigma)\psi(\sigma+w)\,d\sigma,$$

which we rewrite as

$$T_\lambda\psi = \langle H_\lambda, \psi\rangle e_1^\lambda + N_\lambda\psi, \tag{2.18}$$

where

$$e_1^\lambda(s) = \frac{1}{s^\lambda E(s)}, \qquad s\in[w, c+w], \tag{2.19}$$

$$\langle H_\lambda, \psi\rangle = x\int_0^c g(\sigma)\sigma^{\lambda-1}E(\sigma)\psi(\sigma+w)\,d\sigma \tag{2.20}$$

defines a bounded linear functional on X_1, and

$$(N_\lambda\psi)(s) = \frac{-x}{s^\lambda E(s)}\int_s^c g(\sigma)\sigma^{\lambda-1}E(\sigma)\psi(\sigma+w)\,d\sigma \tag{2.21}$$

defines a compact operator on X_1. Moreover N_λ is nilpotent, i.e.

$$N_\lambda^p = 0, \tag{2.22}$$

where p is the smallest integer such that $p \geq (c+w)/w$. Let

$$e_k^\lambda = N_\lambda^{k-1}e_1^\lambda, \qquad k=1,\ldots,p, \tag{2.23}$$

then $e_1^\lambda,\ldots,e_p^\lambda$ are linearly independent vectors in X_1. By iteration of (2.18) we obtain

$$T_\lambda^p\psi = \langle H_\lambda, T_\lambda^{p-1}\psi\rangle\cdot e_1^\lambda + \langle H_\lambda, T_\lambda^{p-2}\psi\rangle\cdot e_2^\lambda + \cdots + \langle H_\lambda, \psi\rangle\cdot e_p^\lambda, \tag{2.24}$$

implying that all eigenvectors of T_λ can be written as a linear combination of $e_1^\lambda,\ldots,e_p^\lambda$. Now suppose that $T_\lambda\psi=\psi$ for some $\lambda\in\Omega$ and $\psi\in X_1$, then $\psi = \psi_1 e_1^\lambda + \cdots + \psi_p e_p^\lambda$ for some $\psi_i\in\mathbb{C}$, $i=1,\ldots,p$. Substitution of this expression in (2.18) and using (2.23) leads to the following identity:

$$\langle H_\lambda, e_1^\lambda + \cdots + e_p^\lambda\rangle = 1, \tag{2.25}$$

which is called the *characteristic equation.*

Theorem 2.12. $\lambda\in\sigma(A_w)\cap\Omega$ *if and only if* $\langle H_\lambda, e_1^\lambda+\cdots+e_p^\lambda\rangle = 1$. *Every closed vertical strip inside* Ω, $\{\lambda\,|\,\xi_1\leq \operatorname{Re}\lambda\leq\xi_2\}$ *where* $\xi_1\leq\xi_2$, *contains at most finitely many elements of* $\sigma(A_w)$.

A similar result is proved in [8].

From Theorem 2.12 we conclude that there exists an $\varepsilon>0$ that

$$\sigma(A_w)\cap\{\lambda\,|\operatorname{Re}\lambda\geq-\varepsilon\} = \{0\}. \tag{2.26}$$

We end this section with a brief study of the adjoint operator of A_w. In the Appendix we shall prove that the adjoint operator A_w^* defined on

$$X^* = \{\Psi\,|\,\Psi \text{ is a bounded variation function on } [0, c+w] \text{ and } \Psi(c+w)=0\}, \tag{2.27}$$

is given by

$$(A_w^*\Psi)(s) = s\frac{d\Psi}{ds}(s) - x\int_{s-w}^s g(\sigma)\,d\Psi(\sigma), \tag{2.28}$$

having a domain

$$\mathscr{D}(A_w^*)=\left\{\Psi\in X^*\,|\,\Psi \text{ is absolutely continuous and } s\to s\frac{d\Psi(s)}{ds}\in X^*\right\}. \quad (2.29)$$

For $\Psi\in X^*$ and $\phi\in X$ we define

$$\langle\Psi,\phi\rangle=\int_0^{c+w}\phi(s)\,d\Psi(s).$$

The following result is straightforward.

Theorem 2.13. *If Ψ is an eigenvector of A_w^* corresponding to an eigenvalue $\lambda\in\Omega$, then Ψ satisfies*

$$\Psi(s)=-s^{\lambda}\int_s^{c+w}\sigma^{-\lambda-1}\left(\int_{\sigma-w}^{\sigma}xg(\eta)\,d\Psi(\eta)\right)d\sigma. \quad (2.30)$$

If $\lambda\neq 0$ then $\Psi(0)=0$. If $\lambda=0$ then $\Psi(0)<0$ and Ψ is increasing.

Remark 2.2: Notice that for $\Psi\in X^*$ we have $\langle\Psi, 1\rangle=-\Psi(0)$.

Because of the algebraic simplicity of the dominant eigenvalue $\lambda=0$, and Theorem 2.11 we have the following invariant decomposition of X.

$$X=N(A_w)\oplus R(A_w), \quad (2.31)$$

and $N(A_w)=\{\alpha\cdot 1\,|\,\alpha\in\mathbb{C}\}$.

Let P be the projection on $N(A_w)$ corresponding with this decomposition, and let Ψ_w be the eigenvector of A_w^* associated with the dominant eigenvalue $\lambda=0$, and normalized by the condition $\Psi_w(0)=-1$, then

$$P\psi=\langle\Psi_w,\psi\rangle\cdot 1. \quad (2.32)$$

Observe that $P1=\langle\Psi_w, 1\rangle\cdot 1=-\Psi_w(0)\cdot 1=1$.

3. The backward equation

Here we shall examine the initial value problem (1.4)–(1.5), or equivalently (1.7). We obtain existence and uniqueness results by proving that A_w generates a strongly continuous semigroup on X. The method of proof is very similar to the one used by Diekmann et al. in [4], where they investigate the evolution of a size-structured cell population reproducing by fission. (In [4] however, the forward equation is studied.) The idea is to integrate the partial differential equation along its characteristics and to use a variation-of-constants formula, and this will give us the solution as a series.

In the second part of this section, we prove a sort of asymptotic compactness result for the semigroup, which enables us to characterize the behaviour of the solutions for large t.

A_w as defined by (1.8)-(1.9) can be written as the sum of a closed and a bounded operator.

$$A_w = B + C, \tag{3.1}$$

where

$$(B\psi)(s) = -s\frac{d\psi}{ds} - xg(s)\psi(s), \tag{3.2}$$

$$(C\psi)(s) = xg(s)\psi(s+w), \tag{3.3}$$

where the domain $D(B)$ of B is given by

$$\mathscr{D}(B) = \left\{\psi \in X | \psi \text{ is absolutely continuous and } s \to s\frac{d\psi}{ds} \text{ is continuous}\right\}.$$

A straightforward computation shows that B generates a strongly continuous semigroup $S_0(t)$ given by

$$(S_0(t)\psi)(s) = \frac{E(s\,e^{-t})}{E(s)}\psi(s\,e^{-t}), \qquad s \in [0, c+w], \qquad t \geq 0. \tag{3.4}$$

Now a standard perturbation lemma (see e.g. [16]) yields that $A_w = B + C$ generates a strongly continuous semigroup as well.

Theorem 3.1. *A_w generates a strongly continuous semigroup $T_w(t)$.*

One can prove this in the following way.

Consider Cn as the inhomogeneous part of the equation $dn/dt = Bn + Cn$, and apply the variation-of-constants formula. It follows that $n(t)$ has to be a solution of the integral equation

$$n(t) = S_0(t)\phi + \int_0^t S_0(t-\tau)Cn(\tau)\,d\tau. \tag{3.5}$$

The result follows from a standard contraction and continuation argument.

Remark 3.1: In [16] one uses the Hille-Yosida conditions to prove the result.

Now iteration gives us the solution $n(t) = T_w(t)\phi$ as a series

$$T_w(t)\phi = \sum_{n=0}^{\infty} S_n(t)\phi, \qquad t \geq 0, \tag{3.6}$$

where this series converges in the operator norm. $S_n(t)$ is determined by the recurrent relation

$$S_{n+1}(t)\phi = \int_0^t S_0(t-\tau)CS_n(\tau)\phi\,d\tau, \qquad n = 0, 1, 2, \ldots \tag{3.7}$$

For the initial value problem (1.4)-(1.5) this means that there does exist a unique solution in the following sense. Let the operator D on $C(\mathbb{R}^+ x[0, c+w] \to \mathbb{R})$ be given by

$$(Dn)(s, t) = \lim_{h \to 0} \frac{1}{h}(n(s\,e^h, t+h) - n(s, t)),$$

then the initial value problem

$$(Dn)(s,t) = -xg(s)n(s,t) + xg(s)n(s+w,t), \qquad n(s,0) = \phi(s)$$

has a unique solution. In other words the solution $n(s,t) = (T_w(t)\phi)(s)$ is differentiable along the characteristics of the partial differential equation (1.4). If moreover $\phi \in \mathscr{D}(A)$, then the solution is differentiable in s and t separately.

We are especially interested in the behaviour of the solutions $n(s,t)$ for large t. The characterization of this behaviour would be relatively easy if $T_w(t)$ were compact after finite time. (See [4].) Unfortunately $S_0(t)$ which contributes to $T_w(t)$ for all $t \geq 0$, never becomes compact. However, we can prove that this contribution becomes smaller and smaller.

Lemma 3.2. $\|S_0(t)\| \leq C e^{-\gamma x t}$, $t \geq 0$, *for some positive constant C not depending on t.*

Proof: Let $\phi \in X$, $\|\phi\| \leq 1$.

$$|(S_0(t)\phi)(s)| = \left|\frac{E(s e^{-t})}{E(s)}\phi(s e^{-t})\right|$$

$$= \left|\frac{s^{\gamma x} e^{-\gamma x t}\tilde{E}(s e^{-t})}{s^{\gamma x}\tilde{E}(s)}\phi(s e^{-t})\right| \leq C e^{-\gamma x t}$$

where we have used (2.3) and the fact that $\tilde{E}(s)$ is bounded from above and below.

Lemma 3.3. $U(t) := \sum_{n=1}^{\infty} S_n(t)$ *is compact for all* $t \geq 0$.

Proof: A simple calculation shows that

$$(S_1(t)\phi)(s) = x\int_0^t g(s e^{-t+\tau})\frac{E(s e^{-t+\tau})}{E(s)}\frac{E(s e^{-t} + w e^{-\tau})}{E(s e^{-t+\tau} + w)}\phi(s e^{-t} + w e^{-\tau})\, d\tau.$$

One can apply the Arzelà-Ascoli theorem (cf. [18]) to establish the compactness of $S_1(t)$, provided that the derivative of g is bounded. Because of assumption (A) this is indeed the case. Using recurrence relation (3.7), it follows immediately that $S_n(t)$ is compact for all $n \geq 1$. This and the convergence of the series (3.6) with respect to the norm topology yields the result.

Now let

$$\nu := \min\{\varepsilon, \gamma x\}, \tag{3.8}$$

where ε is characterized by (2.26). Let P be the projection on $N(A_w)$, given by (2.32).

Theorem 3.4. *For all* $\eta > 0$ *there exists a constant* $K(\eta) > 0$ *such that*

$$\|T_w(t)\phi - P\phi\| \leq K(\eta)\, e^{-(\nu-\eta)t}\|\phi\| \tag{3.9}$$

for all $\phi \in X$ *and* $t \geq 0$.

Proof: Let $\lambda \in \mathbb{C}$ be such that $\operatorname{Re}\lambda > -\gamma x$, hence $|e^{\lambda t}| > e^{-\gamma x t}$. Obviously $T_w(t) - e^{\lambda t}I = S_0(t) + U(t) - e^{\lambda t}I$, where $U(t) = \sum_{n=1}^{\infty} S_n(t)$. Lemma 3.2 yields that $r(S_0(t)) \leq e^{-\gamma x t}$. Therefore $S_0(t) - e^{\lambda t}I$ is invertible. Thus $T_w(t) - e^{\lambda t}I = (S_0(t) - e^{\lambda t}I)(I + (S_0(t) - e^{\lambda t}I)^{-1}U(t))$. Now from the invertibility of $S_0(t) - e^{\lambda t}I$

and the compactness of $(S_0(t)-e^{\lambda t}I)^{-1}U(t)$ we conclude that

$$e^{\lambda t}\in\sigma(T_w(t))\Rightarrow e^{\lambda t}\in P\sigma(T_w(t)).$$

If $\lambda\in\mathbb{C}$ is such that $\operatorname{Re}\lambda\leqslant-\gamma x$ then $\lambda\in\sigma(A_w)$, according to Theorem 2.5. Now, using the spectral mapping results

$$e^{t\sigma(A_w)}\subseteq\sigma(T_w(t))\quad\text{and}\quad P\sigma(T_w(t))\subseteq e^{tP\sigma(A_w)}\cup\{0\}$$

(see e.g. [16]) we conclude that

$$\sigma(T_w(t))=\{0\}\cup\{e^{t\lambda}|\operatorname{Re}\lambda\leqslant-\gamma x\vee\lambda\in P\sigma(A_w)\cap\Omega\}$$

for all $t\geqslant0$. In Sect. 2 we found the following decomposition of X.

$$X=N(A_w)\oplus R(A_w).$$

Let $\hat{T}_w(t)$ be the restriction of $T_w(t)$ to $R(A_w)$. Then $\hat{T}_w(t)$ defines a strongly continuous semigroup on $R(A_w)$ having infinitesimal generator $\hat{A}_w$, where $\hat{A}_w$ is the restriction of A_w to $R(A_w)$. It follows that $\sigma(\hat{A}_w)=\sigma(A_w)\backslash\{0\}$ and $\sigma(\hat{T}_w(t))=\sigma(T_w(t))\backslash\{1\}$. Therefore $r(\hat{T}_w(t))=e^{-\nu t}$, $t\geqslant0$. Now a result of Hale ([7, Lemma 7.4.2]) yields: for all $\eta>0$ there exists a constant $K(\eta)>0$ such that for all $\phi\in R(A_w)$ and $t\geqslant0$:

$$\|\hat{T}_w(t)\phi\|\leqslant K(\eta)\,e^{-(\nu-\eta)t}\|\phi\|.$$

Let $\phi\in X$, then $T_w(t)\phi=T_w(t)(P\phi+(I-P)\phi)=P\phi+\hat{T}_w(t)(I-P)\phi$. Hence

$$\|T_w(t)\phi-P\phi\|\leqslant K(\eta)\,e^{-(\nu-\eta)t}\|(I-P)\phi\|\leqslant K(\eta)\,e^{-(\nu-\eta)t}\|\phi\|.$$

We can state our main result now.

Corollary 3.5. *Let $n(t,s)$ be the solution of* (1.7), *then*

$$\lim_{t\to\infty}n(t,\cdot)=\int_0^{c+w}\phi(s)\,d\Psi_w(s)\cdot 1$$

in the sup-norm.

Remark 3.2: Notice that $T_w(t)1=1$, $t\geqslant0$. A semigroup satisfying this property is sometimes called a Markov-semigroup. (See e.g. [3]).

4. The guzzler limit

As we did mention in the Introduction Metz and van Batenburg [14] started from a more general model than we did. The forward equation (1.1) was obtained from this general model by a limit transition accounting for very small handling times. They even went one step further by letting the prey weight w tend to zero while letting prey density x tend to ∞, in order to arrive at a rather simple equation. Note that it is necessary to let simultaneously increase the prey density x. (Otherwise there would be nothing left to eat.) In this section we shall give a rigorous justification of this limit transition. We assume that

$$\xi=xw\tag{4.1}$$

and

$$c^* = c + w \tag{4.2}$$

remain constant. It follows from the interpretation that ξ stands for the total prey biomass in the predator's environment, and that c^* denotes the maximum gut content. Although this is not explicit in our notation, the prey capture rate may depend on w. We assume that

$$g(s) \to g_0(s), \qquad w \to 0, \tag{4.3}$$

uniformly in $s \in [0, c^*]$, and g_0 is Lipschitz continuous.

A formal Taylor expansion of the backward Eq. (1.4) around $w = 0$, neglecting higher order terms yields

$$\frac{\partial n}{\partial t}(s, t) \approx -s \frac{\partial n}{\partial s}(s, t) + xwg(s) \frac{\partial n}{\partial s}(s, t).$$

If we let $w \to 0$, we obtain

$$\frac{\partial n}{\partial t}(s, t) = (\xi g_0(s) - s) \frac{\partial n}{\partial s}(s, t), \tag{4.4}$$

where we have used (4.1) and (4.3). We call (4.4) the *limiting backward equation*. The associated forward equation is given by

$$\frac{\partial p}{\partial t}(s, t) = -\frac{\partial}{\partial s}((\xi g_0(s) - s) p(s, t)), \tag{4.5a}$$

supplied with the boundary conditions

$$p(s, t) = 0, \qquad s \leqslant 0 \quad \text{and} \quad s \geqslant c^*. \tag{4.5b}$$

Remark 4.1: We have to add the boundary condition $p(s, t) = 0$ if $s \leqslant 0$, which is not present for $w > 0$, because the characteristic curves associated with (4.5a) are directing inwards at $s = 0$.

An important feature of (4.4) and (4.5a) is the absence of "jump terms": the catch of prey has become a deterministic process. The mantid's satiation now obeys the ordinary differential equation

$$\frac{ds}{dt} = \xi g_0(s) - s. \tag{4.6}$$

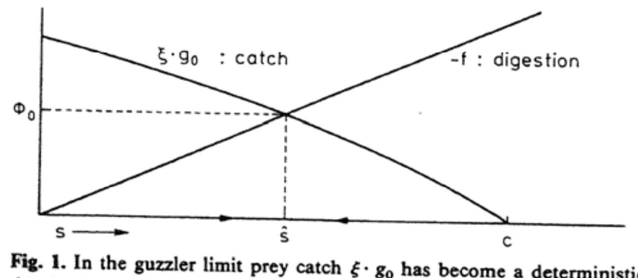

Fig. 1. In the guzzler limit prey catch $\xi \cdot g_0$ has become a deterministic process. The satiation s of the predator tends to $\hat{s}$, and the functional response tends to Φ_0 (see Sect. 7)

Observe that (4.6) has a unique solution because the expression at the right-hand side defines a Lipschitz continuous function because of (4.3). (4.4) is written abstractly as

$$\frac{dn}{dt} = A_0 n, \tag{4.7}$$

where A_0 is given by

$$(A_0\psi)(s) = -(s - \xi g_0(s))\frac{d\psi}{ds} \tag{4.8}$$

having a domain

$$D(A_0) = \left\{ \psi \in X \,|\, \psi \text{ is absolutely continuous and the function } s \mapsto (s - \xi g_0(s))\frac{d\psi(s)}{ds} \text{ is an element of } X \right\}.$$

In this section we shall justify the formal limit transition by showing that (for identical initial data) solutions of $dn/dt = A_w n$, where A_w is given by (1.8)–(1.9) converge to solutions of (4.7) if $w \to 0$. Let

$$q(s) = \xi g_0(s) - s, \qquad 0 \leq s \leq c^*, \tag{4.9}$$

and let $\hat{s}$ be the (unique) solution of $q(\hat{s}) = 0$. (Notice that assumption (A) guarantees that $\hat{s}$ is uniquely determined.) Now let

$$\begin{aligned} Q_\ell(s) &= \int_0^s \frac{d\sigma}{q(\sigma)}, && 0 \leq s < \hat{s}, \\ Q_r(s) &= -\int_s^{c^*} \frac{d\sigma}{q(\sigma)}, && \hat{s} < s \leq s^*. \end{aligned} \tag{4.10}$$

Observe that Q_ℓ, Q_r are well-defined and C^1 on $[0, \hat{s})$ and $(\hat{s}, c^*]$ respectively. The solution of (4.4) supplied with the initial condition $n(s, 0) = \phi(s)$ is given by

$$\begin{aligned} n(s, t) &= \phi(Q_\ell^{-1}(t + Q_\ell(s))), && 0 \leq s < \hat{s}, \\ n(s, t) &= \phi(\hat{s}), && s = \hat{s}, \\ n(s, t) &= \phi(Q_r^{-1}(t + Q_r(s))), && \hat{s} < s \leq c^*, \end{aligned} \tag{4.11}$$

where Q_ℓ^{-1} and Q_r^{-1} denote the inverse functions of Q_ℓ and Q_r respectively. It follows directly that the mapping $\phi \to n(\cdot, t)$, where $n(s, t)$ is given by (4.11), defines a strongly continuous semigroup on X which we denote with $T_0(t)$. The following result is straightforward.

Theorem 4.1. $\lim_{t \to \infty} T_0(t)\phi = \phi(\hat{s}) \cdot 1$, $\phi \in X$.

Theorem 4.2. *For all* $\phi \in X$ *we have* $\lim_{w \to \infty} T_w(t)\phi = T_0(t)\phi$, *and this limit is uniform for* t *in bounded intervals.*

Proof: We use a Trotter–Kato type theorem to establish this result. Let D be the subspace of X consisting of C^1-functions. First we shall prove that for every $f \in D$ there exists an element $\psi \in D$ such that $(I - A_0)\psi = f$. Let $Q(s) := Q_\ell(s)$,

$s < \hat{s}$, $Q(s) := Q_r(s)$, $s > \hat{s}$. It follows immediately that

$$\psi(s) = -e^{Q(s)} \int_{\hat{s}}^{s} \frac{f(\sigma)\, e^{-Q(\sigma)}}{q(\sigma)}\, d\sigma$$

defines a solution of $\psi(s) - q(s)\, d\psi/ds = f(s)$. Suppose that $q(s) = \alpha(\hat{s} - s)$, then

$$\psi(s) = \frac{1}{\alpha|s-\hat{s}|^p} \int_{\hat{s}}^{s} \frac{f(\sigma)|\sigma-\hat{s}|^p}{(\sigma-\hat{s})}\, d\sigma,$$

where $p = 1/\alpha$. If $f \in D$, then

$$f(\sigma) = f(\hat{s}) + (\sigma - \hat{s}) f'(\hat{s}) + o(|\sigma - \hat{s}|)$$

for σ in a neighbourhood of $\hat{s}$. Substituting this in the expression for ψ, we find that for s in a neighbourhood of $\hat{s}$

$$\psi(s) = f(\hat{s}) + \frac{f'(\hat{s})}{\alpha(p+1)}(s-\hat{s}) + o(|s-\hat{s}|).$$

Thus for this special choice of q, it follows that $D \subseteq (I - A_0)D$. The same result can be proved for arbitrary q obtained from (4.9). (Here we have used the Lipschitz-continuity of g.) Moreover, it follows that for all $\psi \in D$ we have $\lim_{w\to 0} \|A_w\psi - A_0\psi\| = 0$, where we have used (4.3). Now the Trotter–Kato theorem (See [16, Chapter 3, Theorem 4.5]) yields the result.

A straightforward computation shows that $\sigma(A_0) = \{\lambda \in \mathbb{C} | \mathrm{Re}\,\lambda \le 0\}$. The eigenvector of A_0 corresponding to the eigenvalue $\lambda = 0$ is I. The adjoint operator A_0^* has the eigenvector

$$\Psi_0(s) = -H(\hat{s} - s) \tag{4.12}$$

corresponding to the eigenvalue $\lambda = 0$. Here H denotes the Heaviside function, i.e. $H(x) = 0$, $x < 0$, $H(x) = 1$, $x > 0$.

5. The forward equation

In Sect. 3 we solved the backward equation (1.4). The solutions were seen to be represented by a strongly continuous semigroup $T_w(t)$. Solutions of the forward equation (1.1) are to be regarded as linear functionals on the space X of continuous functions and they are called weak * solutions (cf. [1]). The idea becomes more clear if we integrate (1.1a) from s to $c + w$. We obtain

$$\frac{\partial P(s,t)}{\partial t} = s\frac{\partial}{\partial s}(P(s,t)) - x \int_{s-w}^{s} g(\sigma)\, dP(\sigma, t), \tag{5.1a}$$

where $P(s,t) = -\int_s^{c+w} p(\sigma, t)$. Now $P(\cdot, t)$ is a bounded variation function normalized by the condition

$$P(s,t) = 0, \qquad s \geq c + w, \tag{5.1b}$$

i.e. $P(\cdot, t) \in X^*$, $t \geq 0$, where X^* is given by (2.27). Equation (5.1) has to be supplemented with the initial condition

$$P(s, 0) = P_0(s), \tag{5.2}$$

where $P_0(s) = -\int_s^{c+w} p_0(\sigma)\, d\sigma$, and $p_0(\cdot)$ is given by (1.1c). (5.1)–(5.2) can be rewritten as

$$\frac{dP}{dt} = A_w^* P, \quad P(0) = P_0, \tag{5.3}$$

where A_w^* is given by (2.28)–(2.29). The solution of (5.3) which we denote by $P(s, t; P_0)$ is characterized by the following relation (see (1.6)):

$$\int_0^{c+w} \phi(s)\, dP(s, t; P_0) = \int_0^{c+w} n(s, t; \phi)\, dP_0(s), \qquad \phi \in X, \tag{5.4}$$

where $n(\cdot, t; \phi) = T_w(t)\phi$ is the solution of the backward equation (1.4).

Up till now we did not mention what topology X^* is endowed with. The sense in which solutions of the integrated forward equation (5.1) should be interpreted, namely being linear functionals on the space of continuous functions X, yields that we should work with the weak $*$ topology on X^*. This topology is characterized if we define what convergence of a sequence in X^* means: let $\{\Psi_n\}_{n\in\mathbb{N}}$ be a sequence in X^*, and let $\Psi \in X^*$. We say that $\Psi_n \to \Psi$ in the weak $*$ topology of X^* if for all $\phi \in X$

$$\int_0^{c+w} \phi(s)\, d\Psi_n(s) \to \int_0^{c+w} \phi(s)\, d\Psi(s), \qquad n \to \infty.$$

(See e.g. [1, 18].)

Now let us return to our forward equation (5.1). Condition (1.2) can be rewritten as

$$\int_0^{c+w} dP_0(s) = 1. \tag{5.5}$$

If P_0 satisfies (5.5), then so does the solution $P(\cdot, t; P_0)$ of (5.3) for all $t \geq 0$. (See (1.2)). Now we shall reformulate Theorem 3.4 in terms of $P(\cdot, t; P_0)$. Let Ψ_w be the eigenvector of A_w^* associated with the dominant eigenvalue 0. (See Sect. 2.)

Corollary 5.1. *Let ν be given by* (3.8) *and let $\eta > 0$ be arbitrary. If P_0 satisfies* (5.5) *then*

$$P(\cdot, t; P_0) = \Psi_w + \mathcal{O}(e^{-(\nu-\eta)t}), \qquad t \to \infty$$

in the weak $*$ topology of X^*.

We define the family of operators $T_w^*(t)$ by

$$T_w^*(t) P_0 = P(\cdot, t; P_0). \tag{5.6}$$

Then $T_w^*(t)$ is the adjoint operator of $T_w(t)$ for all $t \geq 0$, and $T_w^*(t)$ defines a weak $*$ semigroup on X^* (see [1]), i.e.

(i) $T_w^*(t_1) T_w^*(t_2) = T_w^*(t_1 + t_2)$,

(ii) $T_w^*(0)=I$,

(iii) $\lim_{t\downarrow 0}\langle T_w^*(t)\Psi, \phi\rangle=\langle\Psi, \phi\rangle$, for all $\phi\in X$, $\Psi\in X^*$.

A_w^* is the weak * infinitesimal generator of the weak * semigroup $T_w(t)$, i.e.

$$\lim_{t\downarrow 0}\left\langle\frac{T_w^*(t)-I}{t}\Psi, \phi\right\rangle=\langle A_w^*\Psi, \phi\rangle, \quad \text{for all } \phi\in X \text{ and } \Psi\in\mathcal{D}(A_w^*).$$

More details can be found in the book of Butzer and Behrens [1].

Also Theorem 4.1, characterizing the asymptotic behaviour of the limiting backward equation $dn/dt=A_0n$, can be reformulated in terms of bounded variation functions. As above we can associate a weak * semigroup $T_0^*(t)$ with the solutions of the integrated limiting forward equation (4.5).

Corollary 5.2. *Let Ψ_0 be given by* (4.12). *If P_0 satisfies* (5.5) *then $\lim_{t\to\infty} T_0^*(t)P_0=\Psi_0$, with respect to the weak * topology of X^*.*

This means that solutions of the non-integrated limiting forward equation (4.5) converge in distribution-sense to the delta function $\delta(s-\hat{s})$.

From Theorem 4.2 it can be easily seen what happens to solutions of the forward equation (1.1) if the prey weights w become very small.

Corollary 5.3. *Let P_0 satisfy* (5.5). *Then $\lim_{w\to 0} T_w^*(t)P_0=T_0^*(t)P_0$ in the weak * topology of X^*, and this limit is uniform for t in bounded intervals.*

So far, it is not clear whether the result of Corollary 5.3 is also valid for $t\to\infty$. If this is true then it follows from the Corollaries 5.1 and 5.2 that $\Psi_w\to\Psi_0$ if $w\to 0$. This can indeed be proved.

Theorem 5.4. $\lim_{w\to 0}\langle\Psi_w, \phi\rangle=\langle\Psi_0, \phi\rangle$ *for all $\phi\in X$.*

Proof: Let $t>0$ be fixed. Then $T_w^*(t)\Psi_w=\Psi_w$. If $\phi\in X$, $\|\phi\|\leq 1$, then

$$|\langle\Psi_w, \phi\rangle|=\left|\int_0^{c+w}\phi(s)\, d\Psi_w(s)\right|\leq\left|\int_0^{c+w} d\Psi_w(s)\right|=1,$$

where we have used that Ψ_w is increasing, $\Psi_w(0)=-1$, $\Psi_w(c+w)=0$. (See Sect. 2.) Therefore Ψ_w is an element of the closed unit ball in X^*, for all $w>0$. Alaoglu's theorem (see [18, Theorem III.10.2]) states that this unit ball is weak * compact. As a consequence the set $\{\Psi_w|w>0\}$ has at least one limit point within the closed unit ball. Let χ be such a limit point. Then there exists a sequence $\{w_k\}_{k\in\mathbb{N}}$ such that $w_k\to 0$ if $k\to\infty$ and $\Psi_{w_k}\to\chi$, $k\to\infty$ with respect to the weak * topology of X^*. Now

$$\begin{aligned}|\langle T_0^*(t)\chi-\chi, \phi\rangle|&=|\langle T_0^*(t)\chi-T_{w_k}^*(t)\chi+T_{w_k}^*(t)\chi-T_{w_k}^*(t)\Psi_{w_k}+\Psi_{w_k}-\chi, \phi\rangle|\\&=|\langle\chi, T_0(t)\phi-T_{w_k}(t)\phi\rangle+\langle\chi-\Psi_{w_k}, T_{w_k}(t)\phi\rangle+\langle\Psi_{w_k}-\chi, \phi\rangle|\\&\leq|\langle\Psi_{w_k}, T_0(t)\phi-T_{w_k}(t)\phi\rangle|+|\langle\chi-\Psi_{w_k}, T_0(t)\phi-\phi\rangle|\\&\leq\|T_0(t)\phi-T_{w_k}(t)\phi\|+|\langle\chi-\Psi_{w_k}, T_0(t)\phi-\phi\rangle|.\end{aligned}$$

If we let $k\to\infty$, then this expression tends to zero, from which we conclude

$$T_0^*(t)\chi=\chi.$$

Thus $\langle \chi, T_0(t)\phi\rangle = \langle \chi, \phi\rangle$ for all $\phi \in X$, and this relation is valid for all $t \geq 0$. Now letting $t \to \infty$ and using Theorem 4.1 we find

$$\langle \chi, \phi\rangle = \phi(\hat{s})\langle \chi, I\rangle = \lim_{k\to\infty} \phi(\hat{s})\langle \Psi_{w_k}, I\rangle = \phi(\hat{s}).$$

Therefore $\chi = \Psi_0$, and this result is independent of the choice of the sequence $\{w_k\}_{k\in\mathbb{N}}$. This yields the result.

6. The inhomogeneous equation

Here we shall study the inhomogeneous equation (1.11) which we first rewrite in terms of bounded variation functions. Let

$$Z(s, t) = \int_s^{c+w} z(\sigma, t)\, d\sigma.$$

Integration of (1.11a) from s to $c+w$ yields that Z must obey

$$\frac{\partial Z}{\partial t} = s\frac{\partial Z}{\partial s} - x\int_{s-w}^{s} g(\sigma)\, dZ(\sigma, t) + H(s, t), \tag{6.1}$$

where $H(t) = H(t, \cdot)$ is the bounded variation function given by

$$H(t, s) = -x\int_{s-w}^{c+w} g(\sigma)\, dP(\sigma, t) + x\int_0^{c+w} g(\sigma)\, dP(\sigma, t)\cdot\int_s^{c+w} dP(\sigma, t), \tag{6.2}$$

where $P(s, t)$ is the solution of (5.1)–(5.2), i.e. $P(s, t) = (T_w^*(t)P_0)(s)$, and P_0 satisfies (5.5). Obviously

$$\langle H(t), I\rangle = 0. \tag{6.3}$$

From (1.11b)–(1.11c) it follows that (6.1) has to be supplied with the boundary and initial conditions

$$Z(s, t) = 0, \qquad s \geq c+w \tag{6.4a}$$

$$Z(s, 0) = 0, \qquad 0 \leq s \leq c+w. \tag{6.4b}$$

Now we can rewrite (6.1), (6.4) as an abstract Cauchy problem.

$$\frac{dZ}{dt} = A_w^* Z + H(t), \qquad Z(0) = 0. \tag{6.5}$$

Taking the innerproduct of (6.5) with an arbitrary element $\phi \in \mathcal{D}(A_w)$ we find the ordinary differential equation:

$$\frac{d}{dt}\langle Z(t), \phi\rangle = \langle Z(t), A_w\phi\rangle + \langle H(t), \phi\rangle, \qquad \langle Z(0), \phi\rangle = 0. \tag{6.6}$$

The solution of this equation is given by

$$\langle Z(t), \phi\rangle = \int_0^t \langle H(\tau), T_w(t-\tau)\phi\rangle\, d\tau. \tag{6.7}$$

The remainder of this section is devoted to the study of the large-time behaviour of this solution. We need the following result. Let the bounded variation function H_w be given by

$$H_w(s) = -x \int_{s-w}^{c+w} g(\sigma)\, d\Psi_w(\sigma) + x \int_0^{c+w} g(\sigma)\, d\Psi_w(\sigma) \cdot \int_s^{c+w} d\Psi_w(\sigma). \quad (6.8)$$

Lemma 6.1. *Let ν be given by* (3.8). *For all $\eta > 0$ there exists a constant $L(\eta) > 0$ such that for all $\phi \in X$*

$$\left| \int_0^{c+w} \phi(s)\, dH(s,t) - \int_0^{c+w} \phi(s)\, dH_w(s) \right| \leq L(\eta)\, e^{-(\nu-\eta)t} \|\phi\|.$$

Proof:

$$\left| \int_0^{c+w} \phi(s)\, dH(s,t) - \int_0^{c+w} \phi(s)\, dH_w(s) \right|$$

$$= \left| \int_0^{c+w} \phi(s) \cdot \left\{ xg(s-w)\, dP(s-w,t) - x\, dP(s,t) \cdot \int_0^{c+w} g(\sigma)\, dP(\sigma,t) \right\} \right.$$

$$\left. - \int_0^{c+w} \phi(s) \left\{ xg(s-w)\, d\Psi_w(s-w) - x\, d\Psi_w(s) \cdot \int_0^{c+w} g(\sigma)\, d\Psi_w(\sigma) \right\} \right|.$$

Corollary 5.1 states that for every $\phi \in X$

$$\left| \int_0^{c+w} \phi(s)\, dP(s,t) - \int_0^{c+w} \phi(s)\, d\Psi_w(s) \right| \leq K(\eta)\, e^{-(\nu-\eta)t} \|\phi\|,$$

for some positive constant $K(\eta)$. This and the continuity of g yield the result.

Theorem 6.2. *Let for all $\phi \in X$, $\langle Z(t), \phi \rangle$ be defined by* (6.7). *Then*

$$\lim_{t\to\infty} \langle Z(t), \phi \rangle = \langle H_w, -A_w^{-1}(I-P)\phi \rangle,$$

where P is the projection on $N(A_w)$ given by (2.32).

Proof: Let $\phi \in X$ and ψ its projection on $R(A_w)$, i.e. $\psi = (I-P)\phi$. Then

$$\langle Z(t), \phi \rangle = \int_0^t \langle H(\tau), T_w(t-\tau)(P\phi + \psi) \rangle\, d\tau = \int_0^t \langle H(\tau), T_w(t-\tau)\psi \rangle\, d\tau,$$

where we have used that $\langle H(\tau), T_w(t-\tau)P\phi \rangle = \langle H(\tau), \langle \Psi_w, \phi \rangle \cdot 1 \rangle = 0$, because of (6.3). Hence

$$\langle Z(t), \phi \rangle = \int_0^t \langle H_w, T_w(t-\tau)\psi \rangle\, d\tau + \int_0^t \langle H(\tau) - H_w, T_w(t-\tau)\psi \rangle\, d\tau.$$

Let $\eta > 0$. Lemma 6.1 and Theorem 3.4 yield that

$$\left| \int_0^t \langle H(\tau) - H_w, T_w(t-\tau)\psi \rangle\, d\tau \right| \leq \int_0^t L(\eta)\, e^{-(\nu-\eta)\tau} \|T_w(t-\tau)\psi\|\, d\tau$$

$$\leq K(\eta) L(\eta) \int_0^t e^{-(\nu-\eta)\tau} e^{-(\nu-\eta)(t-\tau)} \|\psi\|\, d\tau$$

$$= K(\eta) L(\eta)\, t\, e^{-(\nu-\eta)t} \|\psi\|,$$

Finally

$$\int_0^t \langle H_w, T_w(t-\tau)\psi\rangle\, d\tau = \left\langle H_w, \int_0^t T_w(\tau)\psi\, d\tau \right\rangle \to \langle H_w, -A^{-1}\psi\rangle.$$

if $t\to\infty$, where we have used a standard result from semigroup theory. (See e.g. [16].)

This proves the theorem.

We shall give a more comprehensible reformulation of this result. Let $Z_w \in X^*$ be defined by

$$A_w^* Z_w = -H_w$$
$$\langle Z_w, I\rangle = 0.$$

(Existence of Z_w is guaranteed by the Fredholm Alternative ($\langle H_w, I\rangle = 0$). The second condition guarantees uniqueness.)

Let $Z(s, t)$ be the weak * solution of (6.1), defined by (6.7).

Corollary 6.3. *$Z(s, t) \to Z_w(s)$, $t\to\infty$ in the weak * topology of X^*.*

Remark 6.1: It doesn't make sense to study the inhomogeneous equation that is obtained if one lets $w\to 0$ in (1.11). To understand this, one should remember that the solution z of (1.11) is needed to calculate the variance var(W) of prey catch W per unit of time (see Remark 1.4). However, if $w\to 0$ then the catching process becomes deterministic, yielding that var(W) vanishes, and hence $Z_w(s)\to 0$ if $w\to 0$.

7. The functional response

In this paper we define the functional response $\Phi_w(\xi)$ as the total weight of prey caught per unit of time per predator, where $\xi = xw$ is the density of prey weight in the mantid's environment.

Remark 7.1: Observe that Φ_w is a function of two independent variables, ξ and w. One might also choose x and w or ξ and x. However in practical cases, w can be chosen a constant and the functional reponse is a function of ξ only. In many cases biologists prefer to work with x instead of ξ. In our case ξ is a better choice because later on, we shall take the limit, $w\to 0$, $x\to\infty$ such that $\xi = xw$ remains constant, and we want to examine what happens to the functional response in this case.

$\Phi_w(\xi)$ can be calculated from

$$\Phi_w(\xi) = \xi \int_0^{c+w} g(s)\, d\Psi_w(s), \tag{7.1}$$

where Ψ_w is the (positive) eigenvector of A_w^* corresponding to the dominant eigenvalue $\lambda = 0$, normalized by the condition

$$\langle \Psi_w, I\rangle = \int_0^{c+w} d\Psi_w(s) = 1. \tag{7.2}$$

In experiments, $\Phi_w(\xi)$ is found to be increasing and concave and to have a finite limit for $\xi \to \infty$. We have tried to prove these properties by means of analytical methods, but we have not succeeded so far. However, if we let w tend to zero, keeping $\xi = xw$ and $c^* = c + w$ constant, then we find that $\Psi_0(s) = -H(s - \hat{s})$. From (7.1) we find that for $w = 0$ the functional response $\Phi_0(\xi)$ is given by

$$\Phi_0(\xi) = \xi g_0(\hat{s}) = \hat{s}, \tag{7.3}$$

where $\hat{s}$ is the unique solution of

$$\xi g_0(s) = s \qquad \text{(See Fig. 1).}$$

It is clear that $\hat{s}$ depends on ξ, and a straightforward computation shows that $\Phi_0(\xi)$ is increasing. Moreover $\lim_{\xi\to\infty} \Phi_0(\xi) = c^* = c$.

Example: If $g(s)$ is linear, $g(s) = \gamma(1 - s/c)^+$, the $^+$ meaning that negative values are replaced by zero, then $g_0(s) = \gamma(1 - s/c^*)^+$ and $\Phi_0(\xi) = \hat{s} = \gamma c^* \xi / (c^* + \gamma\xi)$.

The usefulness of $\Phi_0(\xi)$ is demonstrated by the following result, which says that $\Phi_0(\xi)$ approximates $\Phi_w(\xi)$ for small w.

Theorem 7.1. *For all $\xi > 0$ we have*

$$\lim_{w\to 0} \Phi_w(\xi) = \Phi_0(\xi).$$

Proof: (7.1) says that $\Phi_w(\xi) = \xi\langle \Psi_w, g\rangle$. Hence

$$\begin{aligned}|\Phi_w(\xi) - \Phi_0(\xi)| &= \xi|\langle \Psi_w, g\rangle - \langle \Psi_0, g_0\rangle| = \xi|\langle \Psi_w, g - g_0\rangle + \langle \Psi_w - \Psi_0, g_0\rangle| \\ &\leq \xi\|g - g_0\| + \xi|\langle \Psi_w - \Psi_0, g_0\rangle|\end{aligned}$$

and this tends to zero if $w \to 0$ because of (4.3) and Theorem 5.4.

Remark 7.2: It follows from the proof of Theorem 7.1 that

$$\frac{\Phi_w(\xi)}{\xi} \to \frac{\Phi_0(\xi)}{\xi}$$

in the sup-norm.

We were able to compute $\Phi_w(\xi)$ for a special case, namely $c \leq w$. Biologically, this means that the predator's gut can contain at most two preys. After consuming a prey, the predator will not show prey catching behaviour until (part of) the previous meal is digested. Now let

$$\psi_w = \frac{d}{ds}\Psi_w(s). \tag{7.4}$$

Then $s \to s\psi_w(s)$ defines an L_1-function. (2.30) yields

$$\frac{d}{ds}(s\psi_w(s)) - xg(s)\psi_w(s) + xg(s-w)\psi_w(s-w) = 0.$$

If we substitute $\theta(s) = s\psi_w(s)/E(s)$ where E is given by (2.2) in the first two terms we obtain

$$\frac{d\theta}{ds} = -xg(s-w)\cdot\frac{1}{E(s)}\psi_w(s-w).$$

Integration from s to $c+w$ and the fact that $\psi_w(c+w)=0$ yield

$$\theta(s)=x\int_s^{c+w} g(\sigma-w)\,\frac{1}{E(\sigma)}\,\psi_w(\sigma-w)\,d\sigma$$

and we obtain

$$\psi_w(s)=\frac{xE(s)}{s}\int_s^{c+w}\frac{g(\sigma-w)}{E(\sigma)}\,\psi_w(\sigma-w)\,d\sigma. \tag{7.5}$$

From (7.2) we conclude that

$$\int_0^{c+w}\psi_w(s)\,ds=1. \tag{7.6}$$

Observe that (7.4)–(7.6) are also valid if $c>w$. Now the functional response can be computed from

$$\Phi_w(\xi)=\xi\int_0^{c+w} g(\sigma)\psi_w(\sigma)\,d\sigma. \tag{7.7}$$

With respect to $\psi_w(s)$ we can prove the following: $\psi_w(s)$ is continuous on $(0, c+w]$, $\psi_w(s)=\mathcal{O}(s^{\gamma x-1})$, $s\downarrow 0$, $\psi_w\in L_1[0, c+w]$, $\psi_w(s)\geq 0$ a.e. on $[0, c+w]$.

Now let us assume that $c\leq w$, then $E(s)=1$, $c\leq s\leq c+w$. From (7.5) we find that $\psi_w(s)=N.\,E(s)/s$ if $0\leq s\leq w$ for some constant N. For $w\leq s\leq c+w$ we have

$$\psi_w(s)=\frac{x}{s}\int_s^{c+w} g(\sigma-w)N\frac{E(\sigma-w)}{\sigma-w}\,d\sigma=\frac{N}{s}(1-E(s-w)).$$

Now N should be computed from (7.6).

$$\begin{aligned}1&=N\left\{\int_0^w\frac{E(s)}{s}\,ds+\int_w^{c+w}\frac{1-E(s-w)}{s}\,ds\right\}\\&=N\left\{\int_c^{c+w}\frac{ds}{s}+\int_0^c E(s)\left(\frac{1}{s}-\frac{1}{s+w}\right)ds\right\}\\&=N\left\{\log\frac{c+w}{c}+w\int_0^c\frac{E(s)}{s(s+w)}\,ds\right\}.\end{aligned}$$

Now

$$\Phi_w(\xi)=\xi\int_0^{c+w} g(s)\psi_w(s)\,ds=\xi N\int_0^c g(s)\,\frac{E(s)}{s}\,ds=wN(1-E(0))=wN$$

if $\xi>0$, and $\Phi_w(\xi)=0$ if $\xi=0$.

Thus we have proved the following result.

Theorem 7.2. *If $c\leq w$ then*

$$\begin{aligned}&\Phi_w(\xi)=0\quad \text{if } \xi=0\\&\Phi_w(\xi)=w\left(\log\left(\frac{c+w}{c}\right)+w\int_0^c\frac{E(s)}{s(s+w)}\,ds\right)^{-1}\quad \text{if } \xi>0.\end{aligned} \tag{7.8}$$

Observe that $\Phi_w(\xi)$ given by (7.8) is increasing and concave. Moreover

$$\lim_{\xi\to\infty} \Phi_w(\xi) = w/\log\left(\frac{c+w}{c}\right). \tag{7.9}$$

Remark 7.3: From probabilistic considerations it follows that (7.9) is also valid if $c > w$. (See [15].)

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Appendix

In this appendix we shall prove that the adjoint operator A_w^* of A_w is given by

$$(A_w^*\Psi)(s) = s\frac{d\Psi}{ds} - x\int_{s-w}^{s} g(\sigma)\, d\Psi(\sigma) \tag{1}$$

having a domain

$$\mathscr{D}(A_w^*) = \left\{ \Psi\in X^* \,\middle|\, \Psi \text{ is absolutely continuous and } s\to s\frac{d\Psi}{ds}\in X^* \right\}. \tag{2}$$

Let $\lambda\in\mathbb{R}$, $\lambda>0$ be arbitrary. Then

$$\mathscr{D}(A_w^*) = R(((\lambda I - A_w)^{-1})^*). \tag{3}$$

Theorem 2.1 says that $\lambda\psi - A_w\psi = h$ if and only if $\psi - \hat{T}_\lambda\psi = U_\lambda h$. Where $\hat{T}_\lambda$ and U_λ are given by (2.9) and (2.10) respectively. Let X^* be given by (2.27).

Lemma A.1.

$$(U_\lambda^* F)(s) = -\int_s^{c+w} \sigma^{\lambda-1}E(\sigma)\left(\int_\sigma^{c+w} \frac{dF(\eta)}{\eta^\lambda E(\eta)}\right) d\sigma, \quad \textit{for all } F\in X^*.$$

Proof: Let $\phi\in X$ and $F\in X^*$. Then

$$\begin{aligned}\langle F, U_\lambda\phi\rangle &= \int_0^{c+w} (U_\lambda\phi)(s)\, dF(s)\\ &= \int_0^{c+w} \frac{1}{s^\lambda E(s)}\left\{\int_0^s \sigma^{\lambda-1}E(\sigma)\phi(\sigma)\, d\sigma\right\} dF(s)\\ &= \int_0^{c+w} \frac{1}{s^p\tilde{E}(s)}\left\{\int_0^s \sigma^{p-1}\tilde{E}(\sigma)\phi(\sigma)\, d\sigma\right\} dF(s)\end{aligned}$$

where we have used (2.3) and where $p=\lambda+\gamma x$. Because this integral is absolutely convergent, we can apply Fubini's theorem and change order of integration.

$$\begin{aligned}\langle F, U_\lambda\phi\rangle &= \int_0^{c+w} \sigma^{\lambda-1}E(\sigma)\phi(\sigma)\left\{\int_\sigma^{c+w} \frac{dF(s)}{s^\lambda E(s)}\right\} d\sigma,\\ &= \langle G, \phi\rangle,\end{aligned}$$

where

$$G(s) = -\int_s^{c+w} \sigma^{\lambda-1}E(\sigma)\left(\int_\sigma^{c+w} \frac{dF(\eta)}{\eta^\lambda E(\eta)}\right) d\sigma.$$

We also have $\langle F, U_\lambda\phi\rangle = \langle U_\lambda^* F, \phi\rangle$ and therefore $U_\lambda^* F = G$, which yields the result.

Obviously $(\lambda I - A_u)^{-1} = (I - \hat{T}_\lambda)^{-1} U_\lambda$, hence

$$((\lambda I - A_u)^{-1})^* = U_\lambda^*(I - T_\lambda^*)^{-1}. \tag{4}$$

From (3) and (4) it is clear that

$$\mathscr{D}(A_u^*) = R(U_\lambda^*). \tag{5}$$

Theorem A.2. $\mathscr{D}(A_u^*) = V \stackrel{\text{def}}{=} \{\Psi \in X^* | \Psi$ *is absolutely continuous and* $s \mapsto s\, d\Psi(s)/ds$ *is an element of* $X^*\}$.

Proof: (i) Suppose $\Psi \in \mathscr{D}(A_u^*)$, then $\Psi \in R(U_\lambda^*)$. Let $F \in X^*$ be such that $U_\lambda^* F = \Psi$. It follows from Lemma A.1 that

$$\Psi(s) = -\int_s^{c+w} \sigma^{\lambda-1} E(\sigma) \left(\int_\sigma^{c+w} \frac{dF(\eta)}{\eta^\lambda E(\eta)} \right) d\sigma.$$

A straightforward computation shows that Ψ is absolutely continuous on $[\varepsilon, c+w]$ for every $\varepsilon > 0$. Moreover, using Fubini's theorem it follows directly that Ψ is continuous on $[0, c+w]$. This yields that Ψ is absolutely continuous on $[0, c+w]$. Obviously

$$s\Psi'(s) = s^\lambda E(s) \int_s^{c+w} \frac{dF(\eta)}{\eta^\lambda E(\eta)},$$

and the right-hand expression defines an element of X^*. Thus $\mathscr{D}(A_u^*) \subset V$.

(ii) Now suppose that $\Psi \in V$. We shall prove that there exists an element $F \in X^*$ such that $U_\lambda^* F = \Psi$. Let

$$F(s) = -s\frac{d\Psi}{ds} - \int_s^{c+w} (\lambda + xg(\sigma))\, d\Psi(\sigma). \tag{6}$$

Clearly $F \in X^*$. From Lemma A.1 we know that

$$(U_\lambda^* F)(s) = -\int_s^{c+w} \sigma^{\lambda-1} E(\sigma) \left(\int_\sigma^{c+w} \frac{dF(\eta)}{\eta^\lambda E(\eta)} \right) d\sigma.$$

First we compute the expression

$$\begin{aligned} \int_\sigma^{c+w} \frac{dF(\eta)}{\eta^\lambda E(\eta)} &= \frac{F(\eta)}{\eta^\lambda E(\eta)} \Bigg]_\sigma^{c+w} + \int_\sigma^{c+w} F(\eta) \cdot \left(\frac{\lambda + xg(\eta)}{\eta^{\lambda+1} E(\eta)} \right) d\eta \\ &= \frac{-F(\sigma)}{\sigma^\lambda E(\sigma)} + \int_\sigma^{c+w} F(\eta) \left(\frac{\lambda + xg(\eta)}{\eta^{\lambda+1} E(\eta)} \right) d\eta, \qquad \text{if } \sigma > 0. \end{aligned}$$

If we substitute (6), we obtain

$$\begin{aligned} \int_\sigma^{c+w} \frac{dF(\eta)}{\eta^\lambda E(\eta)} = \frac{\Psi'(\sigma)}{\sigma^{\lambda-1} E(\sigma)} &+ \frac{1}{\sigma^\lambda E(\sigma)} \int_\sigma^{c+w} (\lambda + xg(\eta))\, d\Psi(\eta) \\ &- \int_\sigma^{c+w} \eta \Psi'(\eta) \cdot \frac{\lambda + xg(\eta)}{\eta^{\lambda+1} E(\eta)}\, d\eta \\ &- \int_\sigma^{c+w} \frac{\lambda + xg(\eta)}{\eta^{\lambda+1} E(\eta)} \left(\int_\eta^{c+w} (\lambda + xg(\xi))\, d\Psi(\xi) \right) d\eta. \end{aligned} \tag{7}$$

Again, Fubini's theorem says that we may change order of integration in the last expression at the right-hand side

$$\begin{aligned} \int_\sigma^{c+w} \frac{\lambda + xg(\eta)}{\eta^{\lambda+1} E(\eta)} \left(\int_\eta^{c+w} (\lambda + xg(\xi))\, d\Psi(\xi) \right) d\eta &= \int_\sigma^{c+w} (\lambda + xg(\xi)) \left(\int_\sigma^\xi \frac{\lambda + xg(\eta)}{\eta^{\lambda+1} E(\eta)}\, d\eta \right) d\Psi(\xi) \\ = \frac{1}{\sigma^\lambda E(\sigma)} \int_\sigma^{c+w} (\lambda + xg(\xi))\, d\Psi(\xi) &- \int_\sigma^{c+w} \frac{\lambda + xg(\xi)}{\xi^\lambda E(\xi)}\, d\Psi(\xi). \end{aligned}$$

Substitution in (7) yields

$$\int_{\sigma}^{c+w} \frac{dF(\eta)}{\eta^{\lambda}E(\eta)} = \frac{\Psi'(\sigma)}{\sigma^{\lambda-1}E(\sigma)}.$$

Consequently

$$(U_{\lambda}^{*}F)(s) = -\int_{s}^{c+w} \sigma^{\lambda-1}E(\sigma)\frac{\Psi'(\sigma)}{\sigma^{\lambda-1}E(\sigma)}\,d\sigma = \Psi(s).$$

Therefore $\Psi \in R(U_{\lambda}^{*}) = \mathscr{D}(A_{w}^{*})$.

Now suppose that $\phi \in \mathscr{D}(A_{w})$ and $\Psi \in \mathscr{D}(A_{w}^{*})$. Then Ψ is absolutely continuous. Let $\psi(s) = d\Psi/ds$, then ψ is an L_1-function.

$$\begin{aligned}
\langle \Psi, A_w\phi\rangle &= \int_0^{c+w} (A_w\phi)(s)\,d\Psi(s)\\
&= \int_0^{c+w}\left(-s\frac{d\phi}{ds} - xg(s)\phi(s) + xg(s)\phi(s+w)\right)\psi(s)\,ds\\
&= -s\phi(s)\psi(s)\Big]_0^{c+w}\\
&\quad + \int_0^{c+w}\phi(s)\left\{\frac{d}{ds}(s\psi(s)) - xg(s)\psi(s) + xg(s-w)\psi(s-w)\right\}ds\\
&= \int_0^{c+w}\phi(s)\,dG(s),
\end{aligned}$$

where

$$\begin{aligned}
G(s) &= -\int_s^{c+w}\left(\frac{d}{ds}(s\psi(s)) - xg(s)\psi(s) + xg(s-w)\psi(s-w)\right)ds\\
&= s\psi(s) - x\int_{s-w}^{s} g(\sigma)\psi(\sigma)\,d\sigma = s\frac{d\Psi}{ds} - x\int_{s-w}^{s} g(\sigma)\,d\Psi(\sigma).
\end{aligned}$$

Hence $\langle \Psi, A_w\phi\rangle = \langle G, \phi\rangle = \langle A_w^{*}\Psi, \phi\rangle$. Thus

$$(A_w^{*}\Psi)(s) = G(s) = s\frac{d\Psi}{ds} - x\int_{s-w}^{s} g(\sigma)\,d\Psi(\sigma).$$

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Nonlinear Structured Population Dynamics: Some Examples and Open Problems

1. Introduction

So far, we have restricted our attention to time-homogeneous linear models, and we have indicated that in general the solutions of the corresponding linear, autonomous partial differential equations grow or decay exponentially with time.

In general, the circumstances which a population encounters, are not constant but rather are, directly or indirectly, influenced by the population itself. As an example, one might think of the situation where the individuals are all consuming from a common resource which is supplied at a constant rate. If the population density is large, then the individuals have to be content with a smaller meal, and this may affect their behaviour (c.f. section I.2): for instance it may have an effect on the reproductive capacity, resulting in a lower number of births, eventually causing a decrease of the total population number. A similar phenomenon occurs if the individuals of a cell population produce some chemical substance which has an inhibiting effect on mitosis.

The incorporation of some structure is usually indispensable if one tries to build these negative feedback effects into a model in a biological justified manner, since this requires a rather detailed mechanistic description of the functioning of the individuals. The incorporation of feedback phenomena usually leads to nonlinear mathematical equations.

In this chapter we shall consider three nonlinear problems from structured population dynamics. These examples have in common that in all three cases we are able to characterize the asymptotic behaviour of the solutions completely. The model in section 2 describes the growth of a cell population reproducing by unequal fission and living in a chemostat. In this model the dynamics of the substrate and total biomass are described by a well-studied two-dimensional ODE-system. In the *stochastic threshold model* of section 3, also describing the dynamics of a size-structured cell population under chemostat conditions, the nonlinearity disappears after a simple transformation and a scaling of the time. In both these models the concept of omega-limit set, known from dynamical systems theory (c.f. section I.8, in particular theorem 8.1), is used to characterize the large time behaviour of solutions. In section 4 we consider a model describing the bone marrow stem cell population, and there we exploit Lyapunov function techniques (c.f. theorem I.8.2) and monotonicity arguments to prove global stability of equilibria. Although these worked examples might suggest the contrary, the theory of nonlinear structured population models (except for age-dependent models: see Webb (1985)) is still in its infancy. Therefore we have added a section five in which we have tried to explain what kind of difficulties one might have to cope with in the near future.

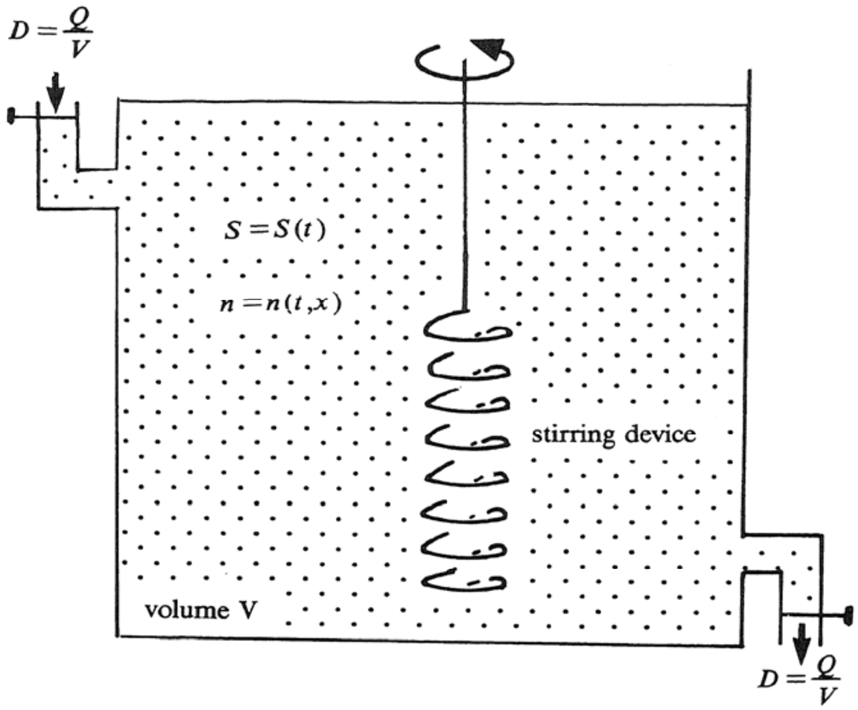
2. A Chemostat Model For a Cell Population Reproducing By Unequal Fission

2.1. *The model*

We consider a population of cells contained in some perfectly stirred tank of volume V. Fresh medium containing substrate essential for maintenance and growth is supplied at a constant rate Q. At the same rate medium containing both cells and unused substrate is removed from the tank. In the literature such a device is called a *chemostat.* The population in a chemostat is called a *continuous culture* (see Herbert, Elsworth & Telling (1956) and Waltman (1983)). The ratio $D = Q / V$ is called the *dilution rate,* and is a control variable of the process. We assume that the environmental influence on the behaviour of individual cells is fully described by the availability of one particular compound of the medium, and we call this compound the limiting substrate. We denote its concentration at time t by $S(t)$. We assume that the internal state of the cells is fully characterized by their size x and that the growth of an individual is at every time instant proportional to its size, and this proportionality factor depends on the substrate concentration S at that particular moment only. More precisely: as long as no wash-out or division occurs (we neglect death) the size of a cell increases according to the differential equation

$$\frac{dx}{dt} = \gamma(S(t))x, \tag{2.1}$$

where γ is some function of S which we assume to be given. We let $b(x)$ be the division rate of a cell with size x, and we assume that the ratio p of the birth size of a daughter cell to the division size of her mother is a random variable described by a smooth probability density function $d(p)$, which is independent of the mother's division size. Obviously $d(p)$ is symmetric



Schematic representation of a chemostat

around $p = \frac{1}{2}$. Moreover

$$\int_0^1 d(p)dp = 1. \tag{2.2}$$

We refer to KOCH & SCHAECHTER (1962) for more biological details.

The model can be described by the nonlinear system:

$$\frac{\partial n}{\partial t}(t,x)+\frac{\partial}{\partial x}(\gamma(S(t))xn(t,x)) = -Dn(t,x) \tag{2.3}$$

$$-b(x)n(t,x)+2\int_0^1 \frac{d(p)}{p}b(\frac{x}{p})n(t,\frac{x}{p})dp,$$

$$\frac{dS}{dt}(t) = D(S^{in}-S(t)) - \frac{1}{\theta}\gamma(S(t))\int_0^\infty xn(t,x)dx, \tag{2.4}$$

where $n(t,x)$ is the unknown size distribution, i.e. $\int_{x_1}^{x_2} n(t,x)$ is the number of individuals per unit of volume with size between x_1 and x_2. By S^{in} we denote the input substrate concentration and θ is the so-called yield constant, i.e. the ratio *biomass of the organisms formed/mass of substrate used.* The last term at the right-hand side of (2.4) denotes the uptake of substrate by the population. Throughout this section we make the following assumptions.

ASSUMPTIONS 2.1

A_γ: $\gamma(S) = \dfrac{k_1 S}{1+k_2 S}$, $S \geqslant 0$, where $k_1, k_2 > 0$.

A_d: $d(p) > 0$, $p \in (\frac{1}{2}-\Delta, \frac{1}{2}+\Delta)$ where $0 < \Delta < \frac{1}{2}$, and $d(p) = 0$ outside this interval, d is symmetric around $p = \frac{1}{2}$, satisfies (2.2) and is continuously differentiable on $(\frac{1}{2}-\Delta, \frac{1}{2}+\Delta)$.

A_b: b is continuous on $[0,1)$, $b(x) = 0$, $x \leqslant a$ and $b(x) > 0$, $x \in (a,1)$, for some $0 < a < 1$, $\lim_{x \uparrow 1} \int_a^x b(\xi) d\xi = \infty$, and the function $x \to \dfrac{b(x)}{\overline{\gamma} x} \cdot \exp[-\int_a^x \dfrac{b(\xi)}{\overline{\gamma}\xi} d\xi]$ is bounded. Here $\overline{\gamma} = \lim_{S \to \infty} \gamma(S) = \dfrac{k_1}{k_2}$.

The function $\gamma(S)$ in A_γ is sometimes called the Monod-Michaelis-Menten function. The assumption A_γ is only made for simplicity: essential is that $\gamma(0) = 0$, γ is strictly increasing and bounded. Condition A_b guarantees among others that all cells have divided before reaching the maximum size $x = 1$. For an interpretation of the last condition in A_b we refer to section 3 of this chapter (see also Heijmans (1984), section 9).

From these assumptions it follows that the minimum possible size is given by $\alpha = a(\frac{1}{2}-\Delta)$, and we have to supply (2.3) - (2.4) with the boundary condition

$$n(t,\alpha) = 0, \quad t \geqslant 0. \tag{2.5}$$

Additionally we impose the initial conditions

$$n(0,x) = n_0(x), \quad \alpha \leqslant x \leqslant 1, \tag{2.6}$$

$$S(0) = S_0. \tag{2.7}$$

In the following subsection we consider the linear system that is obtained if the substrate concentration S is not governed by the differential equation (2.4) but is, instead, kept constant. In subsection 2.3 we discuss a two-dimensional ODE-system related to the model and finally in subsection 2.4 we study the asymptotic behaviour of solutions using techniques from dynamical systems theory.

2.2. Constant food density

A good starting point is an investigation of the linear problem that is obtained if we assume that S and therefore $\gamma = \gamma(S)$ does not depend on time. The analysis of the linear problem that is obtained if we substitute $\gamma(S(t)) = \gamma$ in (2.3) and omit (2.4), proceeds along the lines of chapter III.

Let

$$E(x) = exp(-\int_a^x \frac{b(\xi)}{\gamma\xi} d\xi). \tag{2.8}$$

We make the following compatibility condition on n_0 (c.f. sections III.2 and III.7)

$$n_0(\cdot)/E(\cdot) \in L^1[\alpha,1]. \tag{2.9}$$

Let the Banach space X be defined as

$$X = \{\phi | \phi(\cdot)/E(\cdot) \in L^1[\alpha,1]\}, \tag{2.10}$$

supplied with the norm:

$$\|\phi\|_X = \int_\alpha^1 |\phi(x)| / E(x) dx, \ \phi \in X.$$

Note that X does depend on γ. We define the cone X_+ by:

$$\phi \in X_+ \ \text{ iff } \ \phi(x)/E(x) \geqslant 0, \ \alpha \leqslant x \leqslant 1.$$

Let the closed operator A_γ on X be defined as

$$(A_\gamma\psi)(x) = -\frac{d}{dx}(\gamma x \psi(x)) - D\psi(x) - b(x)\psi(x) +$$

$$+ 2 \int_{\frac{1}{2}-\Delta}^{\frac{1}{2}+\Delta} \frac{d(p)}{p} b(\frac{x}{p})\psi(\frac{x}{p}) dp,$$

with domain

$\mathfrak{D}(A_\gamma) = \{\psi \in X \mid \psi$ is absolutely continuous, the function

$$x \to -\frac{d}{dx}(\gamma x . \psi(x)) - b(x)\psi(x) + 2 \int_{\frac{1}{2}-\Delta}^{\frac{1}{2}+\Delta} \frac{d(p)}{p} b(\frac{x}{p})\psi(\frac{x}{p}) dp \in X$$

and $\psi(\alpha) = 0\}$,

then we can rewrite the linear system as

$$\frac{dn}{dt}(t) = A_\gamma n(t), \ n(0) = n_0,$$

and it can be shown relatively easy that A_γ is the generator of a strongly continuous semigroup $U_\gamma(t)$, $t \geq 0$ on X (c.f. HEIJMANS (1984)). The large time behaviour of solutions follows via a spectral mapping theorem for strongly continuous semigroups (see (5.7)-(5.8) of chapter I) from the spectrum of the generator A_γ. In HEIJMANS (1984) (see also section I.6, chapter II and section III.6) it is shown that A_γ has a strictly dominant eigenvalue λ_d with corresponding eigenvector $n_d \in X_+$ and dual eigenvector $F_d \in X_+^*$ which are quasi-interior and strictly positive respectively (c.f. section I.6). Let the element $F \in X_+^*$ be defined by

$$<F,\phi> = \int_\alpha^1 x\phi(x)dx, \quad \phi \in X. \tag{2.11}$$

Biologically this quantity can be interpreted as the total biomass represented by ϕ. An easy calculation shows

$$<F,A_\gamma\phi> = (\gamma-D)<F,\phi>, \quad \phi \in \mathfrak{D}(A). \tag{2.12}$$

From $<F,n_d>>0$ and $A_\gamma n_d = \lambda_d n_d$ it follows that

$$\lambda_d = \gamma - D, \tag{2.13}$$

and moreover that we can choose $F_d = F$. Observe that F_d does not depend on γ, whereas n_d does: $n_d = n_d(\gamma)$. We normalize n_d by

$$<F,n_d> = 1. \tag{2.14}$$

Now the following result holds (c.f. theorem I.5.3).

THEOREM 2.2. *There is an $\epsilon_0 > 0$ such that for all $\epsilon \in (0,\epsilon_0)$ there exists a constant $M(\epsilon) > 0$ such that for all $n_0 \in X$*

$$\|U_\gamma(t)n_0 - e^{(\gamma-D)t}.<F,n_0>n_d\|_X \leq M(\epsilon)e^{(\gamma-D-\epsilon)t}\|n_0\|_X.$$

We call n_d the stable size distribution. Note that, in contrast with the results of section III.8, a stable size distribution does exist although $g(2x) = 2g(x)$ for all x. This, of course, is due to the fact that d is not a delta function but smooth.

REMARK 2.3. Let $n_0 \in X$ and $n(t) = U_\gamma(t)n_0$, $t \geq 0$. Let $W(t) = <F,n(t)>$, $t \geq 0$, then $W(t)$ satisfies the ordinary differential equation

$$\frac{dW}{dt}(t) = (\gamma-D)W(t), \quad W(0) = <F,n_0>.$$

2.3. An O.D.E. system related to the nonlinear P.D.E.
If S and therefore γ does depend on time t, then remark 2.3 is still valid in the sense that

$$\frac{dW}{dt}(t) = (\gamma(S(t))-D)W(t), \quad t > 0 \tag{2.15}$$

where $W(t) = <F,n(t)>$ and $n(t),S(t)$ is the solution of (2.3)-(2.7) (taking its existence for granted for the moment). Equation (2.4) can be rewritten as

$$\frac{dS}{dt}(t) = D(S^{in}-S(t))-\frac{1}{\theta}\gamma(S(t))W(t), \quad t > 0. \tag{2.16}$$

Additionally we impose the initial conditions

$$W(0) = W_0 \overset{def}{=} <F,n_0>, \tag{2.17}$$

$$S(0) = S_0, \tag{2.18}$$

where n_0 is given by (2.6) and S_0 by (2.7). So now we have obtained a two-dimensional O.D.E. system sometimes called the *Monod equations,* which has been extensively investigated in the literature (e.g. HERBERT et al. (1956), HSU, HUBBELL AND WALTMAN (1977) and WALTMAN (1983)). For the following results we refer to the paper by HSU (1977), where the more general situation that several species are competing for the same limiting substrate, has been considered. First we note that the initial value problem (2.15)-(2.18) is only meaningful if we assume

$$W_0 \geqslant 0, \quad S_0 \geqslant 0.$$

THEOREM 2.4. *If $W_0 > 0$ and $S_0 \geqslant 0$ then the solution $W(t)$, $S(t)$ of (2.15)-(2.18) exists for all $t \geqslant 0$ and is positive and bounded.*

Obviously (2.15)-(2.18) always has the trivial equilibrium $W = 0$, $S = S^{in}$. A nontrivial equilibrium only exists if D is not too large. Let

$$D_{crit} = \frac{k_1 S^{in}}{1+k_2 S^{in}}, \tag{2.19}$$

where k_1, k_2 are given by assumption 2.1. A_γ. If $D < D_{crit}$ then there exists the unique nontrivial equilibrium W^*, S^* given by

$$W^* = \theta(S^{in}-\frac{D}{k_1-k_2 D}), \quad S^* = \frac{D}{k_1-k_2 D}. \tag{2.20}$$

REMARK 2.5. We note that $R(t) = S(t)+\frac{1}{\theta}W(t)$ obeys the initial value problem $\frac{dR}{dt} = D(S^{in}-R)$, $R(0) = S_0 + \frac{1}{\theta}W_0$, and has the solution $R(t) = S^{in}(1-e^{-Dt})+(S_0+\frac{1}{\theta}W_0).e^{-Dt}, t \geqslant 0$. So $\lim_{t\to\infty} R(t) = S^{in}$.

THEOREM 2.6. *Let* $W_0 > 0$ *and* $S_0 \geqslant 0$. *If* $D \geqslant D_{crit}$ *then* $\lim_{t\to\infty} W(t) = 0$, $\lim_{t\to\infty} S(t) = S^{in}$. *If* $D < D_{crit}$ *then* $\lim_{t\to\infty} W(t) = W^*$, $\lim_{t\to\infty} S(t) = S^*$.

REMARK 2.7. Let for $W,S > 0$, $\mathcal{V}$ be defined as

$$\mathcal{V}(S,W) = (S - S^* - S^* \log\frac{S}{S^*}) + \frac{k_1}{\theta(k_1 - k_2 D)}(W - W^* - W^* \log\frac{W}{W^*}).$$

Then

$$\dot{\mathcal{V}}(S,W) = -\frac{(S-S^*)^2}{S(1+k_2 S)}.(-(k_1 - k_2 D)S^{in} - k_2 DS) \leqslant 0$$

if $D \leqslant D_{crit}$ and the global stability of W^*,S^* follows from the invariance principle (see theorem I.8.2).

2.4. The nonlinear PDE problem

Let us return to our original problem (2.3)-(2.7) and assume that $n_0(x) \geqslant 0$, $\alpha \leqslant x \leqslant 1$, and $S_0 \geqslant 0$. The observation that the nonlinear function $\gamma(S(\cdot))$ can be computed à priori from (2.15)-(2.18) makes the proof of existence and uniqueness of solutions a relatively easy one. However, we have to impose a condition on n_0 which is more or less the nonlinear analogue of the compatibility condition, and prescribes the behaviour of n_0 in $x = 1$. A precise statement of this condition, which we shall omit since it is too technical (instead we refer to HEIJMANS (1984)) involves the feeding history of the population during some finite time interval. We think that the fact that we need such a condition is due to our particular approach of the problem and at this point we do not know how to avoid it. Let $Z = \mathbb{R} \times L^1[\alpha,1]$ with norm $\|(S_0,n_0)\|_Z = |S_0| + \|n_0\|_{L^1}$. Let C be the subset of Z consisting of all pairs (S_0,n_0) satisfying $S_0 \geqslant 0$, $n_0(x) \geqslant 0$, $\alpha \leqslant x \leqslant 1$, and this compatibility condition. Let $(S_0,n_0) \in C$. We call $\{(S(t),n(t)) \mid t \geqslant 0\} \subseteq Z$ a solution of (2.3)-(2.7) iff

i) $S(t)$ is differentiable for $t > 0$,
ii) $n(t,x)$ is differentiable along the characteristics of the differential operator $\frac{\partial}{\partial t} + \gamma(S(t))x\frac{\partial}{\partial x}$, $t > 0$, $\alpha < x < 1$,
iii) $S(t),n(t)$ obey (2.3)-(2.7).

The proof of the following result can be found in HEIJMANS (1984).

THEOREM 2.8. *For all* $(S_0,n_0) \in C$ *there exists a unique solution* $\{(S(t),n(t)) \mid t \geqslant 0\} \subseteq C$.

If we want to emphasize the dependence on the initial data we shall write $(S(t,S_0,n_0), n(t,S_0,n_0))$ instead of $(S(t),n(t))$.

One of our main interests is again the large time behaviour of solutions. Like in theorem 2.6 we have to distinguish between two cases. If $D \geqslant D_{crit}$ then the only equilibrium is the trivial equilibrium $(S^{in},0)$. However if $D < D_{crit}$ then there exists a unique nontrivial equilibrium (S^*,n^*) where S^* is given by (2.20) and $n^* = W^* \cdot n_d(D)$, with W^* given by (2.20) and $n_d(D)$ the positive eigenvector of A_D associated with the dominant eigenvalue $\lambda_d = D - D = 0$ of A_D, normalized by (2.14). We can prove the following global stability result (compare theorem 2.6).

THEOREM 2.9. *Let* $(S_0,n_0) \in C, n_0 \neq 0$ *and let* $(S(t),n(t))$ *be the solution of (2.3)-(2.7). If* $D \geqslant D_{crit}$ *then* $\lim_{t\to\infty}(S(t),n(t)) = (S^{in},0)$. *If* $D < D_{crit}$, *then* $\lim_{t\to\infty}(S(t),n(t)) = (S^*,n^*)$.

The rest of this section is concerned with a sketch of the proof of this result. The missing (technical) details can be found in HEIJMANS (1984).

We can associate with solutions of (2.3)-(2.7) a dynamical system $T(t)$ on C in the following standard way.

$$T(t)(S_0,n_0) = (S(t),n(t)),\ t \geqslant 0, (S_0,n_0) \in C.$$

Let us first consider the case $D \geqslant D_{crit}$. Let $(S_0,n_0) \in C$ and $(S(t),n(t)) = T(t)(S_0,n_0)$. Obviously

$$\|(S(t),n(t)) - (S^{in},0)\| = |S(t) - S^{in}| + \|n(t)\|_{L^1}$$

$$\leqslant |S(t) - S^{in}| + \frac{1}{\alpha}\int_{\alpha}^{1} xn(t,x)dx = |S(t) - S^{in}| + \frac{1}{\alpha}W(t)$$

where $W(t) = \langle F,n(t)\rangle$. Now theorem 2.6 yields the result.

From now on we assume that $D < D_{crit}$. Let $(S_0,n_0) \in C$, $n_0 \neq 0$ and let $\Gamma^+(S_0,n_0)$ be the orbit starting in (S_0,n_0) (see section I.8). It can be proved that $\Gamma^+(S_0,n_0)$ is bounded and precompact. Therefore the omega-limit set $\Omega(S_0,n_0)$ is non-empty, compact and invariant, and moreover $(S(t),n(t)) \to \Omega(S_0,n_0)$ as $t \to \infty$. It can also be shown that $\Omega(S_0,n_0) \subseteq C$. Now let $(\Sigma,\nu) \in \Omega(S_0,n_0)$, then we obtain from theorem 2.6 that $\Sigma = S^*$ and $\langle F,\nu\rangle = W^*$. The invariance of $\Omega(S_0,n_0)$ yields that for all $t \geqslant 0$ there exists an element $(\Sigma^{-t},\nu^{-t}) \in \Omega(S_0,n_0)$ such that

$$T(t)(\Sigma^{-t},\nu^{-t}) = (\Sigma,\nu).$$

Since $S(s;\Sigma^{-t},\nu^{-t}) = S^*$ for all $s \geqslant 0$ we have $n(s;\Sigma^{-t},\nu^{-t}) = U_D(s)\nu^{-t}$, $s \geqslant 0$. In words: for initial pairs belonging to the omega-limit set the nonlinear problem reduces to the linear one with $\gamma(S(t))$ replaced by $\gamma(S^*) = D$. From theorem 2.2 we conclude that for $s \geqslant 0$:

$$\|U_D(s)\nu^{-t} - n^*\|_{L^1} \leqslant \|U_D(s)\nu^{-t} - n^*\|_X \leqslant Me^{-\epsilon s}\|\nu_{-t}\|_X \leqslant M'e^{-\epsilon s},$$

where M' can be chosen independently of ν^{-t}, since $\Omega(S_0,n_0)$ is precompact. In these expressions X is the Banach space defined in (2.10), and γ is equal to D. Substituting $s=t$ and using that $U_D(t)\nu^{-t} = \nu$ yields

$$\|\nu-n^*\|_{L^1} \leqslant M'e^{-\epsilon t},$$

and from the fact that this inequality is valid for all $t \geqslant 0$ we conclude that $\nu = n^*$. Thus we have shown that $\Omega(S_0,n_0) = (S^*,n^*)$ and the result follows.

In essence this section shows that the asymptotic behaviour of solutions of the nonlinear PDE agrees with the asymptotic behaviour of solutions of the corresponding nonlinear ODE-system. In the *Final Remarks* of section 5 we mention a class of structured population models which can be reduced to two-dimensional ODE-systems

3. The Stochastic Threshold Model

In the chapters II, III and IV of this thesis we assume that fission can be described by a fixed function $b(x)$ being the probability per unit of time that a cell with size x divides. There is an alternative probabilistic view of the fission process due to Diekmann, Lauwerier, Aldenberg and Metz (1983) which we shall describe below.

Again we consider the model of chapter III, but now we assume that any cell has a predestinated size at which it divides, but these division sizes may differ from one cell to another. In mathematical terms: we assume that there exists a function $\beta(x)$ such that $\int_{x_1}^{x_2}\beta(x)dx$ is the chance of an arbitrary cell to divide at a size between x_1 and x_2, and this chance is completely independent of the time needed to grow from x_1 to x_2. Let $g(x)$ denote the growth rate of cells with size x. As before we denote by a the minimum size at which fission can occur. Let $X(t,x)$ be the size of an individual at time t, if its size at time 0 were x, i.e. $X(t,x) = G^{-1}(t+G(x))$ where $G(x) = \int_{a/2}^{x} \frac{d\xi}{g(\xi)}$.

Now consider a cohort of N_0 cells passing size a at time $t=0$. Then

$$N(t) = N_0(1-\int_a^{X(t,a)} \beta(\xi)d\xi)$$

cells reach time t without having divided (we neglect death for the moment). Therefore the division rate is given by

$$-\frac{1}{N(t)}\frac{dN}{dt}(t) = \frac{\beta(x)}{1-\int_a^x\beta(\xi)d\xi}.g(x) = \delta(x)\cdot g(x),$$

where we have substituted $x=X(t,a)$ and where

$$\delta(x)=\frac{\beta(x)}{1-\int_a^x\beta(\xi)d\xi},$$

and we find the following equation for the size distribution $n(t,x)$:

$$\frac{\partial n}{\partial t}(t,x) + \frac{\partial}{\partial x}(g(x)n(t,x)) \tag{3.1}$$
$$= -g(x)\delta(x)n(t,x)+4g(2x)\delta(2x)n(t,2x).$$

As long as g does not depend on time, we can identify this equation and equation 2.1 of chapter III (with $\mu \equiv 0$) by putting $b(x) = g(x)\delta(x)$. If, however, g does depend on time, e.g. through food supply, then the two equations are essentially different. For a nice and clear exposition of these more or less subtle differences we refer to the paper of DIEKMANN et al (1983).

In this section we examine the case that the cell population lives in a chemostat. We refer to the former section for a description of this device, and we shall use the same notation here.

Let individual growth be given by

$$\frac{dx}{dt} = \gamma(S)g(x). \tag{3.2}$$

DIEKMANN et al (1983) call this the *structural nutrient hypothesis.* The model is described by the following nonlinear system:

$$\frac{\partial n}{\partial t}(t,x) + \frac{\partial}{\partial x}(\gamma(S(t))g(x)n(t,x)) = -Dn(t,x) \tag{3.3}$$
$$-\gamma(S(t))b(x)n(t,x)+ 4\gamma(S(t))b(2x)n(t,2x),$$

$$\frac{dS}{dt}(t) = D(S^{in}-S(t)) - \frac{1}{\theta}\gamma(S(t))\int_{a/2}^{1} g(x)n(t,x)dx, \tag{3.4}$$

where $b(x) = g(x)\delta(x)$. This system still has to be supplemented with boundary and initial conditions

$$n(t,a/2) = 0, \ t \geqslant 0, \tag{3.5}$$

$$n(0,x) = n_0(x), \ a/2 \leqslant x \leqslant 1, \tag{3.6}$$

$$S(0) = S_0. \tag{3.7}$$

Throughout this section we make the following assumptions:

ASSUMPTIONS 3.1.

A_g: g is continuous and strictly positive on $[a/2,1]$ and $g(2x) < 2g(x)$, $x \in [a/2,1/2]$.

A_γ: $\gamma(S) = \dfrac{k_1 S}{1+k_2 S}$, $S \geqslant 0$, where $k_1,k_2 > 0$.

A_β: β is continuous on $[0,1]$, $\beta(x) = 0$, $x \leqslant a$ and $\beta(x) > 0$,

$$x \in (a,1), \int_a^1 \beta(x)dx = 1.$$

From A_β it follows that the function b satisfies:

i) $\lim_{x \uparrow 1} \int_a^x b(\xi)d\xi = \infty$,

ii) The function $x \rightarrow \frac{b(x)}{g(x)} \exp[-\int_a^x \frac{b(\xi)}{g(\xi)} d\xi]$ is bounded.

(Compare this last assumption to assumption 2.1. A_b.) Let

$$E(x) = \exp(-\int_a^x \frac{b(\xi)}{g(\xi)}) = 1 - \int_a^x \beta(\xi)d\xi.$$

As in chapter III we make the following compatibility condition on n_0:

$$n_0(\cdot)/E(\cdot) \in L^1[a/2,1], \tag{3.8}$$

and we look for solutions $S(t), n(t)$ of (3.3)-(3.7) satisfying $n(t,\cdot)/E(\cdot) \in L^1[a/2,1]$ (here the concept of solution is the same as in subsection 2.4).

Let X be the Banach space consisting of all functions ϕ satisfying $\phi(\cdot)/E(\cdot) \in L^1[a/2,1]$ with norm $\|\phi\|_X = \int_{a/2}^1 |\phi(x)|/E(x)dx$. Let C be the subset of $Z = \mathbb{R} \times X$ consisting of all pairs (S_0,n_0) satisfying $S_0 \geqslant 0$, $n_0(x)/E(x) \geqslant 0$ a.e. on $[a/2,1]$ with the norm on Z defined as $\|(S_0,n_0)\|_Z = |S_0| + \|n_0\|_X$. Let the closed operator A with domain $\mathfrak{D}(A) \subseteq X$ be defined as

$$(A\psi)(x) = -\frac{d}{dx}(g(x)\psi(x)) - b(x)\psi(x) + 4b(2x)\psi(2x), \tag{3.9}$$

$$\mathfrak{D}(A) = \{\psi \in X \mid g\psi \text{ is absolutely continuous,} \tag{3.10}$$

$$x \rightarrow -\frac{d}{dx}(g(x)\psi(x)) - b(x)\psi(x) + 4b(2x)\psi(2x) \in X$$

$$\text{and } \psi(a/2) = 0\},$$

then one can show as in chapter III that A is the infinitesimal generator of a strongly continuous, linear semigroup $U(t), t \geqslant 0$ on X. Moreover, from assumption 3.1-A_g it follows that A has an algebraically simple strictly dominant real eigenvalue $\lambda_d > 0$ with positive eigenvector ϕ_d and dual eigenvector F_d, normalized in such a way that

$$\langle F_d, \phi_d \rangle = 1 \text{ and } \int_{a/2}^1 x\phi_d(x) = 1. \tag{3.11}$$

Now for every $\phi \in X$ the asymptotic behaviour of $T(t)\phi$ is given by

$$\|U(t)\phi - e^{\lambda_d t} <F_d,\phi>\phi_d\|_X \leq Me^{(\lambda_d-\epsilon)t}\|\phi\|_X, \quad t \geq 0 \tag{3.12}$$

for some constants $M, \epsilon > 0$.

REMARK 3.2. The main difference with chapter III is that here we are working on L^1 and in chapter III on C. However the results obtained there can be extended without difficulty to the present case because of the boundedness of β. See also HEIJMANS (1984).

We can rewrite (3.3)-(3.5) abstractly as

$$\frac{dn}{dt} = \gamma(S)An - Dn, \tag{3.13}$$

$$\frac{dS}{dt} = D(S^{in} - S) - \frac{1}{\theta}\gamma(S)L(n), \tag{3.14}$$

where the bounded linear functional $L: X \rightarrow \mathbb{R}$ is given by

$$L(\phi) = \int_{a/2}^{1} g(x)\phi(x)dx, \quad \phi \in X.$$

With standard techniques it can be shown that for every $(S_0,n_0) \in C$ the nonlinear system (3.3)-(3.7) has a unique solution $(S(t),n(t)) \in C$. In this section we shall only describe the asymptotic behaviour of solutions. Let for the rest of this section $(S_0,n_0) \in C, n_0 \neq 0$ and $(S(t),n(t)) = T(t)(S_0,n_0)$, $t \geq 0$, where $T(t)$ is the nonlinear semigroup on C associated with solutions of (3.3)-(3.7).

We decompose X in the following way

$$X = \text{span}\{\phi_d\} \oplus \tilde{X},$$

where $\tilde{X} = \Re(\lambda_d I - A)$. For an element $\psi \in X$ we denote by $\tilde{\psi}$ its projection on $\tilde{X}$ with respect to this decomposition. We substitute in (3.13)-(3.14)

$$n(t) = W(t)\phi_d + \tilde{n}(t), \quad t \geq 0, \tag{3.15}$$

where

$$W(t) = <F_d,n(t)> \text{ and } \tilde{n}(t) \in \tilde{X}, t \geq 0.$$

Then

$$\frac{dW}{dt}(t) = (\lambda_d\gamma(S(t)) - D)W(t), \; W(0) = W_0 \overset{def}{=} <F_d,n_0>, \tag{3.16}$$

$$\frac{d\tilde{n}}{dt}(t) = \gamma(S(t))A\tilde{n}(t) - D\tilde{n}(t), \; \tilde{n}(0) = \tilde{n}_0, \tag{3.17}$$

$$\frac{dS}{dt}(t) = D(S^{in} - S(t)) - \frac{1}{\theta}\gamma(S(t)).\{L_d W(t) + L(\tilde{n}(t))\}, \tag{3.18}$$

$$S(0) = S_0,$$

where $L_d = L(\phi_d) > 0$. Now let (compare remark 2.5)

$$R(t) = S(t) + \frac{1}{\theta}\int_{a/2}^{1} xn(t,x)dx,\ t \geqslant 0, \tag{3.19}$$

then $R(t)$ obeys the initial value problem

$$\frac{dR}{dt}(t) = D(S^{in} - R(t)),\ R(0) = R_0 = S_0 + \frac{1}{\theta}\int_{a/2}^{1} xn_0(x)dx,$$

with solution

$$R(t) = S^{in} + (R_0 - S^{in})e^{-Dt}, t \geqslant 0,$$

and this gives us the following relation

$$S(t) + \frac{1}{\theta}W(t) + \frac{1}{\theta}\int_{a/2}^{1} x\tilde{n}(t,x)dx = S^{in} + (R_0 - S^{in})e^{-Dt}, t \geqslant 0. \tag{3.20}$$

For $t \geqslant 0$ we put

$$\tau(t) = \int_0^t \gamma(S(t'))dt'. \tag{3.21}$$

Obviously the solutions $W(t), \tilde{n}(t)$ of (3.16), (3.17) are given by

$$W(t) = e^{-Dt + \lambda_d \tau(t)}.W_0,\ t \geqslant 0, \tag{3.22}$$

$$\tilde{n}(t) = e^{-Dt}U(\tau(t))\tilde{n}_0,\ t \geqslant 0, \tag{3.23}$$

where U is the linear semigroup generated by A. We can prove the following result.

LEMMA 3.3. *$\tau(t) \to \infty$ as $t \to \infty$.*

PROOF. Suppose not. The monotonicity of $\tau(t)$ implies that $\lim_{t\to\infty}\tau(t)$ exists and is finite. Therefore $\lim_{t\to\infty}\gamma(S(t)) = 0$, yielding that $\lim_{t\to\infty}S(t) = 0$. Substitution of (3.22) and (3.23) in (3.20) and letting $t \to \infty$ gives $0 = S^{in}$ which is a contradiction. □

From (3.23), (3.12) and the fact that $<F_d, \tilde{n}_0> = 0$ we obtain

$$\|\tilde{n}(t)\|_X \leqslant Me^{-Dt}.e^{(\lambda_d - \epsilon)\tau(t)}\|\tilde{n}_0\|_X,\ t \geqslant 0, \tag{3.24}$$

and since $-Dt + \lambda_d\tau(t)$ is bounded from above (which follows from (3.20), (3.22), (3.24) and lemma 3.3) we obtain from lemma 3.3 that $\tilde{n}(t) \to 0$ as $t \to \infty$. So, asymptotically we have

$$\int_{a/2}^{1} xn(t,x)dx \sim W(t)\int_{a/2}^{1} x\phi_d(x)dx = W(t),$$

So for large t, $W(t)$ is approximately the total biomass and this explains the use of the notation $W(t)$ in (3.15).

Let $\Gamma^+(S_0,n_0)$ denote the orbit starting in (S_0,n_0), (c.f. section I.8) then obviously $\Gamma^+(S_0,n_0)$ is bounded. From the compactness of the semigroup $U(t)$, $t \geqslant 0$, after finite time, lemma 3.3, and the boundedness of solutions we easily obtain that $\Gamma^+(S_0,n_0)$ is precompact. Therefore (see section I.8) the omega limit set $\Omega(S_0,n_0)$ is nonempty, compact and invariant.

Since the contribution $\tilde{n}(t)$ to the total solution $n(t)$ is relatively small (we have $\|\tilde{n}(t)\|_X \,/\, \|n(t)\|_X \sim e^{-\epsilon\tau(t)}, t \to \infty$) we expect that the asymptotic behaviour of $(S(t),n(t))$ is determined by the corresponding two-dimensional system (3.16), (3.18), with $L(\tilde{n}) = 0$ substituted:

$$\frac{dW}{dt} = (\lambda_d\gamma(S)-D)W(t),\ t \geqslant 0,\ W(0) = W_0, \tag{3.25}$$

$$\frac{dS}{dt} = D(S^{in}-S)-\frac{L_d}{\theta}\gamma(S)W,\ t \geqslant 0,\ S(0) = S_0. \tag{3.26}$$

The system (3.25)-(3.26) always has the trivial equilibrium $(S^{in},0)$. If D is not too large, i.e. $D < D_{crit}$, where

$$D_{crit} = \frac{k_1\lambda_d S^{in}}{1+k_2S^{in}}, \tag{3.27}$$

then (3.25)-(3.26) has the non-trivial equilibrium

$$S^* = \frac{D}{k_1\lambda_d-k_2D},\quad W^* = \frac{\theta\lambda_d}{L_d}\left(S^{in}-\frac{D}{k_1\lambda_d-k_2D}\right). \tag{3.28}$$

We note that for (3.25)-(3.26) a global stability result like theorem 2.6 holds. The corresponding equilibrium of (3.3)-(3.7) is given by (S^*,n^*), where $n^* = W^*\phi_d$. Now we can state our main result. We shall prove this result rigorously whereas DIEKMANN et al (1983) only sketched the idea.

THEOREM 3.4. *Let* $(S_0,n_0) \in C$ *and* $n_0 \neq 0$.
a) *If* $D \geqslant D_{crit}$, *then* $\Omega(S_0,n_0) = (S^{in},0)$.
b) *If* $0<D<D_{crit}$, *then* $\Omega(S_0,n_0) = (S^*,n^*)$.

The precompactness of orbits implies that $(S(t),n(t))$ approaches $\Omega(S_0,n_0)$ as $t \to \infty$ (c.f. theorem I.8.1) and therefore theorem 3.4 characterizes the asymptotic behaviour of solutions. The idea of the proof is that solutions of (3.3)-(3.5) starting in the omega-limit set correspond to solutions of the ODE-system (3.25)-(3.26) of which we know a lot (e.g. WALTMAN (1983)).

PROOF OF THEOREM 3.4.
a) We already noticed that $\tilde{n}(t) \to 0$ as $t \to \infty$ which implies that $\tilde{\nu} = 0$ for

every $(\Sigma,\nu) \in \Omega(S_0,n_0)$. Therefore, if $(\Sigma,\nu) \in \Omega(S_0,n_0)$, then ν is of the form $\nu = \omega\phi_d$ for some $\omega \geqslant 0$ and $\Sigma + \frac{1}{\theta}\omega = S^{in}$, because of (3.20). Hence solutions starting in the omega-limit set behave like solutions of the two-dimensional system (3.25)-(3.26). If $D \geqslant D_{crit}$ then the invariance of $\Omega(S_0,n_0)$ implies that $\Omega(S_0,n_0) = (S^{in},0)$.
b) Let us assume that $D < D_{crit}$. Again the behaviour of a solution starting in $\Omega(S_0,n_0)$ is determined by the two-dimensional system (3.25)-(3.26). Obviously (3.3)-(3.5) has two stationary solutions, namely $(S^{in},0)$ and (S^*,n^*). If we can exclude that $(S^{in},0) \in \Omega(S_0,n_0)$ then the invariance of $\Omega(S_0,n_0)$ implies that $\Omega(S_0,n_0) = (S^*,n^*)$. From (3.22) we conclude that $W(t) > 0$, $t \geqslant 0$ (since $W_0>0$). Since $S^* < S^{in}$, there is an $s > 0$ such that $S^* + s < S^{in}$. Because of (3.20) and $\tilde{n}(t) \to 0, t \to \infty$, we have $S(t) + \frac{1}{\theta}W(t) > S^* + s$ for t sufficiently large, say $t \geqslant t_0$. Suppose $W(t) < \frac{1}{2}\theta s$ for some $t \geqslant t_0$, then $S(t) > S^* + \frac{1}{2}s$, and therefore $\frac{dW}{dt}(t) > (\lambda_d\gamma(S^* + \frac{1}{2}s) - D)W(t) > 0$, so this is only possible if $W(t_0) < \frac{1}{2}\theta s$. We may therefore conclude that $W(t) \geqslant \min\{W(t_0), \frac{1}{2}\theta s\}$, $t \geqslant t_0$ which excludes that $(S^{in},0) \in \Omega(S_0,n_0)$.
□

We note that the shape of the stable size distribution $n^* = W^*\phi_d$ does not depend on the control parameter D. On the contrary the stable size distribution obtained in section two (c.f. theorem 2.9) has a shape which depends on D, and this is an important difference between the two models. Moreover these properties can be compared with experimental observations.

4. The Bone Marrow Stem Cell Population

4.1. *The model*

We consider a cell population reproducing by binary fission. We assume that within the cell cycle two phases can be distinguished: the G-phase or resting phase during which cells just 'sit an wait', and the M-phase or mitotic phase. A cell which has entered the M-phase finally passes into mitosis (unless it dies) and its two daughters enter the G-phase. We assume that all individuals in the G-phase are identical (which means among other things that they have the same chance to enter the M-phase) and we denote their number at time t by $P(t)$. Cells in the M-phase, however, can be distinguished from each other according to some one- dimensional quantity x which we shal call maturity, but which can be anything such as age, or some chemical substance (like DNA) within the cell. We let $n(t,x)$ be the maturity distribution, i.e. $\int_{x_1}^{x_2} n(t,x)dx$ is the number of M-cells with maturity between x_1 and x_2. A cell entering the M-phase has maturity $x=0$. As before we conceive of fission as a stochastic process which can be described by a function $b(x) \geqslant 0$. We assume that the maximum attainable maturity is $x=1$, which is certainly true if

$$\int_0^1 \frac{b(x)}{g(x)} dx = \infty,$$

where g stands for the growth of an M-cell.We assume that cells in the M-phase have a constant death rate $\delta > 0$. The death rate of G-cells is denoted by μ, where $\mu > 0$. Finally we let γ be the transition probability, i.e. the chance per unit of time that cells in the G-phase enter the M-phase, and we assume that γ depends on the total G-population, i.e. $\gamma = \gamma(P(t))$.

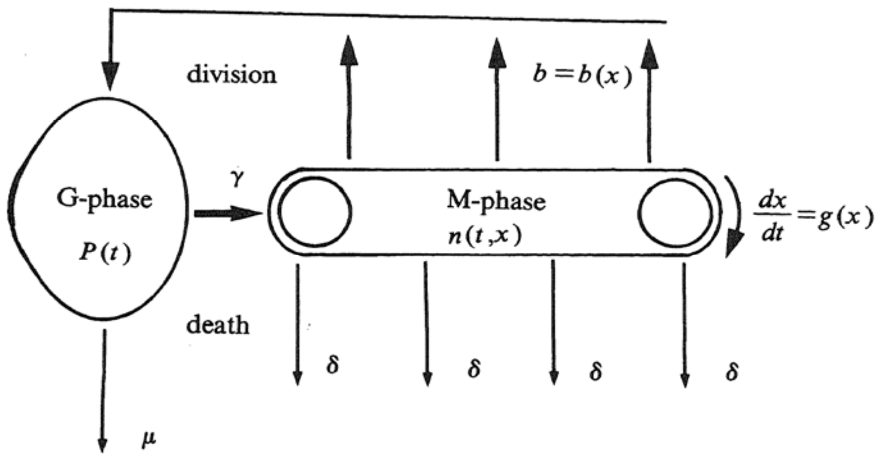


Fig. 1 Schematic representation of the cell cycle

The dynamics of $P(t)$, $n(t,x)$ is governed by the following nonlinear system.

$$\frac{dP}{dt}(t) = -\mu P(t) - \gamma(P(t))P(t) + 2\int_0^1 b(x)n(t,x)dx \tag{4.1}$$

$$\frac{\partial n}{\partial t}(t,x) + \frac{\partial}{\partial x}(g(x)n(t,x)) = -\delta n(t,x) - b(x)n(t,x) \tag{4.2}$$

$$g(0)n(t,0) = \gamma(P(t))P(t) \tag{4.3}$$

$$P(0) = P_0 \geqslant 0 \tag{4.4}$$

$$n(0,x) = n_0(x) \geqslant 0, \ \ 0 \leqslant x \leqslant 1. \tag{4.5}$$

Throughout this section we make the following assumptions on g, b and γ.

ASSUMPTION 4.1

A_g: g is a strictly positive continuous function on $[0,1]$.

A_b: b is nonnegative and continuous on $[0,1)$ and

$$\lim_{x \uparrow 1} \int_a^x b(\xi) d\xi = \infty.$$

A_γ: γ is a Lipschitz-continuous function on $[0,\infty)$, γ is decreasing, and moreover $\lim_{P \to \infty} \gamma(P) = 0$.

KIRK, ORR and FORREST (1970) present a model describing the control of the bone marrow stem cell population, which supplies the circulating blood population with new cells. They assumed that the production process is controlled by some stem cell specific mitotic inhibitor (one of the family of chalones), whose concentation we denote by $C(t)$, and that the mitotic phase is of constant duration. In terms of the model above this last assumption is equivalent to the supposition that all cells divide at reaching maturity $x = 1$. Their first assumption can be build into the model by letting γ depend (in a decreasing manner) on C and assuming that the dynamics of C is described by an O.D.E. KIRK et al. assumed

$$\frac{dC}{dt} = \rho P - \sigma C, \tag{4.6}$$

which describes that the mitotic inhibitor is produced by cells in the G-phase at a rate ρ, and desintegrates at a rate σ. The term $-\mu P$ in (4.1) is due to loss from the G-phase via differentiation into the various channels. KIRK et al (1970) assumed $\delta = 0$ (which is sometimes called the 'normal situation') and solved the system by using analogue computer techniques. The model proposed by KIRK et al (1970) has also been studied by MACKEY (1978,1981) and he calls it the *pluripotential stem cell model.* Mackey extensively examines the situation where the dynamics of C is much faster than the dynamics of P and n, which can be modelled by assuming that the rates ρ and σ in (4.6) are very large. The limiting case is given by $\rho \to \infty$, $\sigma \to \infty$, and in this case (4.6) can be replaced by $C = \frac{\rho}{\sigma} P$ (where only the case that $0 < \lim_{\rho,\sigma \to \infty} \sigma / \rho < \infty$ is interesting), which we might call the *quasi-steady state situation,* and which is one of our modelling assumptions. MACKEY (1978,1981) studies the model (assuming constant duration of the mitotic phase) by standard local methods (linearization around equilibria, examination of the characteristic equation). In this section we shall extend some of his results by exploiting (global) methods from dynamical systems theory.

4.2. Existence and uniqueness of solutions

Let G,E be defined by

$$G(x) = \int_0^x \frac{d\xi}{g(\xi)}, \quad 0 \leq x \leq 1, \tag{4.7}$$

$$E(x) = exp(-\int_0^x \frac{\delta + b(\xi)}{g(\xi)} d\xi), \quad 0 \leq x \leq 1. \tag{4.8}$$

G and E have the same interpretation as in chapters II, III. In addition we define

$$f(P) = P\gamma(P), \quad P \geq 0. \tag{4.9}$$

If $P(t)$ is known for all time $t \geq 0$, then we can express the solution of (4.2)-(4.3) in terms of $P(t)$ in the following way:

$$n(t,x) = f(P(t-G(x)))\frac{E(x)}{g(x)}, \quad 0 \leq x \leq 1, \ t \geq G(x). \tag{4.10}$$

This motivates us to impose the following condition on $n_0(\cdot)$ (see also section 2 and 3 and chapter III):

ASSUMPTION 4.2

$\frac{n_0(\cdot)}{E(\cdot)}$ is a continuous function on [0,1].

Let X be the Banach space consisting of all pairs (ρ,ν) such that $\rho \in \mathbb{R}$, $\nu(\cdot)/E(\cdot) \in C[0,1]$, with norm $\|(\rho,\nu)\| = |\rho| + \sup_{0 \leq x \leq 1} |\nu(x)|/E(x)$. We define the cone X_+ in the following way: $\phi = (\rho,\nu) \in X_+$ if and only if $\rho \geq 0$ and $\nu(x)/E(x) \geq 0$, $0 \leq x \leq 1$. Let $\phi_1 = (\rho_1,\nu_1)$, $\phi_2 = (\rho_2,\nu_2) \in X$, then $\phi_1 \leq \phi_2$ if $\phi_2 - \phi_1 \in X_+$, $\phi_1 < \phi_2$ if $\phi_1 \leq \phi_2$ and $\phi_1 \neq \phi_2$ and finally $\phi_1 \ll \phi_2$ if $\rho_1 < \rho_2$ and $\nu_1(x)/E(x) < \nu_2(x)/E(x)$, $0 \leq x \leq 1$.

We define $X(t,x)$ as the maturity of an individual at time t given that its maturity at time zero was x. Then $X(t,x) = G^{-1}(t+G(x))$ if $-G(x) < t < G(1) - G(x)$.

Let $(P_0,n_0) \in X_+$. Then $(P(t),n(t))$ is called a solution of (4.1)-(4.5) if and only if

(i) $(P(t),n(t)) \in X, \ t \geq 0$,

(ii) $P(t)$ is differentiable for $t > 0$ and

$$\frac{dP}{dt}(t) = -\mu P(t) - f(P(t)) + 2\int_0^1 b(x)n(t,x)dx,$$

(iii) $\lim_{h \to 0} \frac{1}{h} \{g(X(h,x))n(t+h,X(h,x)) - g(x)n(t,x)\}$ exists for all $t > 0$,

$0<x<1$, and

$$\frac{1}{g(x)}\lim_{h\to 0}\frac{1}{h}\{g(X(h,x))n(t+h,X(h,x))-g(x)n(t,x)\}$$
$$= -\delta n(t,x)-b(x)n(t,x) \text{ for } t>0,\ 0<x<1.$$

(iv) $g(0)n(t,0) = f(P(t)),\ t \geqslant 0$

(v) $P(0) = P_0,\ n(0,x) = n_0(x)$ for $0\leqslant x \leqslant 1$.

Condition (iii) says that $n(t,x)$ is differentiable along the characteristics $h \to (t+h, X(h,x))$.

In (4.10) we expressed n in terms of P for $t \geqslant G(x)$. A similar calculation shows that

$$n(t,x) = \frac{E(x)}{g(x)}\frac{g(X(-t,x))}{E(X(-t,x))}n_0(X(-t,x)),\ t \leqslant G(x).$$

Therefore at time $t = G(x)$, where $0<x<1$, $n(t,x)$ is discontinuous in x unless $f(P_0) = g(0)n_0(0)$. We define the subset C of X as

$$C = \{\phi = (\rho,\nu) \in X_+ \mid f(\rho) = g(0)\nu(0)\}.$$

Since the definition of a solution of (4.1)-(4.5) requires that $n(t,\cdot)$ has to be continuous for all $t \geqslant 0$, we should start with initial pairs (P_0,n_0) in C.

If we substitute (4.10) in (4.1) we obtain the integro-differential equation

$$\frac{dP}{dt}(t) = -\mu P(t)-f(P(t))+2\int_0^1 k(x)f(P(t-G(x)))dx \tag{4.11}$$

where

$$k(x) = \frac{b(x)}{g(x)}E(x). \tag{4.12}$$

We can prove the following existence and uniqueness result.

THEOREM 4.3. *Let* $\phi_0=(P_0,n_0)\in C$ *then there exists a unique global solution* $\phi(t)=(P(t),n(t))\in C$ *of the system (4.1)-(4.5).*

One way to obtain this result is to apply standard local existence and uniqueness results for retarded functional differential equations to the integro-differential equation (4.11) (see HALE (1977, chapter II)). Then global existence follows if one can prove boundedness of solutions.

THEOREM 4.4. *Let* $\phi_0 \in C$ *then the solution* $\phi(t)$ *of (4.1)-(4.5) is bounded.*

PROOF. Because of (4.10) it suffices to show that $P(t)$ is bounded. Suppose that $P(t)$ is not bounded. Let $M(t) = P(t)+2N(t)$, where $N(t) = \int_0^1 n(t,x)dx$. Then $\dot{M}(t) = -\mu P(t)-2\delta N(t)+f(P(t))$. Since $P(t)$ is not bounded, we have that $M(t)$ is not bounded, hence there exists an increasing sequence $\{t_n\}$ such that $M(t_n) \to \infty$ and $\dot{M}(t_n) \geqslant 0$. Suppose $\{P(t_n)\}$ is bounded, then $N(t_n) \to \infty$ and therefore $\dot{M}(t_n) < 0$ if n is large enough, since $\delta > 0$. If $P(t_n) \to \infty$ then $\dot{M}(t_n) \leqslant \{\gamma(P(t_n)) - \mu\}P(t_n) \to -\infty$. So this is a contradiction and the theorem is proved. □

We can associate a nonlinear semigroup (or dynamical system) $T(t)$ on C with solutions of (4.1)-(4.5) in the following standard way: let $\phi_0 \in C$ and $\phi(t) \in C, t \geqslant 0$, be the solution of (4.1)-(4.5) (c.f. theorem 4.3), then

$$T(t)\phi_0 = \phi(t), \quad t \geqslant 0.$$

Remark. It is obvious that $T(t)$ is nonnegativity-preserving. Additionally one can easily show that $\phi_0 \in C$, $\phi_0 \neq 0$, implies that $\phi(t) = T(t)\phi_0 >> 0$ for large enough t. This fact shall be exploited in subsection 4.5.

For $\phi_0 \in C$ we denote the orbit startig in ϕ_0 with $\Gamma^+(\phi_0)$ (c.f. section I.8). From (4.10) and theorem 4.4 the following result follows immediately.

Theorem 4.5. *For every* $\phi_0 \in C$ *the orbit* $\Gamma^+(\phi_0)$ *is precompact.*

4.3 Extinction of the population

It is intuitively clear that, if the population becomes extinct, even under the most favourable growth conditions (i.e. $\gamma(P(t)) = \gamma(0)$ for all $t \geqslant 0$), there is no hope for survival under the actual circumstances. Below we shall translate this intuitive idea into rigorous mathematics.

Suppose first that γ does not depend on P but is a constant. Then the problem (4.1)-(4.5) is linear and a straightforward calculation shows that the characteristic equation (c.f. section II) is given by

$$\lambda + \mu + \gamma = 2\gamma \int_0^1 k(x) e^{-\lambda G(x)} dx. \tag{4.13}$$

The easiest way to obtain this is by substitution of $P(t) = e^{\lambda t}$ into equation (4.11). One can easily see that this equation has one real solution λ_d which is strictly dominant, i.e. $\mathrm{Re}\,\lambda < \lambda_d$ for all other solutions λ of (4.13). Since λ_d depends on γ we shall write $\lambda_d(\gamma)$. Now we can state our 'extinction result' which we shall prove below.

Theorem 4.6. *If* $\lambda_d(\gamma(0)) \leqslant 0$, *then for every initial condition* $\phi_0 \in C$ *we have* $T(t)\phi_0 \to 0$ *as* $t \to \infty$.

Remark 4.7. We can reformulate the condition in this theorem. To this end we rewrite (4.13) as

$$\pi_\gamma(\lambda) = \frac{2\gamma}{\lambda + \mu + \gamma} \int_0^1 k(x) e^{-\lambda G(x)} dx = 1.$$

Then $\pi_\gamma(0)$ can be interpreted as the *net reproduction rate,* i.e. the average number of offspring of every newborn cell, if the transition probability is γ. Now $\lambda_d(\gamma(0)) \leq 0$ can be reformulated as $\pi_{\gamma(0)}(0) \leq 1$.

In order to prove theorem 4.6 we shall construct a Lyapunov function (c.f. section I.8) on C. Let

$$r(x) = \frac{2}{E(x)} \int_x^1 k(\xi)d\xi, \quad 0 \leq x \leq 1. \tag{4.14}$$

$r(x)$ can be interpreted as the average number of offspring of a cell in the M-phase with maturity x. If $\delta = 0$ then $r(x) = 2$, $0 \leq x \leq 1$.

We define the continuous function $\mathcal{V}$ on X by:

$$\mathcal{V}(\rho,\nu) = \rho + \int_0^1 r(x)\nu(x)dx, \quad (\rho,\nu) \in X. \tag{4.15}$$

We can give the following intuitive interpretation of $\mathcal{V}$. Obviously a cell in the M-phase has a greater chance to divide eventually than any cell in the G-phase. Since $r(x)$ represents the average number of offspring of an M-cell, the function

$$\nu \rightarrow \int_0^1 r(x)\nu(x)dx$$

represents more or less the average future contribution of the M-population represented by ν to the G-population.

Let $(P_0,n_0) \in C$ and $(P(t),n(t)) = T(t)(P_0,n_0)$, $t \geq 0$, then

$$\frac{d}{dt}\mathcal{V}(P(t),n(t)) = \{(2\theta-1)\gamma(P(t))-\mu\}.P(t), \quad t > 0,$$

where

$$\theta = \int_0^1 k(x)dx.$$

Here we have used that

$$r'(x) = \frac{\delta+b(x)}{g(x)}.r(x) - 2\,\frac{b(x)}{g(x)}.$$

Therefore

$$\dot{\mathcal{V}}(\rho,\nu) = (2\theta-1)f(\rho) - \mu\rho. \tag{4.16}$$

Now suppose that $\lambda_d(\gamma(0)) \leq 0$, then we obtain from (4.13):

$$\mu + \gamma(0) \geq 2\theta\gamma(0) \tag{4.17}$$

and this implies that

$$\dot{\mathcal{V}}(\rho,\nu) = \{(2\theta-1)\gamma(\rho)-\mu\}\rho \leqslant \{(2\theta-1)\gamma(0)-\mu\}.\rho \leqslant 0$$

if $(\rho,\nu) \in C$, which means that V defines a Lyapunov function for $T(t)$ on C if $\lambda_d(\gamma(0)) \leqslant 0$. As in section I.8 let $\mathcal{E}$ be the largest invariant subset of

$$\{(\rho,\nu) \in C \mid \dot{\mathcal{V}}(\rho,\nu) = 0\} = \{(\rho,\nu) \in C \mid \rho = 0\}.$$

Then, because of (4.10) and $f(0) = 0$ we have

$$\mathcal{E} = \{(0,0)\}.$$

Since, moreover, for every $\phi_0 \in C$ the orbit $\Gamma^+(\phi_0)$ is precompact (c.f. theorem 4.5) we obtain from the invariance principle (theorem I.8.2) that $T(t)\phi_0 \to 0$ as $t \to \infty$, and this proves theorem 4.6.

4.4. Existence of a nontrivial equilibrium and monotonicity on a bounded subset

In this and the following subsections we assume that

$$\lambda_d(\gamma(0)) > 0. \tag{4.18}$$

This is equivalent to (c.f. (4.17))

$$\theta > \frac{1}{2} \quad \text{and} \quad \mu+\gamma(0) < 2\theta\gamma(0). \tag{4.19}$$

THEOREM 4.8. *There exists a unique nontrivial equilibrium* $\phi^* = (P^*,n^*)$ *of (4.1)-(4.3) where* P^* *is found from* $\gamma(P^*) = \dfrac{\mu}{2\theta-1}$ *and* $n^*(x) = f(P^*).\dfrac{E(x)}{g(x)}$.

Note that the correctness of this result is guaranteed by (4.19) and properties of γ stated in assumption 4.1- A_γ.

From assumption 4.1- A_γ we conclude that $f(P) = P\gamma(P)$ is increasing for small P. From a biological point of view the following assumption means no restriction of generality.

ASSUMPTION 4.9.
There exists a P_m, $0 < P_m \leqslant \infty$ such that f is increasing on $[0,P_m)$ and nonincreasing on (P_m,∞).

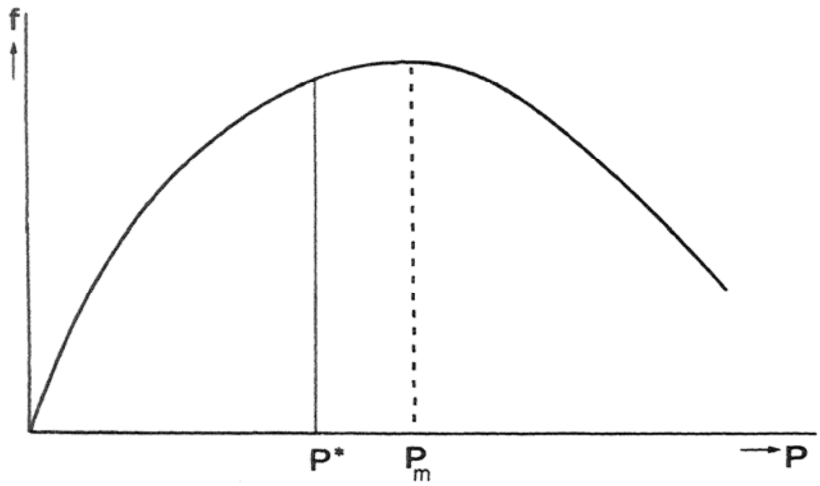
We recall that γ is assumed to be decreasing.

We also make the following

ASSUMPTION 4.10.
$P^* < P_m$.

For future use we note that assumption 4.10 can be reformulated as

$$(2\theta-1)\gamma(P_m) < \mu \tag{4.20}$$



For $P \geqslant 0$ we define $\Phi_P \in C$ by

$$\Phi_P = (P,f(P)\frac{E(\cdot)}{g(\cdot)}). \tag{4.21}$$

Let $P^* < \hat{P} < P_m$ and let the bounded subset $\hat{C} \subseteq C$ be given by

$$\hat{C} = \{\phi \in C \mid \phi << \Phi_{\hat{P}}\}. \tag{4.22}$$

LEMMA 4.11. *$\hat{C}$ is positively invariant under the action of $T(t)$.*

PROOF. Let $\phi_0 \in \hat{C}$ and suppose that $T(t)\phi_0 \notin \hat{C}$ for some $t > 0$. Let $t_0 > 0$ be the smallest t for which this is so, and let $T(t)\phi_0 = (P(t),n(t))$. There are three possibilities:

i) There exists an x, $0 < x \leqslant 1$ such that $\frac{g(x)}{E(x)}\,n(t_0,x) = f(\hat{P})$. Let $h > 0$ be such that $t_0-h > 0$ and $X(-h,x) > 0$, then

$$\frac{g(X(-h,x))}{E(X(-h,x))}\,n(t_0-h,X(-h,x)) = \frac{g(x)}{E(x)}\,n(t_0,x) = f(\hat{P}),$$

as follows directly by integration of (4.2) along characteristics. But this yields $T(t_0-h)\phi_0 \notin \hat{C}$ which is contradictory with the definition of t_0.

ii) Let $g(0)n(t_0,0) = f(\hat{P})$. Then $f(P(t_0)) = f(\hat{P})$ and this implies that $P(t_0) = \hat{P}$.

iii) The third possibility is $P(t_0) = \hat{P}$.

Therefore we may assume $P(t_0) = \hat{P}$. Since $P(t_0-h) < \hat{P}$ for $0 < h \leqslant t_0$

we obtain that $\dot{P}(t_0) \geqslant 0$. On the other hand

$$\dot{P}(t_0) = -\mu\hat{P} - f(\hat{P}) + 2\int_0^1 b(x)n(t_0,x)dx$$

$$< -\mu\hat{P} - f(\hat{P}) + 2\int_0^1 k(x)f(\hat{P})dx$$

$$= (2\theta-1)f(\hat{P}) - \mu\hat{P} < 0$$

because $\hat{P} > P^*$. Thus we have obtained a contradiction, and the result is proved. □

In the sequel we shall need the following technical lemma.

LEMMA 4.12.

a) *Let $\phi \in C$, $\phi >> 0$, then there exists a sequence $\{\phi_k\}_{k\in\mathbb{N}}$ in C such that $0 << \phi_k << \phi$, $k \in \mathbb{N}$ and $\lim_{k\to\infty} \phi_k = \phi$.*

b) *Let $\phi \in \hat{C}$, then there exists a sequence $\{\phi_k\}_{k\in\mathbb{N}}$ in $\hat{C}$ such that $\phi_k >> \phi$, $k \in \mathbb{N}$ and $\lim_{k\to\infty} \phi_k = \phi$.*

PROOF. We shall only prove b). Let $\phi = (\rho,\nu) \in \hat{C}$. Then $\rho < \hat{P}$ and $\frac{g(x)}{E(x)}\nu(x) < f(\hat{P})$, $0 \leqslant x \leqslant 1$. Let $\{a_k\}_{k\in\mathbb{N}}$ be a sequence such that $a_k \to 0$, $k \to \infty$, and for all $k \in \mathbb{N}$, $a_k > 0$ and $\frac{g(x)}{E(x)}\nu(x) + a_k < f(\hat{P})$, $0 \leqslant x \leqslant 1$. Let $\nu_k(x) = \nu(x) + a_k \cdot \frac{E(x)}{g(x)}$ and let $\rho_k \in (\rho,\hat{P})$ be determined by $f(\rho_k) = g(0)\nu_k(0) = g(0)\nu(0) + a_k = f(\rho) + a_k$. Then $\phi_k = (\rho_k,\nu_k)$, $k \in \mathbb{N}$ satisfies the conditions of the lemma. □

Now we shall prove two monotonicity results.

THEOREM 4.13. *$T(t)$ is monotone on $\hat{C}$, i.e. $\phi,\psi \in \hat{C}$ and $\phi \leqslant \psi$ imply that $T(t)\phi \leqslant T(t)\psi$, $t \geqslant 0$.*

PROOF. Let $\phi,\psi \in \hat{C}$, $\phi \leqslant \psi$ and let $\{\psi_k\}_{k\in\mathbb{N}}$ be a sequence in $\hat{C}$ such that $\psi_k \to \psi$, $k \to \infty$ and $\psi_k >> \psi$, $k \in \mathbb{N}$. (cf. lemma 4.12b). We show that $T(t)\phi << T(t)\psi_k$ for all $t > 0$ and $k \in \mathbb{N}$. Suppose there is a $k \in \mathbb{N}$ for which this is not true, and let $t_0 > 0$ be the smallest t for which the strict inequality is not satisfied. Let $T(t)\phi = (P(t;\phi),n(t;\phi))$ and $T(t)\psi_k = (P(t;\psi_k),n(t;\psi_k))$. As in the proof of lemma 4.11 we can show that $P(t_0;\phi) = P(t_0;\psi_k)$. Since $P(t_0-h;\phi) < P(t_0-h;\psi_k)$, $0 < h \leqslant t_0$ we conclude that

$$\dot{P}(t_0;\phi) \geqslant \dot{P}(t_0;\psi_k).$$

This, however, implies that

$$2\int_0^1 b(x)n(t_0,x;\phi)dx \geq 2\int_0^1 b(x)n(t_0,x;\psi_k)dx,$$

which is a contradiction.

Now let $t>0$ be fixed. Then $T(t)\phi << T(t)\psi_k$, $k \in \mathbb{N}$. Letting $k \to \infty$ and using the continuity of $T(t)$ we find

$$T(t)\phi \leq T(t)\psi$$

and the result follows. □

THEOREM 4.14.
a) *If* $0<P<P^*$ *then* $T(t)\Phi_P$ *is increasing in* t.
b) *If* $P^*<P<\hat{P}$ *then* $T(t)\Phi_P$ *is decreasing in* t.

PROOF. We shall only prove a). The proof of b) proceeds along the same lines. Let $0<P<P^*$, and let Q be such that $P<Q<P^*$. Suppose we can show that

$$\Phi_P << T(t)\Phi_Q,\ t>0.$$

Then, letting Q approach P, we obtain

$$\Phi_P \leq T(t)\Phi_P,\ t>0,$$

and now the monotonicity of $T(t)$ gives

$$T(s)\Phi_P \leq T(s)T(t)\Phi_P = T(s+t)\Phi_P,\ s\geq 0,\ t\geq 0$$

which would imply the result. Therefore we shall prove that indeed $\Phi_P << T(t)\Phi_Q$ for all $t>0$. Suppose not. Again let t_0 be the smallest t such that the strict inequality is not satisfied. As in the proof of lemma 4.11 we can show that

$$P = P(t_0;\Phi_Q).$$

Here $T(t)\Phi_Q = (P(t;\Phi_Q),n(t;\Phi_Q))$. Since $P < P(t;\Phi_Q)$, $0 \leq t < t_0$, we obtain

$$\dot{P}(t_0;\Phi_Q) \leq 0.$$

On the other hand

$$\dot{P}(t_0;\Phi_Q) = -\mu P - f(P) + 2\int_0^1 b(x)n(t_0,x;\Phi_Q)dx$$

$$> -\mu P - f(P) + 2\int_0^1 b(x)f(P)\frac{E(x)}{g(x)}dx$$

$$= -\mu P - f(P) + 2\theta f(P) > 0,$$

since $P < P^*$. This is a contradiction, and the result is proved. □

4.5. Global stability of the nontrivial equilibrium

In this section we make again the assumptions 4.9 and 4.10. Let $\hat{P}$ satisfy $P^* < \hat{P} < P_m$ and let the invariant bounded subset $\hat{C}$ be given by (4.22). Now let the initial condition $\phi_0 \neq 0$ be contained in $\hat{C}$. From the remark following theorem 4.4 we obtain that there exists a $t_1 > 0$ such that

$$T(t_1)\phi_0 >> 0.$$

A straightforward calculation shows that there exist $\underline{P}, \overline{P}$ such that

$$0 < \underline{P} \leqslant P^* \leqslant \overline{P} < \hat{P} \text{ and } \Phi_{\underline{P}} \leqslant T(t_1)\phi_0 \leqslant \Phi_{\overline{P}}.$$

Since $\{T(t)\Phi_{\underline{P}}\}_{t \geqslant 0}$ and $\{T(t)\Phi_{\overline{P}}\}_{t \geqslant 0}$ define a precompact increasing and decreasing net respectively we may conclude that both converge to a limit which is a fixed point of $T(t)$. But the only fixed point is ϕ^* and therefore

$$\lim_{t \to \infty} T(t)\Phi_{\underline{P}} = \lim_{t \to \infty} T(t)\Phi_{\overline{P}} = \phi^*.$$

We conclude from $T(t-t_1)\Phi_{\underline{P}} \leqslant T(t)\phi_0 \leqslant T(t-t_1)\Phi_{\overline{P}}$ that

$$\lim_{t \to \infty} T(t)\phi_0 = \phi^*.$$

We have proved the following result.

THEOREM. 4.15. *Let* $\phi_0 \in \hat{C} \setminus \{0\}$, *then* $\lim_{t \to \infty} T(t)\phi_0 = \phi^*$.

Now we can prove our main result.

THEOREM 4.16. *Let* $\phi_0 \in C$, $\phi_0 \neq 0$, *then* $\lim_{t \to \infty} T(t)\phi_0 = \phi^*$.

PROOF.

i) Suppose $P_m = \infty$. Let $\phi_0 \in C$, $\phi_0 \neq 0$. If $f(P) \to \infty$ as $P \to \infty$ then the proof follows from the fact that $\phi_0 \in \hat{C}$ if $\hat{P}$ is large enough. If $f(P) \to f_\infty < \infty$ as $P \to \infty$, then we conclude from (4.10) that for $t > G(1)$ we have $T(t)\phi_0 \in \hat{C}$ if $\hat{P}$ is large enough.

ii) Let $P_m < \infty$. Let $\phi_0 \in C$, $\phi_0 \neq 0$, and $(P(t), n(t)) = T(t)\phi_0$. Suppose $P(t) \geqslant P_m$ for all $t \geqslant t_0$ where $t_0 > 0$. Now let $(\rho,\nu) \in \Omega(\phi_0)$ (i.e. the omega-limit set of ϕ_0: c.f. section I.8) then $\rho \geqslant P_m$, and $\dot{\mathcal{V}}(\rho,\nu) = (2\theta-1)f(\rho) - \mu\rho < 0$ which is impossible. We may conclude that there exists a $t_1 \geqslant G(1)$ such that $P(t_1) < P_m$. Let $\hat{P}$ be such that $P(t_1) < \hat{P} < P_m$ and $-\mu\hat{P} - f(\hat{P}) + 2\theta f(P_m) < 0$ (note that such a $\hat{P}$ exists since $-\mu P_m + (2\theta-1)f(P_m) < 0$). We show that $P(t) < \hat{P}$ for all $t \geqslant t_1$. Suppose not. Let t_2 be the smallest value of t greater than t_1 such that $P(t_2) = \hat{P}$. Then $\dot{P}(t_2) \geqslant 0$. On the other hand

$$\dot{P}(t_2) = -\mu\hat{P} - f(\hat{P}) + 2\int_0^1 b(x)n(t_2,x)dx$$

$$\leqslant -\mu\hat{P} - f(\hat{P}) + 2\int_0^1 k(x) f(P_m)dx$$

$$= -\mu\hat{P} - f(\hat{P}) + 2\theta f(P_m) < 0,$$

which is a contradiction. Therefore $P(t) < \hat{P},\ t \geqslant t_1$, and from (4.10) we conclude that

$$T(t)\phi_0 = (P(t), n(t)) \in \hat{C},\ t \geqslant t_1 + G(1),$$

where $\hat{C}$ is given by (4.22). This proves the result. □

4.6. Final remarks

The results of this section can also be obtained through consideration of the integro-differential equation (4.11). As a matter of fact, (4.11) can be transformed into an integral equation and now application of Fatou's lemma (see e.g. DUNFORD & SCHWARTZ (1958)) also gives the stability result of this section (H.R. Thieme, personal communication). The reason that we did not follow this road is the following. We believe that monotonicity arguments can be applied to many problems from structured population dynamics, including situations for which the mathematical equations cannot be reduced to an an integral equation.

If $\lambda_d(\gamma(0)) \leqslant 0$ (c.f. subsection 4.3) then there does not exist a nontrivial equilibrium and in this case the trivial equilibrium is globally attracting (see theorem 4.6). We obtained this result from the invariance principle. However an easy calculation shows that the monotonicity arguments of the last two subsections can provide an alternative proof.

5. SOME OPEN PROBLEMS IN NONLINEAR STRUCTURED POPULATION DYNAMICS

The examples discussed in section 2-4 of this chapter are quite special. In sections 2 and 3 the problem can in some sense be reduced to a finite-dimensional ODE-system, and the problem of section 4 has some very nice monotonicity properties. This section intends to make clear that in general life is not easy.

Consider a population whose individuals interact with each other indirectly, namely through the environment. The chemostat models described in sections 2 and 3 are nice examples of this situation. Another example is formed by the model describing the control of the bone marrow stem cell population suggested by KIRK et al. (1970) (see also subsection 4.1 of this chapter). Motivated by these examples we write down the following (nonlinear) system of differential equations:

$$\frac{dn}{dt} = A(s)n, \tag{5.1}$$

$$\frac{ds}{dt} = F(s, L(n)). \tag{5.2}$$

Here, for every nonnegative scalar s, $A(s)$ is the infinitesimal generator of a strongly continuous semigroup of linear positive operators on an ordered Banach space X with cone X_+. L denotes a continuous linear positive functional on X and $F:\mathbb{R}_+ \times \mathbb{R}_+ \to \mathbb{R}$ is a smooth function. In order that solutions of (5.2) do not become negative we must impose on F the condition

$$F(0,\ell) \geqslant 0, \quad \ell \geqslant 0.$$

Note that that the examples discussed in sections 2 and 3 and the example discussed in section 4, where $\gamma(P(t))$ in (4.1) and (4.3) is replaced by $\gamma(C(t))$ and the dynamics of $C(t)$ is described by (4.6), fit into this framework.

The system (5.1)-(5.2) can be generalized in several directions, for instance by assuming that s is a vector, or letting L depend on s. However for our purposes the formulation in (5.1)-(5.2) is satisfactory.

We shall now state a number of open questions followed by some remarks which indicate in what direction one might look for an answer: of course these remarks are rather incomplete since they only reflect the personal view of the author.

Existence and uniqueness

Prove existence and uniqueness of solutions for initial data $n(0) = n_0$, $s(0) = s_0$ in some closed subset C of $X_+ \times \mathbb{R}_+$ and show that the solution depends continuously on (n_0, s_0) uniformly for t in compact sets. Associate a nonlinear semigroup (or dynamical system) $T(t)$, $t \geqslant 0$ on C with solutions of (5.1)-(5.2). The ultimate goal is to find verifiable hypotheses about the dependence of A on s, which imply the existence of such a nonlinear semigroup. It might be a good starting point to check under what conditions the semigroups generated by $A(s)$ depend smoothly on s (uniformly in compact t-intervals). Now the Trotter-Kato theorem (see PAZY (1983)) suggests that one should look at the dependence of the resolvent operators $R(\lambda, A(s))$ on s.

Trivial and nontrivial equilibria

Suppose that for every $s \geqslant 0$ the operator $A(s)$ has a strictly dominant algebraïcally simple real eigenvalue $\lambda_d(s)$ with corresponding eigenvector $n_d(s) \in X_+$.

Let $\hat{s}$ be a solution of $F(\hat{s}, 0) = 0$ (in many applications $\hat{s}$ is uniquely determined) then $(0, \hat{s})$ is a trivial equilibrium of (5.1)-(5.2). Let s^* be determined by $\lambda_d(s^*) = 0$ and let $n_d(s^*)$ be normalized by the condition $F(s^*, n_d(s^*)) = 0$, (in practical cases $n_d(s^*)$ is uniquely determined) then

$(n_d(s^*),s^*)$ is a nontrivial equilibrium of (5.1)-(5.2). We note that in a great number of applications (but certainly *not* all) λ_d is a strictly monotone continuous function of s, and in that case there exists a unique nontrivial equilibrium if 0 lies between $\lambda_d(0)$ and $\lambda_d(\infty)$. We note explicitly that the problem of determining all equilibria may sometimes be a very hard one.

Stability, instability and bifurcations

The basic tool for investigating local (in-)stability of an equilibrium is linearization. Let (n^*,s^*) be an equilibrium. We substitute in (5.1)-(5.2)

$$n = n^* + \nu, \; s = s^* + \sigma,$$

and, upon neglecting higher order terms, we obtain

$$\frac{d\nu}{dt} = A(s^*)\nu + \sigma A'(s^*)n^*, \tag{5.3}$$

$$\frac{d\sigma}{dt} = \frac{\partial F}{\partial s}.\sigma + \frac{\partial F}{\partial \ell}.L(\nu), \tag{5.4}$$

where both partial derivatives in (5.4) are evaluated at $(s^*,L(n^*))$. We emphasize that these computations are only formal. Substituting

$$\nu(t) = e^{\lambda t}\nu, \; \sigma(t) = e^{\lambda t}\sigma$$

in (5.3)-(5.4), we obtain the spectral problem

$$(\lambda - A^*)\nu = \sigma B^* n^*, \tag{5.5}$$

$$(\lambda - F_s^*)\sigma = F_\ell^* L(\nu), \tag{5.6}$$

where

$$A^* = A(s^*),\; B^* = A'(s^*),\; F_s^* = \frac{\partial F}{\partial s}(s^*,L(n^*)) \text{ and } F_\ell^* = \frac{\partial F}{\partial \ell}(s^*,L(n^*)).$$

From (5.5) we obtain for $\lambda \notin \sigma(A^*)$

$$\nu = \sigma(\lambda - A^*)^{-1}B^* n^*$$

Substitution into (5.6) gives the *characteristic equation*

$$\lambda - F_s^* = F_\ell^*.L((\lambda - A^*)^{-1}B^* n^*). \tag{5.7}$$

Note that $\lambda \in \sigma(A^*)$ cannot be a solution of (5.7) unless $B^* n^* \in \mathcal{R}(\lambda - A^*)$. Now an important question is: 'How to prove the *principle of linearized stability?* In other words: how to show that the stability of the equilibrium (n^*,s^*) is determined by the position of the complex values λ solving (5.5)-(5.6) (which except for $\sigma(A^*)$ coincide with the roots of (5.7)). We note that in general (5.1)-(5.2) is not semi-linear (see Pazy (1983) for a definition) and therefore the standard theory does not apply.

It is very likely that similar arguments as those used to prove the 'principle of linearized stability' can be used to prove the *Hopf bifurcation theorem* for (5.1)-(5.2) (c.f. Chow & Hale (1983)).

lobal methods

In all the examples discussed in sections 2-4 we managed to prove global ability results for the equilibria. The main techniques came from dynamical 'stems theory, and were *omega-limit sets, Lyapunov functions* and the *variance principle* and last but not least *monotonicity arguments*. An nportant special case is the situation that the semigroup $T(t)$ is monotone on closed invariant subset of the state space C. We refer to HIRSCH (1984) and [ATANO AND HIRSCH (in prep.) for a general exposition on order-preserving stems. We expect that in the future these techniques will play an important le in the study of nonlinear models in structured population dynamics.

nal remarks

If (5.2) is replaced by

$$F(s,L(n)) = 0, \tag{5.8}$$

en we can express s in terms of n, $s = S(n)$, and substitution in (5.1) leads the simpler problem

$$\frac{dn}{dt} = A(S(n))n. \tag{5.9}$$

e call (5.8) a *quasi-steady state assumption,* and the transition from (5.1)-(5.2) (5.9) can be justified, if the dynamics of s is much faster than the dynamics n. In subsection 4.1 a nice example of such a transition is discussed.

The problem studied in section 2 has the nice but also very special property at

$$A(s)^* L = \lambda_d(s)L, \quad s \geqslant 0.$$

this relation is satisfied, then $\ell(t) \stackrel{def}{=} L(n(t))$ obeys

$$\frac{d\ell}{dt} = L(A(s)n) = (A(s)^* L)(n) = \lambda_d(s)L(n) = \lambda_d(s)\ell \tag{5.10}$$

nereas (5.2) can be rewritten as

$$\frac{ds}{dt} = F(s,\ell), \tag{5.11}$$

d the infinite-dimensional system (5.1)-(5.2) has been reduced to the two-nensional system (5.10)-(5.11).

In the literature rather little can be found about nonlinear problems from uctured population dynamics, except for the subclass of age-structured odels, which has been extensively investigated. We refer to CUSHING (1983), (LLENBERG (1982), PRÜSS (1981, 1983a, 1983b) and the book of WEBB (1985) a number of examples. As to size-structured models, we refer to the piring paper by MURPHY (1983) who considers the case that the nonlinearity is contained in the function describing individual growth, and shows how such a problem can be reformulated as an age-dependent problem, if one supplements the original equation with a balance equation whose solution describes size as a function of time and age.

We expect that nonlinear problems from structured population dynamics, such as described by the equations (5.1)-(5.2), can be fitted into the framework of infinite-dimensional dynamical systems. The general theory of infinite-dimensional dynamical systems is growing rapidly nowadays (see HALE, MAGALHAES and OLIVA (1982)) and a further development with a special eye on the application to equations like (5.1)-(5.2) is in our mind desirable.

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SAMENVATTING

DYNAMICA VAN GESTRUCTUREERDE POPULATIES

In dit proefschrift worden een aantal wiskundige modellen uit de populatiedynamica besproken. Uitgangspunt is steeds een biologische populatie waarvan de individuen van elkaar kunnen worden onderscheiden op grond van één of meerdere fysiologische kenmerken zoals leeftijd, gewicht, satiatie enz. Zo'n populatie noemen we gestructureerd.

Het meenemen van een interne structuur schept de mogelijkheid om de dynamica van de populatie te relateren aan de fysiologische processen binnen het individu zoals reproductie, sterfte en groei. Het resultaat is een balansvergelijking (een partiële differentiaalvergelijking) waaruit de frequentieverdeling over de verschillende kenmerk-vectoren op elk tijdstip kan worden berekend, als deze op een eerder tijdstip bekend is. Belangrijke technieken (welke nader worden toegelicht in hoofdstuk I) om oplossingen van lineaire vergelijkingen uit de 'gestructureerde populatiedynamica' te onderzoeken zijn: spectraaltheorie van (positieve) operatoren en de theorie van sterk continue halfgroepen van begrensde (positieve) operatoren. Deze technieken worden toegepast in de hoofdstukken I - IV, waar we varianten van het Bell-Anderson model voor celgroei en -deling bestuderen, en in hoofdstuk V, waar we een model voor het predatiegedrag van een ongewervelde predator bespreken.

In werkelijkheid zullen populaties nooit ongeremd groeien omdat er een wisselwerking bestaat tussen de populatie en haar omgeving: de populatie beïnvloedt haar omgeving welke mede bepalend is voor het gedrag van het individu. Het meenemen van een interne structuur is onontbeerlijk, wil men deze interacties op een biologisch verantwoorde wijze modelleren. De wiskundige problemen die men aldus vindt zijn niet-lineair. In hoofdstuk VI bespreken we een drietal voorbeelden van dergelijke niet-lineaire problemen. In alle drie de gevallen kunnen we een precieze karakterisering van het gedrag van oplossingen geven. In de laatste sectie van hoofdstuk VI laten we zien dat het leven in het algemeen niet zo eenvoudig is.

STELLINGEN
Behorende bij het proefschrift "DYNAMICS OF STRUCTURED POPULATIONS"
door H.J.A.M. HEIJMANS

1. In sectie III.8 van dit proefschrift laten we zien dat corollary III.7.3 ook geldig is als aan voorwaarde B' (sectie III.8) is voldaan. Dit resultaat kan worden uitgebreid tot het geval dat $g(2x) \neq 2g(x)$ voor tenminste één $x \in [\frac{1}{2}a, 1]$ (bedenk dat g continu is).

2. Als de functies g, μ en b in (2.1) van hoofdstuk III van dit proefschrift periodiek van t afhangen, met periode T, en voldoen aan de geijkte gladheids-, begrensdheids- en positiviteitscondities (zie [1]) en als bovendien $g(t,2x) \neq 2g(t,x)$, voor alle t en x, dan wordt het asymptotisch gedrag van oplossingen van

$$\frac{\partial n}{\partial t}(t,x)+\frac{\partial}{\partial x}(g(t,x)n(t,x))=-(\mu(t,x)+b(t,x))n(t,x)+4b(t,2x)n(t,2x)$$

$$n(t,\tfrac{1}{2}a)=0$$

$$n(0,x)=n_0(x)$$

gegeven door: $n(t,x)=e^{\lambda t}.\psi(t,x).(c+e^{-\varepsilon t}O(1)),\ t\to\infty$.

Hierin is $\varepsilon>0$, $\lambda \in \mathbb{R}$ en ψ een continue positieve functie op $\mathbb{R}\times[\frac{1}{2}a,1]$ met periode T. De constante c hangt lineair van de beginconditie n_0 af.

[1] O. Diekmann, H.J.A.M. Heijmans & H.R. Thieme (1985) *On the stability of the cell size distibution, II. Time-periodic developmental rates*, preprint.

3. Beschouw de volgende variant van het celsplitsingsprobleem bestudeerd in hoofdstuk III van dit proefschrift:

$$\frac{\partial n}{\partial t}(t,x)+\frac{\partial}{\partial x}(g(x)n(t,x))=-(\mu(x)+b(x))n(t,x)+4b(2x)n(t-r,2x)$$

$$n(t,\tfrac{1}{2}a)=0$$

$$n(t,x)=n_0(t,x),\ -r\le t\le 0,$$

waarin t,x,g,μ,b,a en n_0 dezelfde betekenis hebben als in hoofdstuk III en waarin $r>0$ een vaste tijdsvertraging is. Laat aan voorwaarden H_g, Hierin is g(r) de groei, en zijn $\mu(r)$ en b(r) resp de kans op doodgaan en splitsen. Als een korrel met straal r splitst dan is z'n straal na splitsing $\rho(r)$. Als men de geeigende aannamen op g,μ,b en ρ maakt, kan men laten zien dat convergentie naar een stabiele verdeling optreedt, hetgeen een sterker resultaat is dan bewezen in [2].

[1] L. Edelstein & Y. Hadar (1983) *A model for pellet size distributions in submerged mycelial cultures*, J. Theor. Biol. 105, 427-452.

[2] M. Chipot & L. Edelstein (1983) *A mathematical theory of size distributions in tissue culture*, J. Math. Biol. 16, 115-130.

6. Zij X een Banachruimte en T een gesloten lineaire operator op X met een niet-lege resolvent verzameling. Laten $\sigma_{Browder}(T)$, $\sigma_{Weyl}(T)$, $\sigma_{Wolf}(T)$ en $\sigma_{Kato}(T)$ resp. het Browder-, Weyl-, Wolf- en Kato-essentiële spectrum zijn (e.g. [1]). Dan is

$$\partial\sigma_{Browder}(T) = \partial\sigma_{Weyl}(T) = \partial\sigma_{Wolf}(T) = \partial\sigma_{Kato}(T).$$

Hierin is ∂V de rand van V als $V\subset\mathbb{C}$.

[1] W. Schappacher (1983) *Asymptotic Behaviour of Linear C_0-Semigroups*, Lecture notes, Quaderni, Bari.

7. Zij H een Hilbertruimte en T een gesloten lineaire operator op H met een een niet-lege resolvent verzameling. Als $\mathbb{C}\backslash\sigma_{Wolf}(T)$ samenhangend is, dan is: $\sigma_{Browder}(T) = \sigma_{Weyl}(T) = \sigma_{Wolf}(T)$.

8. Zij X een Banachruimte en zij $\mathcal{B}(X)$ de Banachalgebra bestaande uit alle begrensde lineaire operatoren op X. Voor een verzameling $\Omega\subset\mathbb{C}$ definiëren we (c.f. [1]): $M_{Browder}(\Omega) = \{T\in\mathcal{B}(X) \mid \sigma_{Browder}(T) \subset \Omega\}$. Op dezelfde wijze worden $M_{Weyl}(\Omega)$, $M_{Wolf}(\Omega)$ en $M_{Kato}(\Omega)$ gedefiniëerd. Als Ω een enkelvoudig samenhangend gebied in $\mathbb{C}$ is, dan is

$$M_{Browder}(\Omega) = M_{Weyl}(\Omega) = M_{Wolf}(\Omega) = M_{Kato}(\Omega)$$

een samenhangende open verzameling in $\mathcal{B}(X)$.

[1] S.T.M. Ackermans (1967) *On the principal extensions of complex sets in a Banachalgebra*, Indag. Math. 29, 146-150.

9. Zij X een Banachruimte en zij $\mathcal{C}(X)$ de ruimte gevormd door alle gesloten lineaire operatoren op X. Zij $\hat{d}$ de afstandsfunctie op $\mathcal{C}(X)$ gedefiniëerd in [1, p.202]. Als $T \in \mathcal{C}(X)$ een Riesz-Schauder operator is (i.e. $0 \notin \sigma_{Browder}(T)$) met dicht domein, dan is er een $\varepsilon>0$ zodat iedere $S \in \mathcal{C}(X)$ welke voldoet aan $\hat{d}(S,T)<\varepsilon$ een Riesz-Schauder operator is.

[1] T.Kato (1976) *Perturbation Theory for Linear Operators*, Springer, Berlin.

10. Zij X een Banachruimte en laat $A \in \mathcal{C}(X)$ de infinitesimale generator van een sterk continue halfgroep $\{T(t;A)\}_{t\geq 0}$ zijn. Zij $\omega_0(T(t;A))$ het type en $\omega_{ess}(T(t;A))$ het essentiële type (zie sectie I.5 van dit proefschrift). Zij $K(X)$ het ideaal der compacte operatoren op X, en laat voor $K \in K(X)$ de sterk continue halfgroep gegenereerd door A+K gegeven zijn door $\{T(t;A+K)\}_{t\geq 0}$. Er geldt:

$$\omega_{ess}(T(t;A)) = \min_{K \in K(X)} \omega_0(T(t;A+K)).$$

11. Zij $f,g \in C^1[0,\infty)$, $f(0) = g(0) = 0$, $f(x)>0$ en $g(x)>0$ als $x>0$. Zij $k \in L^1[0,1]$ een positieve functie en laat voor $x>0$ voldaan zijn aan: $\frac{g(x)}{f(x)} > \int_0^1 k(t)dt$, dan geldt voor elke oplossing $x(t)$ van

$$\dot{x}(t) = -g(x(t)) + \int_0^1 k(s)f(x(t-s))ds,$$

dat $x(t) \to 0$ als $t \to \infty$.

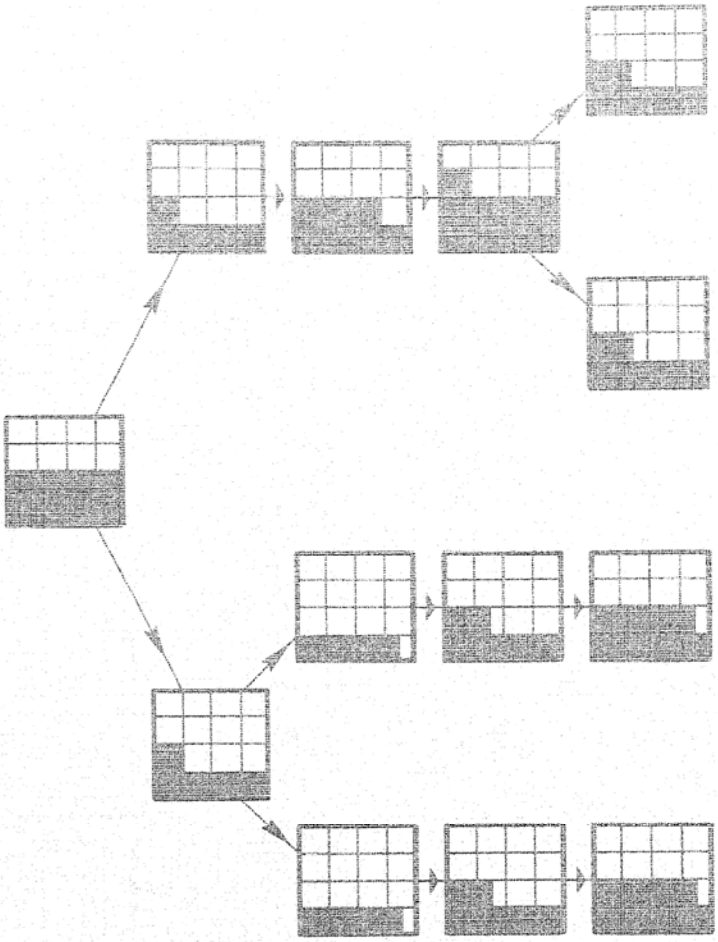
12. De biologie wordt door wiskundigen nog te vaak als grabbelton gebruikt.

13. De mensheid is slim genoeg om ingenieuze wapensystemen te bedenken en dom genoeg om ze te maken.

14. Het lijkt zinvol om na te gaan of een verdere verlaging van de minimumuitkeringen kan worden voorkomen door invoering van shirt-reclame voor de leden van het kabinet.

H.J.A.M. HEIJMANS: DYNAMICS OF STRUCTURED POPULATIONS

DYNAMICS OF STRUCTURED POPULATIONS



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