Aspects of Positivity in Functional Analysis
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MARKOV SEMIGROUPS AND STRUCTURED POPULATION DYNAMICS

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Abstract: An irreducible Markov semigroup of which the essential type is strictly negative, has a prescribed asymptotic behaviour. For a class of structured population models, where the number of individuals is conserved, one can associate a Markov semigroup with the corresponding backward equation, estimate the essential type and establish irreducibility, and thus characterize the large time behaviour of the solutions to the problem.

Introduction

In models from structured population dynamics the basic unit is the individual, and knowledge about individual behaviour as a function of some particular i-state (= individual state e. g. age) must be translated into balance equations for the distribution over all possible i-states as a function of time: often this amounts to a first order PDE with non-local arguments and/or boundary conditions (see [11]). Since in a population model we are dealing with numbers of individuals, the corresponding semigroup is positivity preserving: if moreover the number of individuals in the population is constant then solutions of the associated *backward equation* (see section 2) can be described in terms of a Markov semigroup (e. g. section 1 for a definition). Using known results about the peripheral point spectrum of the generator of a Markov semigroup (under some additional assumptions) one can characterize their large time behaviour.

In section 1 we shall describe the abstract results, which we apply in section 2 to a particular example. In section 3 we indicate how these results can be extended to more general models.

1. Preliminaries

Let E be a Banach lattice and $\{T(t)\}_{t\geq 0}$ a strongly continuous (or C_0-)semigroup of bounded linear operators on E with infinitesimal generator A. By $\mathcal{D}(A)$ we denote the domain of A. The *spectral bound* $s(A)$ is defined by

$$s(A) = \sup\{\mathrm{Re}\,\lambda : \lambda \in \sigma(A)\} \quad \text{if} \quad \sigma(A) \neq \emptyset$$
$$= -\infty \quad \text{if} \quad \sigma(A) \neq \emptyset .$$

Here $\sigma(A)$ is the spectrum of A. By $\sigma_+(A)$ we denote the *peripheral spectrum* of A:

$$\sigma_+(A) = \{\lambda \in \sigma(A) : \mathrm{Re}\lambda = s(A)\}$$

whereas this set is empty if $s(A) = -\infty$. The *(Browder) essential spectrum* $\sigma_{ess}(A)$ is the set consisting of all $\lambda \in \sigma(A)$ which are not a pole of $R(\cdot, A)$ of finite algebraic multiplicity. Here $R(\lambda, A) = (\lambda I - A)^{-1}$, $\lambda \in \mathbb{C} \setminus \sigma(A)$, denotes the resolvent operator.

The *type* $\omega_0(T(t))$ of the semigroup $\{T(t)\}_{t\geq 0}$ can be defined as

$$\omega_0(T(t)) = \lim_{t\to\infty} \frac{1}{t} \log \|T(t)\| . \tag{1.1}$$

In an analogous way we can define the *essential type* $\omega_{ess}(T(t))$, but in order to do so, we need some further terminology.

Let $\mathcal{B}(E)$ be the algebra of bounded linear operators on E. For $L \in \mathcal{B}(E)$ we denote by $|L|_\alpha$ its *(Kuratowski) measure of noncompactness* (e.g. [12, 15]). Then $|\cdot|_\alpha$ defines a seminorm on $\mathcal{B}(E)$ with, among others, the following properties:

$$|L|_\alpha \leq \|L\| , \ L \in \mathcal{B}(E) \tag{1.2.a}$$

$$|LK|_\alpha \leq |L|_\alpha |K|_\alpha , \ L, K \in \mathcal{B}(E) \tag{1.2.b}$$

$$|L + K|_\alpha = |L|_\alpha , \ L, K \in \mathcal{B}(E) , \ K \text{ compact} . \tag{1.2.c}$$

We can define $\omega_{ess}(T(t))$ by

$$\omega_{ess}(T(t)) = \lim_{t\to\infty} \frac{1}{t} \log |T(t)|_\alpha . \tag{1.3}$$

The following relation holds (e. g. [8, 15])

$$\omega_0(T(t)) = \max\{s(A), \ \omega_{ess}(T(t))\} = \max\{s_1(A), \ \omega_{ess}(T(t))\} , \tag{1.4}$$

where $s_1(A) = \sup\{\mathrm{Re}\lambda : \lambda \in \sigma(A) \setminus \sigma_{ess}(A)\}$.

Now let K be a compact Hausdorff space and let $E = C(K)$ be the Banach lattice of continuous functions on K. Let 1 be the element of E which is identically one on K.

Definition. The C_0-semigroup $\{T(t)\}_{t\geq 0}$ on $E = C(K)$ is called a Markov semigroup if for every $t \geq 0$, $T(t)$ is positivity preserving and $T(t)1 = 1$.

$T(t)1 = 1$ implies that $A1 = 0$. For $\phi \in C(K)$, $\|\phi\| \leq 1$, we have $|\phi| \leq 1$, hence $|T(t)\phi| \leq T(t)|\phi| \leq T(t)1 = 1$ yielding that $\|T(t))\| = 1$. So

$$s(A) = \omega_0(T(t)) = 0 .$$

For a smooth introduction into the theory of Markov semigroups we refer to the book of Davies [3].

Theorem. Let $\{T(t)\}_{t\geq 0}$ *define an irreducible Markov semigroup on* $E = C(K)$ *and assume that* $\omega_{ess}(T(t)) < 0$. *Then there is an* $\eta > 0$ *and a strictly positive probability measure* μ *on* K *such that for every* $0 < \varepsilon < \eta$ *there is a constant* $M(\varepsilon) \geq 1$ *such that for every* $\phi \in E$:

$$\| T(t)\phi - < \phi , \mu > 1 \| = M(\varepsilon)e^{-\varepsilon t}\| \phi \| .$$

Here $< \phi , \mu > = \int_K \phi(x)d\mu(x)$.

This result, which we shall apply to a particular problem in structured population dynamics, follows from Davies' result on the peripheral point spectrum of an irreducible Markov semigroup. Davies' results were extended by Greiner ([5, 6]) into several directions.

2. A Markov process: satiation dependent predation

Consider an invertebrate predator whose internal state is completely characterized by the one-dimensional quantity s, which we call *satiation* (= gut content). Assume that this predator feeds on prey with a fixed weight. The predator swallows a prey, once caught, immediately, and thus increases its satiation with a fixed amount w. We refer to the papers of Metz & van Batenburg [9 , 10] for a very general description of the predatory behaviour of some species of predators, e.g. the mantid *Hierodula crassa*.

Let $b(s)$ be the (mean) catch rate of a predator with satiation s.

Assumption. $b \in C[0, c + w]$; b is Lipschitz continuous on $[0, c)$; $b(s) > 0$ on $[0, c)$, and $b(s) = 0$ on $[c, c + w]$.

So the maximum attainable satiation is $s = c + w$. Between two catches the satiation of the predator decreases due to digestion. We assume (and this assumption is justified by experiments) that digestion $-\frac{ds}{dt}$ is proportional to satiation,

$$\frac{ds}{dt} = - as ,$$

and without loss of generality we may set $a = 1$. Let $n(t, s)$ denote the satiation density at time t , i. e. for a measurable subset $\Omega \subseteq [0, c + w]$ the probability that the satiation S_t at time t lies in Ω is given by $\int_\Omega n(t, s)ds$. In particular: $\int_0^{c+w} n(t, s)ds = 1$. Then $n(t, s)$ satisfies the balance equation

$$\frac{\partial n}{\partial t}(t, s) - \frac{\partial}{\partial s}(sn(t, s)) = - b(s)n(t, s) + b(s-w)n(t, s - w) \tag{2.1.a}$$

$$n(t, s) = 0, s \geq c + w . \tag{2.1.b}$$

This equation is called the *forward equation* (e. g. [4]). The associated *backward equation* is given by

$$\frac{\partial m}{\partial t}(t, s) + s \frac{\partial m}{\partial s}(t, s) = - b(s)m(t, s) + b(s)m(t, s + w). \tag{2.2}$$

The remainder of this section will be devoted to the investigation of equation (2.2) supplied with an initial condition of the form:

$$m(0, s) = \phi(s), 0 \leq s \leq c + w . \tag{2.3}$$

where $\phi \in E := C[0, c + w]$. Suppose we can solve the initial value problem (2.2)-(2.3) for every $\phi \in E$. Then we can think of a solution $n(t, \cdot ; \psi)$ of the forward equation (2.1) with initial data

$$n(0, \cdot ; \psi) = \psi(\cdot) ,$$

where ψ is a Borel measure on $[0, c + w]$, as a linear functional on $E = C[0, c + w]$. For $\phi \in C[0, c + w]$:

$$\int_0^{c+w} \phi(s)n(t, ds; \psi) = \int_0^{c+w} m(t, s; \phi) \psi(ds)$$

where $m(t, \cdot ; \phi)$ is the solution of (2.2)-(2.3) . We call such solutions $n(t, \cdot ;\psi)$ *weak* solutions.*

Remark. In probability theory one often works with transition probabilities instead of densities. Let S_t be the stochastic variable denoting satiation at time t . Let

$$P(t, s_0, s) = \text{Prob}(S_t \geq s \mid S_0 = s_0) .$$

Then in terms of n

$$P(t, s_0, s) = \int_s^{c+w} n(t, d\sigma; \delta_{s_0})$$

where δ_{s_0} is the Dirac measure at $s = s_0$. Then P obeys (c. f. [7]):

$$\frac{\partial P}{\partial t} = s\frac{\partial P}{\partial s} - \int_{s-w}^{s} b(\sigma)\, \partial_s P(t, s_0, \sigma)d\sigma .$$

We write (2.2)-(2.3) abstractly as

$$\frac{dm}{dt}(t) = Am(t), \; m(0) = \phi \in E , \tag{2.4}$$

where A is the closed operator on E with domain

$$\mathcal{D}(A) = \{\phi \in W^{1,1}_{loc}[0, c + w] : s \to s\phi'(s) \in E\}$$

given by

$$(A\phi)(s) = - s\phi'(s) - b(s)\phi(s) + b(s)\phi(s + w).$$

Remark. The abstract forward equation looks as follows:

$$\frac{dn}{dt} = A'n(t) \;, \; n(0) = \psi,$$

where A' is the adjoint of A .

We will show the following

- A generates a Markov semigroup $\{T(t))\}_{t\geq 0}$
- $\omega_{ess}\,(T(t)) < 0$
- $\{T(t))\}_{t\geq 0}$ is irreducible.

We write

$$A = A_0 + B ,$$

where the closed operator A_0 with domain $\mathcal{D}(A_0) = \mathcal{D}(A)$ is given by

$$(A_0\phi)(s) = - s\phi'(s) - b(s)\phi(s)$$

and B is the bounded linear operator

$$(B\phi)(s) = b(s)\phi(s + w).$$

Defining

$$E(s) = \exp\left(-\int_s^c \frac{b(\sigma)}{\sigma}\, d\sigma\right)$$

it is easy to see that A_0 generates the strongly continuous positive semigroup $\{T_0(t)\}_{t\geq 0}$ given by

$$(T_0(t)\phi(s) = \frac{E(se^{-t}}{E(s)}\,\phi(se^{-t}),\ s \in [0, c+w],\ t \geq 0 .$$

Now a standard perturbation result yields that $A = A_0 + B$ also generates a strongly continuous semigroup $\{T(t)\}_{t\geq 0}$. Note that this result also follows from the positivity of $R(\lambda, A)$ for $\lambda \in \mathbb{R}$ large enough (e. g. [1]). We have

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

where

$$T_i(t) = \int_s^t T_0(t-s)\, B\, T_{i-1}(s)ds ,\ t \geq 0 ,\ i \geq 1 .$$

Since B defines a positive operator we find that $\{T(t)\}_{t\geq 0}$ is a positive semigroup. Obviously $1 \in D(A)$ and $A1 = 0$, hence $T(t)1 = 1$.

Proposition. *A generates a Markov semigroup* $\{T(t)\}_{t\geq 0}$.

We can write down the following explicit expression for $T_1(t)$:

$$(T_1(t)\phi(s) = \int_0^t b(se^{-t+\tau})\,\frac{E(se^{-t+\tau}}{E(s)}\,\frac{E(se^{-t}+ we^{-\tau}}{E(se^{-t+\tau}+ w}\,\phi(se^{-t} + we^{-\tau})d\tau .$$

Application of the Arzela-Ascoli theorem gives that $T_1(t)$ is compact for all $t \geq 0$, and it follows that $U(t) = \Sigma_{i=1}^{\infty} T_i(t)$ is compact if $t \geq 0$. By (1.2)

$$|T(t)|_\alpha = |T_0(t) + U(t)|_\alpha = |T_0(t)|_\alpha \leq \|\, T_0(t)\, \|$$

and from (1.1) and (1.3) we find

$$\omega_{ess}(T(t)) \leq \omega_0(T_0(t)) .$$

From the Lipschitz continuity of b it follows that there exist positive constants $0 < m_1 \leq m_2 < \infty$ such that

$$m_1 \cdot s^\gamma \leq E(s) \leq m_2 \cdot s^\gamma ,$$

where $\gamma = b(0) > 0$. Now

$$\frac{m_1}{m_2} e^{-\gamma t} \le \| T_0(t) \| = \| T_0(t) 1 \| \le \frac{m_2}{m_1} e^{-\gamma t} ,$$

therefore $\omega_0(T_0(t)) = -\gamma < 0$ and we have proved

Proposition. $\omega_{ess}(T(t)) \le -\gamma < 0$.

Finally we have to show

Proposition. $\{T(t)\}_{t\ge 0}$ *is irreducible.*

Proof. VOIGT [14] has proved that a closed ideal in E is invariant under $\{T(t)\}_{t\ge 0}$ if and only if it is invariant under both $\{T_0(t)\}_{t\ge 0}$ and B . Now let J be a closed ideal in E . Then J is of the form: $J = \{\phi \in C[0, c+w]$: ϕ vanishes on $\Omega\}$, for some closed subset $\Omega \subseteq [0, c+w]$ (see [13]). Now suppose that J is invariant under $\{T_0(t)\}_{t\ge 0}$ and under B . Then

i) $s \in \Omega \Longrightarrow se^{-t} \in \Omega,\ t \ge 0$
ii) $s \in \Omega\ ,\ s \le c \Longrightarrow s + w \in \Omega$.

This is only possible if $\Omega = \emptyset$ or $\Omega = [0, c+w]$ corresponding to the cases $J = E$ and $J = \{0\}$ respectively, which proves the irreducibility of $\{T(t)\}_{t\ge 0}$. □

So we may apply the theorem of section 1 which says that there exists a strictly positive probability measure μ on $[0, c+w]$ and an $\eta > 0$ such that for every such that for every ε , $0 < \varepsilon < \eta$ there is an $M(\varepsilon) \ge 1$ such that for every $\phi \in C[0, c+w]$:

$$\| T(t)\phi - <\phi, \mu> 1 \| \le M(\varepsilon) e^{-\varepsilon t} \| \phi \| .$$

In terms of the solutions $n(t, \cdot, \psi)$ of the forward equation (2.1), where ψ is a probability measure on $[0, c+w]$, this can be translated into

$$n(t, \cdot, \psi) \to \mu,\ t \to \infty ,$$

exponentially with respect to the weak * topology. We call μ the *stable satiation density.*

3. Extensions to some other population models

The example discussed in the previous section in special in the sense that $\int_0^{c+w} n(t, ds)$ is a conserved quantity. Although in general population models this

is not true due to births and deaths, one can sometimes transform the problem in such a way that a similar relation is satisfied. We shall illustrate this idea by means of the cell fission model without death (e. g. [3]).
Consider a cell population whose individuals can be characterized by their size x. The population reproduces by equal fission of individuals cells. Let $g(x)$ be the growth rate and $b(x)$ the division rate.

Assumption. i) $g \in C^1[0, 1]$; $g(x) > 0$ on $[0, 1]$; $g(1) = 0$ and $g'(1) \neq 0$.
ii) b is Lipschitz continuous on $[0, 1]$; $b(x) > 0$ on $(0, 1]$.

Let $n(t, x)$ be the size density at time t , then n obeys the balance equation.

$$\frac{\partial n}{\partial t}(t, x) + \frac{\partial}{\partial x}(g(x)n(t, x)) = - b(x)n(t, x) + 4b(2x)n(t, 2x) \tag{3.1.a}$$

$$n(t, 0) = 0 . \tag{3.1.b}$$

Note that we do not have conservation of number due to factor 4 . The *backward equation* takes the form

$$\frac{\partial m}{\partial t}(t,x) - g(x) \frac{\partial m}{\partial x}(t,x) = - b(x)m(t,x) + 2b(x)m(t, \frac{1}{2}x), \tag{3.2}$$

which we can write abstractly as

$$\frac{dm}{dt}(t) = Am(t) ,$$

where A is the closed operator on $E = C[0, 1]$ with domain

$$\mathcal{D}(A) = \{\phi \in W^{1,1}_{loc}[0, 1]: g \cdot \phi' \in C[0, 1]\}$$

given by

$$(A\phi)(x) = g(x)\phi'(x) - b(x)\phi(x) + 2b(x)\phi(\tfrac{1}{2}x).$$

Proposition. There is an $\alpha > 0$ and an element $\phi_\alpha \in C[0, 1]$, $\phi_\alpha(x) > 0$, $x \in [0, 1]$, such that $A\phi_\alpha = \alpha\phi_\alpha$.

This proposition will be proved at the end of this section. So ϕ_α satisfies

$$g(x)\phi'_\alpha(x) = b(x)\phi_\alpha(x) - 2b(x)\phi_\alpha(\tfrac{1}{2}x) + \alpha\phi_\alpha(x) .$$

Substituting in (3.1)

$$v(t,x) = e^{-\alpha t} \phi_\alpha(x)n(t,x)$$

we obtain the following equation for v :

$$\frac{\partial v}{\partial t}(t,x) + \frac{\partial}{\partial x}(g(x)v(t,x)) = -\beta(x)v(t,x) + 2\beta(2x)v(t, 2x)$$

$$v(t, 0) = 0 ,$$

where

$$\beta(x) = 2b(x) \cdot \frac{\phi_\alpha(\frac{1}{2}x)}{\phi_\alpha(x)} ,$$

and we see immediately that

$$\frac{d}{dt}\int_0^1 v(t,x)dx = 0$$

so we can apply the same techniques as we did in § 2.

Remark. Abstractly this last relation can be written as: $\frac{d}{dt}< 1, v(t) > = 0$. Note that formally

$$\frac{d}{dt}< 1, v(t) > = \frac{d}{dt}< 1, e^{-\alpha t}\phi_\alpha\cdot n(t) >$$

$$= -\alpha< 1, e^{-\alpha t}\phi_\alpha \cdot n(t)> + < 1, e^{-\alpha t}\phi_\alpha\cdot \frac{dn}{dt}(t)> .$$

Now $<1, e^{-\alpha t}\phi_\alpha\cdot\frac{dn}{dt}(t)> = e^{-\alpha t}< \phi_\alpha, A'n(t)> = e^{-\alpha t}< A\phi_\alpha , n(t)> = \alpha e^{-\alpha t}<\phi_\alpha, n(t) >$ $= \alpha<1, e^{-\alpha t}\phi_\alpha\cdot n(t) >$, and indeed $\frac{d}{dt}< 1 , v(t) > = 0$. Here A' stands for the adjoint of A .

Proof of proposition. Let $E(x) = \exp(-\int_0^x \frac{\lambda + b(\xi)}{g(\xi)}d\xi)$. If $\operatorname{Re}\lambda + b(1) > 0$ then $E_\lambda(1) = 0$. Now $A\phi = \lambda_\phi$ can be rewritten as $K_\lambda\phi = \phi$, where for $\operatorname{Re}\lambda + b(1) > 0$, $K_\lambda : C[0, 1]\to C[0, 1]$ is the *compact* operator

$$(K_\lambda\phi)(x) = \frac{2}{E_\lambda(x)}\int_x^1 \frac{b(\xi)}{g(\xi)} E_\lambda(\xi)\,\phi(\frac{1}{2}\xi)d\xi.$$

If λ is real, $\lambda + b(1) > 0$ then K_λ is a positive operator with spectral radius $r(K_\lambda) > 0$, hence $r(K_\lambda) \in P\sigma(K_\lambda)$. Let $\phi_\lambda > 0$ be such that $K_\lambda\phi_\lambda = r_\lambda\phi_\lambda$, where $r_\lambda = r(K_\lambda)$. (Such a ϕ_λ does exist). If $\phi_\lambda = 0$ on $[0,\frac{1}{2}]$ then $K_\lambda\phi_\lambda = r_\lambda\phi_\lambda = 0$ which is a contradiction. So $\phi_\lambda(x) > 0$ for at least one $x \in (0,\frac{1}{2})$ but this implies immediately that $\phi_\lambda(x) > 0$ for every $0 \le x \le 1$ (also in $x = 1$!). Since

$$(K_0 1)(x) = \frac{2}{E_0(x)} \int_x^1 \frac{b(\xi)}{g(\xi)} E_0(\xi) d\xi = 2$$

we find $K_0 1 \geq 2 \cdot 1$ hence $r(K_0) \geq 2$. Since $\lambda \to r(K_\lambda)$ is continuous and $r(K_\lambda) \to 0$ as $\lambda \to \infty$ we find an $\alpha > 0$ such that $r(K_\alpha) = 1$. Now the result follows. □

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