On a size-structured two-phase population model with infinite states-at-birth

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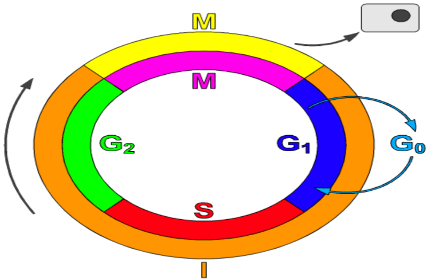
Overview of the talk

- introduction of the mathematical model
- positive operators, quasicontractive semigroups
- asymptotic behavior of solutions, balanced/asynchronous exponential growth
- outlook, conclusion

Biological motivation

Many living things can experience "active" and "resting" phases in their life cycles, e.g. cells, hibernating animals, plants etc.

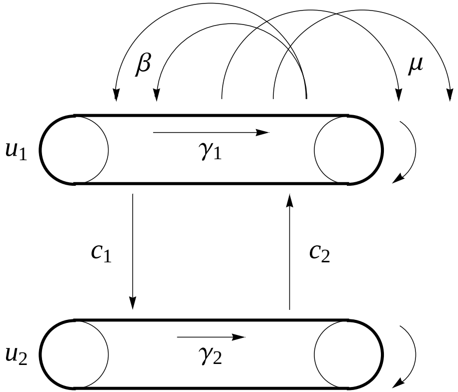


Cell cycle with resting phase G_0.

Biological motivation

In both the active and resting phases do the individuals grow, while only in the active phase do they proliferate and die.

Individuals are structured by size $s \in [0, m]$ and can be born at different, distributed sizes.



The model

We study the following linear size-structured model

$$u_{1,t}(s,t) + \underbrace{(\gamma_1(s)u_1(s,t))_s}_{growth} = \underbrace{-\mu(s)u_1(s,t)}_{mortality} + \underbrace{\int_0^m \beta(s,y)u_1(y,t)\mathrm{d}y}_{recruitment}$$
$$- c_1(s)u_1(s,t) + c_2(s)u_2(s,t),$$
$$u_{2,t}(s,t) + (\gamma_2(s)u_2(s,t))_s = \underbrace{c_1(s)u_1(s,t) - c_2(s)u_2(s,t)}_{exchange\ between\ classes},$$

with boundary and initial conditions

$$\gamma_1(0)u_1(0,t) = 0, \quad u_1(s,0) = u_1^0(s),$$
$$\gamma_2(0)u_2(0,t) = 0, \quad u_2(s,0) = u_2^0(s).$$

Assumptions on the model parameters

We assume bounded mortality and transition rates

$$\mu,\ c_1,\ c_2 \in L_+^\infty([0,m]),$$

and smooth and positive growth rates

$$0 < \gamma_1,\ \gamma_2 \in C^1([0,m]).$$

The function $\beta(s,y)$ gives the rate at which an active individual of size y produces offspring of the size s and satisfies

$$\beta \in C([0,m]^2).$$

Related works

- H. J. A. M. Heijmans, *Math. Z.* **191** (1986), treats size-structured populations with linear semigroups
- O. Arino *et al.*, *J. Math. Anal. Appl.* **215** (1997), investigated age structured cell populations with quiescence,
- À. Calsina and J. Saldaña, *Math. Models Methods Appl. Sci.* **16** (2006), consider distributed states in the recruitment term

The abstract Cauchy problem

Let $\mathcal{X} = L^1(0,m) \times L^1(0,m)$ and define

$$\mathcal{A}\,\mathbf{u} = \begin{pmatrix} -\gamma_1 \frac{d}{ds} u_1 \\ -\gamma_2 \frac{d}{ds} u_2 \end{pmatrix}$$

$$\mathrm{Dom}(\mathcal{A}) = \left\{ \mathbf{u} \in W^{1,1}(0,m) \times W^{1,1}(0,m) \,|\, \mathbf{u}(0) = \mathbf{0} \right\}$$

and on $\mathcal{X}$

$$\mathcal{B}\,\mathbf{u} = \begin{pmatrix} -\left(\frac{d}{ds}\gamma_1 + \mu + c_1\right) u_1 + \int_0^m \beta(\,\cdot\,, y) u_1(y)\,\mathrm{d}y + c_2 u_2 \\ -\left(\frac{d}{ds}\gamma_2 + c_2\right) u_2 + c_1 u_1 \end{pmatrix}.$$

The abstract Cauchy problem on the state space $\mathcal{X}$ is

$$\frac{d}{dt}\,\mathbf{u} = (\mathcal{A} + \mathcal{B})\,\mathbf{u}, \quad \mathbf{u}(0) = \mathbf{u}_0,$$

where $\mathbf{u_0} = (u_1^0, u_2^0)$.

Existence and positivity of solutions

Our plan is to apply the following

Theorem

Let $\mathcal{Y}$ be a Banach lattice and let $\mathcal{L} : Dom(\mathcal{L}) \to \mathcal{Y}$ be a linear operator. The following statements are equivalent.

(i) *$\mathcal{L}$ is the generator of a positive contractive semigroup.*

(ii) *$\mathcal{L}$ is densely defined, $Rg(\lambda\mathcal{I} - \mathcal{L}) = \mathcal{Y}$ for some $\lambda > 0$, and $\mathcal{L}$ is dispersive.*

Corollary 7.15 in Ph. Clément *et al.*, *One-Parameter Semigroups*, North–Holland, Amsterdam 1987.

Definitions

A C_0 semigroup $\mathcal{T}(t)$ is called *contractive* if

$$||\mathcal{T}(t)|| \leq e^{\omega t}, \quad t \geq 0,$$

for some $\omega \leq 0$. An operator $\mathcal{L}$ is called *dispersive*, if it is p-dissipative with respect to the canonical half-norm

$$p(y) = ||y^+||_{\mathcal{Y}},$$

where $y^+ = y \vee 0$ (and $y^- = (-y)^+$), that is

$$p(y) \leq p(y - \lambda \mathcal{L} y), \quad \lambda \geq 0, \quad y \in \mathrm{Dom}(\mathcal{L}).$$

Equivalent definition of dispersivity

Let $\mathcal{L} : \mathrm{Dom}(\mathcal{L}) \to \mathcal{Y}$ be a linear operator and $\mathcal{Y}^*$ be the dual space of $\mathcal{Y}$. Then $\mathcal{L}$ is dispersive if for every $y \in \mathrm{Dom}(\mathcal{L})$ there exists $\phi_y \in \mathcal{Y}^*$ with $0 \leq \phi_y$, $||\phi_y||_{\mathcal{Y}^*} \leq 1$ and $\langle y, \phi_y \rangle = ||y^+||_{\mathcal{Y}}$ such that

$$\langle \mathcal{L}y, \phi_y \rangle \leq 0,$$

where $\langle \cdot\,, \cdot \rangle$ is the canonical pairing of $\mathcal{Y}$ and $\mathcal{Y}^*$.

W. Arendt *et al.*, *One-Parameter Semigroups of Positive Operators*, Springer-Verlag, Berlin, (1986).

Existence and positivity of solutions

Theorem

The operator $\mathcal{A}+\mathcal{B}$ generates a positive strongly continuous quasicontractive semigroup $\{\mathcal{T}(t)\}_{t\geq 0}$ of bounded linear operators on $\mathcal{X}$.

Proof.

Verify the conditions in (ii) of the previous theorem for the operator $\mathcal{A}+\mathcal{B}-\omega\mathcal{I}$ by using

$$\phi_u(s) = \begin{cases} (1,1) & \text{if} \quad u_1(s) > 0,\ u_2(s) > 0, \\ (1,0) & \text{if} \quad u_1(s) > 0,\ u_2(s) \leq 0, \\ (0,1) & \text{if} \quad u_1(s) \leq 0,\ u_2(s) > 0, \\ (0,0) & \text{if} \quad u_1(s) \leq 0,\ u_2(s) \leq 0 \end{cases}.$$

□

Asymptotic behavior of solutions

A strongly continuous semigroup $\{\mathcal{S}(t)\}_{t\geq 0}$ on a Banach space $\mathcal{Y}$ with generator $\mathcal{O}$ and *spectral bound*

$$s(\mathcal{O}) = \sup\{\,\mathrm{Re}(\lambda)\ :\ \lambda \in \sigma(\mathcal{O})\,\}$$

exhibits *balanced (asynchronous) exponential growth* if there exists a (rank one) projection Π on $\mathcal{Y}$ such that

$$\lim_{t\to\infty} \|e^{-s(\mathcal{O})\,t}\,\mathcal{S}(t) - \Pi\| = 0.$$

Balanced exponential growth requires that the spectral bound $s(\mathcal{O})$ is a dominant eigenvalue, and that the semigroup $\mathcal{S}$ is essentially compact, i.e. $\omega_{ess}(\mathcal{S}) < s(\mathcal{O})$, where $\omega_{ess}(S)$ stands for the essential growth bound of the semigroup.

Spectrum of the generator

Lemma

The spectrum of $\mathcal{A}+\mathcal{B}$ can contain only isolated eigenvalues of finite algebraic multiplicity.

Proof.

It is enough to show that $R(\lambda, \mathcal{A})$ is compact for λ large enough. We can solve the resolvent equation

$$(\lambda \mathcal{I} - \mathcal{A})\, \mathbf{u} = \mathbf{h}$$

and show that the solution belongs to $W^{1,1}(0,m) \times W^{1,1}(0,m)$ which is compactly embedded in $\mathcal{X}$ by the Rellich-Kondrachov theorem (recall that $\mathcal{A}$ is a diagonal matrix of differentiation operators). □

Spectrum of the generator

The previous lemma implies that the essential spectrum of $\mathcal{A}+\mathcal{B}$ is empty. For the essential compactness of the semigroup $\mathcal{T}(t)$, i.e. $\omega_{ess}(\mathcal{T}) < s(\mathcal{A}+\mathcal{B})$, we need to show that the point spectrum $\sigma_P(\mathcal{A}+\mathcal{B})$ is not empty.

Theorem

The generator $\mathcal{A}+\mathcal{B}$ has a non-empty point spectrum.

Difficulty: the eigenvalue equation

$$(\mathcal{A}+\mathcal{B}-\lambda\mathcal{I})\mathbf{u} = 0$$

cannot be solved explicitly due to coupling terms and the distributed recruitment term.

Spectrum of the generator

Proof.

We use a different operator splitting

$$\mathcal{A} + \mathcal{B} = \mathcal{A}_0 + \mathcal{B}_0,$$

where

$$\mathcal{A}_0\,\mathbf{u} = \begin{pmatrix} -\frac{d}{ds}(\gamma_1 u_1) - (\mu + c_1)u_1 + \int_0^m \beta(\,\cdot\,, y)u_1(y)\,\mathrm{d}y \\ -\frac{d}{ds}(\gamma_2 u_2) - c_2 u_2 \end{pmatrix},$$

$$\mathcal{B}_0\,\mathbf{u} = \begin{pmatrix} c_2 u_2 \\ c_1 u_1 \end{pmatrix}$$

(i.e. $\mathcal{A}$ is diagonal and all influx terms due to coupling are contained in $\mathcal{B}_0$).

Spectrum of the generator

We fix a separable kernel β^* that satisfies

$$0 \leq \beta^*(s,y) = \beta_1(s)\beta_2(y) \leq \beta(s,y)$$

and denote by $\mathcal{A}_0^*$ the corresponding operator with rank-one birth process defined by β^*. Then we can show that

$$-\infty < s(\mathcal{A}_0^*) \leq s(\mathcal{A}_0) \leq s(\mathcal{A}_0 + \mathcal{B}_0) = s(\mathcal{A} + \mathcal{B}).$$

The first inequality follows from solving a characteristic equation for the operator $\mathcal{A}_0^*$, the second and third follow from a perturbation theorem for generators of positive semigroups. $\square$

Eventual compactness of the semigroup

Lemma

The semigroup $\{\mathcal{T}(t)\}_{t\geq 0}$ generated by the operator $\mathcal{A}+\mathcal{B}$ is eventually compact.

Proof.

We use yet another operator splitting

$$\mathcal{A}_1\,\mathbf{u} = \begin{pmatrix} -\frac{d}{ds}\,(\gamma_1 u_1) - (\mu + c_1)u_1 + c_2 u_2 \\ -\frac{d}{ds}\,(\gamma_2 u_2) - c_2 u_2 + c_1 u_1 \end{pmatrix} = \begin{bmatrix} \text{growth, coupling} \\ \text{and loss} \end{bmatrix}$$

$$\mathcal{B}_1\,\mathbf{u} = \begin{pmatrix} \int_0^m \beta(\,\cdot\,,y)u_1(y)\,\mathrm{d}y \\ 0 \end{pmatrix} = [\text{birth}].$$

Using the Fréchet-Kolmogorov compactness criterion in L^1 and the continuity of β we show that the operator $\mathcal{B}_1$ is compact. The semigroup $\mathcal{T}_1(t)$ generated by $\mathcal{A}_1$ is nilpotent. □

Previous results combined

Theorem

The semigroup $\mathcal{T}(t)$ generated by the operator $\mathcal{A}+\mathcal{B}$ exhibits balanced exponential growth.

Proof.

The eventual compactness of the semigroup $\mathcal{T}(t)$ implies eventual norm continuity. It follows that the boundary spectrum

$$\sigma_+(\mathcal{A}+\mathcal{B}) = \sigma(\mathcal{A}+\mathcal{B}) \cap (s(\mathcal{A}+\mathcal{B}) + i\mathbb{R})$$

equals $s(\mathcal{A}+\mathcal{B})$ which is a pole of the resolvent with finite algebraic multiplicity. □

K.-J. Engel and R. Nagel, *One-Parameter Semigroups for Linear Evolution Equations*, Springer, New York 2000.

Asynchronous exponential growth

Theorem

Assume that there exists an $\varepsilon_0 > 0$ such that for all $0 < \varepsilon \leq \varepsilon_0$

$$\int_0^{\varepsilon} \int_{m-\varepsilon}^{m} \beta(s, y)\, \mathrm{d}y\, \mathrm{d}s > 0$$

and that the transition rates satisfy

$$\inf \, supp\, c_1 = 0, \quad \text{and} \quad \sup \, supp\, c_2 = m.$$

Then the semigroup $\mathcal{T}(t)$ generated by $\mathcal{A} + \mathcal{B}$ exhibits asynchronous exponential growth.

Irreducibility

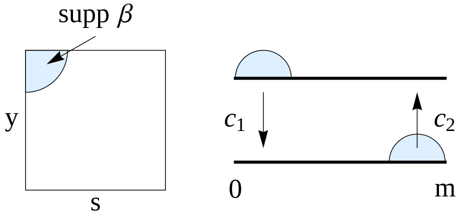
Proof.

It only remains to show that the semigroup $\mathcal{T}(t)$ is *irreducible*, i.e. for every $\mathbf{0} \neq \mathbf{u} \in \mathcal{X}_+$ and $\mathbf{0} \neq \mathbf{u}^* \in \mathcal{X}_+^*$ there exists a t_0 such that

$$\langle \mathcal{T}(t_0)\mathbf{u}, \mathbf{u}^* \rangle > 0.$$

In fact, we have for t sufficiently large that

$$\operatorname{supp} \mathcal{T}(t)\mathbf{u} = [0, m] \times [0, m].$$



□

Concluding remarks

- The conditions on asynchronous exponential growth are natural, if they are not satisfied, then the size space can be reduced appropriately.
- Coupling to a quiescent phase can "shift" the spectral radius of the resulting matrix in both directions (K. Hadeler and H. Thieme, *J. Math. Biol.* **57** (2008)). The same holds for the infinite-dimensional setting.
- A natural extension would be to make the model nonlinear by making the coupling terms dependent on the total population size.

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Thank you for your attention

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