Size-structured populations with distributed states at birth

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Overview of the talk

- review of age-structured population models
- size-structured models:
  - distributed states at birth,
  - resting states,
  - steady states for nonlinear problems,
  - size diffusion and Wentzell boundary conditions,
  - hierarchical competitions
- outlook, conclusion

Linear age-structured population models

Introduced by Lotka & McKendrick (1911, 1926), the model reads

$$\underbrace{u_t(a,t) + u_a(a,t)}_{\textit{aging}} = \underbrace{-\mu(a)u(a,t)}_{\textit{mortality}},$$

$$u(0,t) = \underbrace{\int_0^{a_m} \beta(r)u(r,t)\mathrm{d}r}_{\textit{recruitment}}, \quad u(a,0) = u_0(a),$$

this is solved with the methods of characteristics, renewal equations and the theory of semigroups of operators on the state space $L^1(0,a_M)$.

Nonlinear version

Gurtin & MacCamy (1974)

$$u_t(a,t) + u_a(a,t) = -\mu(a,U)u(a,t),$$
$$u(0,t) = \int_0^{a_m} \beta(r,U)u(r,t)\mathrm{d}r, \quad u(a,0) = u_0(a),$$

where

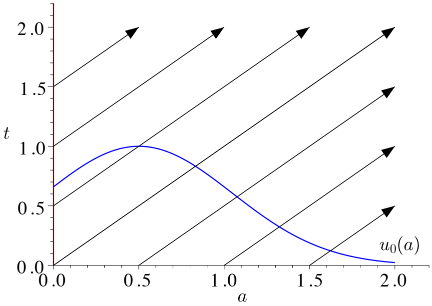
$$U(t) = \int_0^{a_m} w(r)u(r,t)\mathrm{d}r$$

is the (weighted) total population. Results are local and global existence theory, existence and stability of steady states, balanced growth etc. (Webb, Diekmann, Iannelli, Gyllenberg, Thieme, Magal and many others).

Summary

Age stuctured models are characterized by

- all individuals are born at age zero,
- all individuals age at the same rate as time progresses, and
- age differences between individuals remain the same throughout their lives.



Many biologically relevant problems require a different interpretation of the structuring variable.

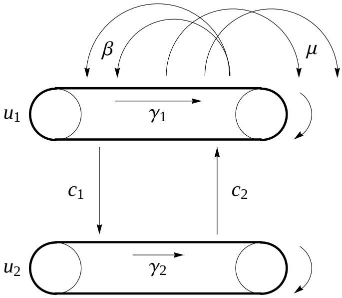
Introduction of size structure

"Size" can mean many things, for example size, mass, energy content, pathogen load etc. Other new possibilities are

- size-dependent growth rates,
- distributed states at birth, and
- "size-diffusion".

Example 1: “active” and “resting” phases

Individuals grow in both the active (u_1) and resting (u_2) phases, but proliferate and die only in the active phase.



e.g. quiescent cells in a cell cycle model.

Example 1: The model

We study the following linear size-structured model

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

with boundary and initial conditions

$$
\begin{aligned}
\gamma_1(0)u_1(0,t) = 0, &\quad u_1(s,0) = u_1^0(s), \\
\gamma_2(0)u_2(0,t) = 0, &\quad u_2(s,0) = u_2^0(s).
\end{aligned}
$$

JZF & PH, *Positivity* **14**:501-514 (2010)

Example 1: The abstract Cauchy problem

Equation (1) can be written as an abstract Cauchy problem

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

on the state space $\mathcal{X} = (L^1(0, m))^2$ where $\mathcal{A} \approx \partial_s$ is the unbounded part (defined on $W^{1,1}$).

Theorem

The operator $\mathcal{A} + \mathcal{B}$ generates a positive quasicontractive C_0-semigroup $\{\mathcal{T}(t)\}_{t \geq 0}$ of bounded linear operators on $\mathcal{X}$.

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

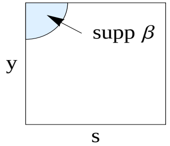
Example 1: Asymptotic behavior

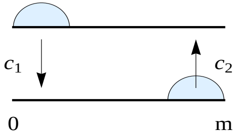
A C_0-semigroup $\mathcal{S}(t)$ on a Banach space $\mathcal{Y}$ with generator $\mathcal{O}$ and *spectral bound* $s(\mathcal{O}) = \sup\{\mathrm{Re}(\lambda) : \lambda \in \sigma(\mathcal{O})\}$ exhibits *asynchronous exponential growth* if there exists a rank one projection Π on $\mathcal{Y}$ such that

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

Theorem

Under some reasonable "mixing conditions" on the birth rate β and the transition rates c_1 and c_2, the semigroup $\mathcal{T}(t)$ generated by $\mathcal{A} + \mathcal{B}$ exhibits asynchronous exponential growth.





Example 2: Structured parasite populations

Sea lice infest farmed fish, causing growth reduction, external wounds and secondary infections. A single equation simplifies the complicated multi-stage life cycle

$$
\begin{aligned}
u(s,t)_t + (\gamma(s,U(t))u(s,t))_s = \\
& -\mu(s,U(t))u(s,t) + \int_0^m \beta(s,y,U(t))u(y,t)\,\mathrm{d}y, \\
\gamma(0,U(t))u(0,t) = 0, \quad & U(t) = \int_0^m u(s,t)\,\mathrm{d}s.
\end{aligned} \tag{2}
$$

JZF, Darren Green, PH, *Math. Model. Nat. Phenom.* **5**:94-114 (2010)

Example 2: Positive equilibrium solutions

The nonlinear, non-local equilibrium equation of (2)

$$0 = -(\gamma(s, U_*)u_*(s))' - \mu(s, U_*)u_*(s) + \int_0^m \beta(s, y, U_*)u_*(y)\,\mathrm{d}y,$$

$$\gamma(0, u_*)u_*(0) = 0, \qquad U_* = \int_0^m u_*(s)\,\mathrm{d}s$$

can be considered as a U-parametrized zero eigenvalue problem

$$\text{(r.h.s.)} =: \mathcal{B}_U u = 0.$$

Example 2: Separable birth processes

Idea: find a separable underestimator of the birth rate

$$\beta_1^-(s)\beta_2^-(y) \leq \beta(s, y, U^-)$$

such that the operator $\mathcal{B}_{U^-}$ has a dominant real eigenvalue $\lambda_{U^-} > 0$, with corresponding positive eigenvector and a separable overestimator of the birth rate

$$\beta(s, y, U^+) \leq \beta_1^+(s, U^+)\beta_2^+(y)$$

such that the operator $\mathcal{B}_{U^+}$ has a dominant real eigenvalue $\lambda_{U^+} < 0$, with corresponding positive eigenvector and then use the Intermediate Value Theorem.

Example 2: Linearization at steady states

At a steady state u_* of a nonlinear problem, one makes the ansatz $p = u - u_*$ and a Taylor expansion to obtain the *linearized problem*

$$p' = \mathbb{B}(u_*)p.$$

Then it can be shown that under certain conditions on the model ingredients, $\mathbb{B}(u_*)$ generates a positive quasicontractive semigroup.

In another result we characterize the spectrum of $\mathbb{B}(u_*)$ as the roots of a characteristic equation.

Example 3: Size diffusion

We include diffusion in the size space to model "stochastic noise" and consider general, *Wentzell-Robin* boundary conditions

$$
\begin{aligned}
&u_t + (\gamma(s)u)_s = (d(s)u_s)_s - \mu(s)u + \int_0^m \beta(s,y)u(y,t)\,\mathrm{d}y, \\
&[(d(s)u_s(s,t))_s]_{s=0} - b_0 u_s(0,t) + c_0 u(0,t) = 0, \\
&[(d(s)u_s(s,t))_s]_{s=m} + b_m u_s(m,t) + c_m u(m,t) = 0.
\end{aligned} \tag{3}
$$

Hadeler *et al.* 1988, 2010; Goldstein *et al.* 2002-10; JZF & PH *Math. Biosci. Eng.* **8**:503-513 (2011)

Example 3: Interpretation of boundary condition

The boundary conditions can be cast in the *dynamic form*

$$u_t(0,t) = u(0,t)(-\gamma'(0) - \mu(0) - c_0) + u_s(0,t)(b_0 - \gamma(0)) + \int_0^m \beta(0,y)u(y,t)\,\mathrm{d}y.$$

This allows the boundary points to carry mass in the new state space $L^1(0,m) \times \mathbb{R}^2$.

For example, if s is interpreted as pathogen load in a disease model, then $s = 0$ is the uninfected state.

Example 4: Contest competition and hierarchy

Types of competition

- *scramble competition*: all individuals in the population have equal chances in the competition for resources,
- *contest competition*: individuals experience competition differently, depending on their position in some hierarchy.

Trees of different heights competing for light.

Example 4: Infinite-dimensional environments

Instead of the population size $U = \int u \,\mathrm{d}s$ we now have an infinite-dimensional environment

$$E(s,u) = \alpha \int_0^s w(r)u(r)\,\mathrm{d}r + \int_s^m w(r)u(r)\,\mathrm{d}r,$$

with $\alpha \geq 0$, $\alpha \neq 1$.

Calsina & Saldaña 2006; Farkas & Hagen 2009,10; JZF & PH *Discr. Contin. Dyn. Sys. B* to appear (2011)

Example 4: The hierarchical model

For the quasilinear equation

$$u_t(s,t) + (\gamma(s,U(t))u(s,t))_s = -\mu(s,E(s,u))u(s,t) + \int_0^m \beta(s,y,E(y,u))u(y,t)\,\mathrm{d}y, \quad (4)$$

$$\gamma(0,U(t))u(0,t) = 0$$

we show existence of positive steady states as follows:

- approximate the birth process β by separable functions,
- apply a Leray-Schauder type fixed-point theorem in a conical shell in a Banach space
- pass to the limit.

Linearization at steady states

Does the Principle of Linearized Stability (i.e. that the spectral properties of the linearized operator determine asymptotic stability of the steady state of the original equation) hold for a general quasilinear equation

$$u' = \mathbb{A}(u)u + F(u)?$$

This is still an open problem, but there is a transform for the case

$$u' = g(u)\mathbb{A}u + F(u),$$

where g is a scalar function (Grabosch & Heijmans 1990).

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