Positive Equilibrium Solutions in Nonlinear Age-Structured Population Models

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Outline

1. Equilibria in a population model with age and spatial structure
2. Local and global bifurcation results
3. An age-structured predator-prey model

Structured Populations

population of individuals (bacteria, cells, ...)

individuals structured by age (e.g. chronological age, position in cell life cycle) and spatial position

$u = u(t, a, x) \geq 0$	population density, time $t \geq 0$, age $a \in [0, a_m)$, position $x \in \Omega$
$a_m \in (0, \infty)$	maximal age
$\mu(u, a) \geq 0$	death rate (μ smooth)
$\beta(u, a) \geq 0$	birth rate (β smooth)
$\mathrm{div}_x\, (D(u)\nabla_x u)$	nonlinear diffusion ($D(u) \geq d_0 > 0$)

Nonlinear Age-Structured Models with Diffusion

balance equation

$$\partial_t u + \partial_a u = \mathrm{div}_x \left(D(u)\nabla_x u\right) - \mu(u,a)u \ , \quad t>0,\ a\in(0,a_m),\ x\in\Omega$$

age boundary condition

$$u(t,0,x) = \int_0^{a_m} \beta(u,a)u(t,a,x)\,\mathrm{d}a \ , \quad t>0,\ x\in\Omega$$

initial condition

$$u(0,a,x) = \phi(a,x) \ , \quad a\in(0,a_m),\ x\in\Omega$$

spatial boundary condition, e.g. for $\delta = 0,1$

$$\delta u(t,a,x) + (1-\delta)\partial_\nu u(t,a,x) = 0 \ , \quad t>0,\ a\in(0,a_m),\ x\in\partial\Omega$$

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literature: DiBlasio '78-, Webb '82-, Iannelli & Busenberg '83-, Langlais '85-, Thieme '91-, Rhandi & Schnaubelt '95-,...

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aim: positive time-independent solutions

Equilibrium Solutions

For q large let $L_q := L_q(\Omega)$ and $W^2_{q,\mathcal{B}} := W^2_{q,\mathcal{B}}(\Omega)$.

For (u, a) fixed define

$$A(u,a)w := -\mathrm{div}_x\,(D(u)\nabla_x w) + \mu(u,a)w\ , \quad w \in W^2_{q,\mathcal{B}}$$

to obtain an unbounded linear operator

$$A(u,a) : W^2_{q,\mathcal{B}} \subset L_q \to L_q\ .$$

time-independent solutions $u : [0, a_m) \to W^2_{q,\mathcal{B}}$ with $u(a) \geq 0$:

$$\begin{aligned} \partial_a u + A(u,a)\,u &= 0 && \text{in } L_q, \quad a \in (0, a_m), \\ u(0) &= \int_0^{a_m} \beta(u,a)\,u(a)\,\mathrm{d}a && \text{in } L_q, \end{aligned}$$

literature (for $A = \mu$): Prüß '81-, Cushing '84-, Webb '85,...
literature (for $A = -\Delta_x + \mu$): Langlais '85, Delgado & Molina & Suarez '06, '08

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problem: $u \equiv 0$ is a solution

Reformulation

For u fixed, let

$$a \mapsto A(u, a)$$

generate a positive parabolic **evolution operator** $\Pi_u(a, \sigma)$ on L_q,

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$$v(a) := \Pi_u(a,\sigma)\varphi\ , \quad a \in [\sigma, a_m)$$

is the unique strong solution to the linear problem

$$\begin{aligned} \partial_a v \,+\, A(u,a)v \,&= 0\ , \quad a \in (\sigma, a_m) \\ v(\sigma) \,&=\, \varphi\ , \end{aligned}$$

for $\varphi \in L_q$ and $\sigma \in (0, a_m)$.

Also, $v(a) = \Pi_u(a,\sigma)\varphi \geq 0$ for $\varphi \geq 0$.

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is equivalent to

$$u(a) = \Pi_u(a,0)u(0) \ , \ a \in [0,a_m) \ , \quad u(0) = Q(u)u(0) \ ,$$

with "spatial reproduction number"

$$Q(u) := \int_0^{a_m} \beta(u,a)\Pi_u(a,0)\, \mathrm{d}a \in \mathcal{K}_+(L_q) \ .$$

Fixed Point Method

Note:

$$u(a) = \Pi_u(a,0)u(0)\ ,\ \ a \in [0,a_m)\ , \quad u(0)\ =\ Q(u)u(0)\ ,$$

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Growth conditions, e.g. on spectral radius $r(Q(u))$

$\Longrightarrow$ nontrivial positive solutions by a fixed point method in 'conical shells'

Bifurcation Approach

Let $\beta(u,a) := n b(u,a)$.

n bifurcation parameter (intensity of fertility)

Consider

$$\partial_a u + A(u,a)\,u = 0\ , \quad a \in (0, a_m)$$
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where b is normalized such that $r(Q_0) = 1$ for

$$Q_0 := \int_0^{a_m} b(0,a)\Pi_0(a,0)\,\mathrm{d}a \in \mathcal{K}_{sp}(W_{q,\mathcal{B}}^{2-2/q})\ .$$

Krein-Rutman: $r(Q_0)$ simple eigenvalue with eigenvector $B \in \mathrm{int}(W_{q,\mathcal{B}}^{2-2/q,+})$

Local Bifurcation

Theorem

Let

$$\mathbb{W}_q := W_q^1((0,a_m),L_q) \cap L_q((0,a_m),W_{q,\mathcal{B}}^2)\ .$$

Then the problem

$$\partial_a u + A(u,a)u = 0\ , \quad a \in (0,a_m)$$
$$u(0) = n\int_0^{a_m} b(u,a)\,u(a)\,\mathrm{d}a$$

admits a branch $\big\{(n_\varepsilon,u_\varepsilon)\,;\,0<\varepsilon<\varepsilon_0\big\}$ *of nontrivial positive solutions in* $\mathbb{R}^+ \times (\mathbb{W}_q^+ \setminus \{0\})$ *bifurcating from* $(n,u)=(1,0)$ *of the form*

$$u_\varepsilon = \varepsilon\big(\Pi_0(\cdot,0)B + z_\varepsilon\big)\ , \quad 0<\varepsilon<\varepsilon_0\ ,$$

with $n_0=1$, $z_0=0$, *and* $[\varepsilon \mapsto z_\varepsilon] \in C\big([0,\varepsilon_0),\mathbb{W}_q\big)$.

Linearized Problem

Lemma

Let $\mathbb{L}_q := L_q((0,a_m),L_q)$ *and consider the linearized problem*

$$\partial_a u + A(0,a)\,u = 0\ , \quad u(0) = \int_0^{a_m} b(0,a)u(a)\,\mathrm{d}a\ .$$

Then

$$Lu := \left(\partial_a u + A(0,\cdot)u\,,\ u(0) - \int_0^{a_m} b(0,a)u(a)\mathrm{d}a\right)$$

defines a Fredholm operator $L \in \mathcal{L}(\mathbb{W}_q, \mathbb{L}_q \times W_{q,\mathcal{B}}^{2-2/q})$ *with*

$$\dim(\ker(L)) = \operatorname{codim}(\operatorname{rg}(L)) = 1\ .$$

Proof.

Maximal regularity of $A(0,\cdot)$; $r(Q_0)$ simple eigenvalue. □

Sketch of Proof

Existence: The problem is equivalent to

$$Lu = T(n, u) \ ,$$

where L is Fredholm operator of index 0, $T \in C^1$.

Then: **Crandall** & **Rabinowitz**

$\Longrightarrow \exists \ (n_\varepsilon, u_\varepsilon)$ with

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Positivity: any solution $(n_\varepsilon, u_\varepsilon)$ satisfies $u_\varepsilon = \Pi_{u_\varepsilon}(\cdot, 0)u_\varepsilon(0)$ and

$$\frac{1}{\varepsilon}u_\varepsilon(0) = B + z_\varepsilon(0) \in W^{2-2/q,+}_{q,\mathcal{B}}\ .$$

Remarks

(i) Extensions:
abstract result, valid for general elliptic operators A (e.g. lower order terms, dependence on a and x)

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(ii) Direction of bifurcation: $n_\varepsilon = 1 + \zeta\varepsilon + o(\varepsilon)$ (ζ known)

Simpler in some cases:

$$n\, r(Q(u)) = 1 \quad \forall (n, u)$$

Ex.: $\mu(u,a) \geq \mu(0,a)$, $b(u,a) \leq b(0,a)$
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(iii) 'Conjecture': $u \equiv 0$ loses stability when the bifurcation parameter n passes through the critical value $n = 1$.

Remarks (cont.)

(iv) Varying mortality intensity:

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(v) Global bifurcation:

$$A(u, a) = A(0, a) + A_*(u, a)\ , \quad A_* \text{ “lower order” perturbation}$$

$\Longrightarrow$ there is an *unbounded continuum* of nontrivial positive solutions (n, u) in $\mathbb{R}^+ \times \mathbb{W}_q^+$

Proof: unilateral global bifurcation results of López-Gómez and Rabinowitz.

An Age-Structured Predator-Prey Model

$u = u(a,x)$: prey, $v = v(a,x)$: predator

$$
\begin{aligned}
\partial_a u - \Delta_D u &= -u^2 - uv && \text{in } (0,a_m)\times\Omega \ ,\\
u(0,x) &= \eta \int_0^{a_m} b_1(a) u(a,x)\,\mathrm{d}a && \text{in } \Omega \ ,\\
\partial_a v - \Delta_D v &= -v^2 + uv && \text{in } (0,a_m)\times\Omega \ ,\\
v(0,x) &= \xi \int_0^{a_m} b_2(a) v(a,x)\,\mathrm{d}a && \text{in } \Omega \ .
\end{aligned}
$$

coexistence solutions (u,v) with $u>0$ and $v>0$

literature (elliptic case): Dancer '84-; Cosner & Lazer '84-; Blat & Brown '84-; López-Gómez '93-;...

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assumptions: $\quad b_j > 0,\ \int_0^{a_m} b_j(a) e^{-\lambda_1 a}\,\mathrm{d}a = 1.$

solution space: $\quad \mathbb{W}_q := W_q^1(J, L_q(\Omega)) \cap L_q(J, W_{q,D}^2(\Omega))$

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Semi-Trivial Branches

Proposition

For each $\eta > 1$ there is a unique solution $u_\eta \in \mathbb{W}_q^+ \setminus \{0\}$ to

$$\partial_a u - \Delta_D u = -u^2 \ , \quad u(0,\cdot) = \eta \int_0^{a_m} b_1(a) u(a,\cdot)\, \mathrm{d}a \ .$$

The solution u_η depends smoothly and increasingly on η with $\|u_\eta\|_\infty \to \infty$ as $\eta \to \infty$. If $\eta \leq 1$, then there is no nontrivial positive solution.

Proof.

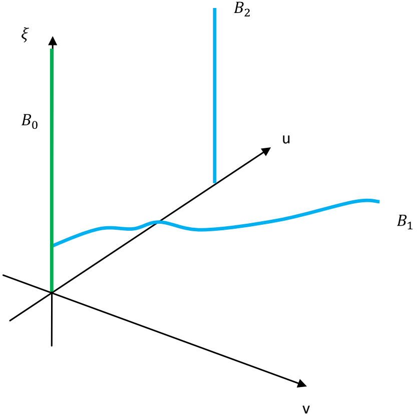
Global bifurcation for

$$A(u) := -\Delta_D + u \ ,$$

comparison principle based on Krein-Rutman (nonlocal initial condition). □

Semi-Trivial Branches ($\eta > 1$ fixed, ξ parameter)

$$B_1 := \{(\xi, 0, v_\xi); \xi > 1\} \ , \quad B_2 := \{(\xi, u_\eta, 0); \xi \geq 0\}$$



Coexistence Steady-States for Parameter ξ

Theorem

If $\eta \leq 1$ there is no nontrivial positive coexistence solution. For $\eta > 1$ there is a unique value $\xi_0(\eta) > 0$ such that a continuum

$$B_3 \subset \mathbb{R}^+ \times (\mathbb{W}_q^+ \setminus \{0\}) \times (\mathbb{W}_q^+ \setminus \{0\})$$

of coexistence solutions emanates to the right from $(\xi_0(\eta), u_\eta, 0) \in B_2$ satisfying the alternatives

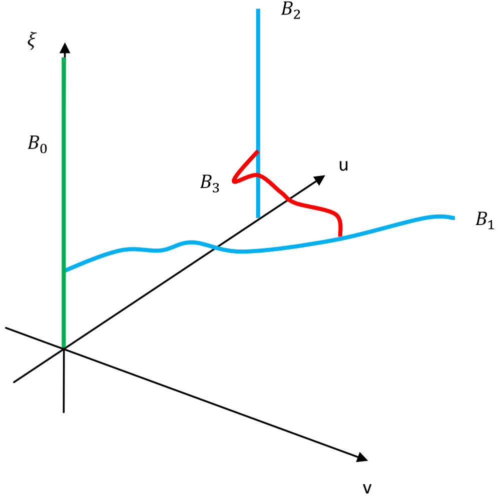
$$(i)\ B_3 \text{ joins } B_2 \text{ with } B_1, \text{ or} \qquad (ii)\ B_3 \text{ is unbounded.}$$

If, in addition,

$$b_2 \in L_1(J, (1 - e^{-sa})^{-1}\mathrm{d}a)$$

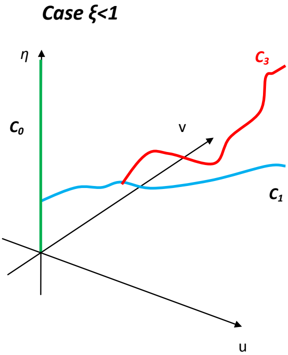
for some $s > 0$, then alternative (i) must occur for $\eta < N$ and if, e.g., $b_2 \geq b_1$, then $N = \infty$.

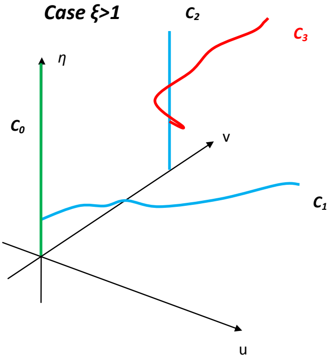
Coexistence Steady-States for Parameter ξ



Coexistence Steady-States for Parameter η

$$C_1 := \{(\eta, u_\eta, 0); \eta > 1\} \ , \quad C_2 := \{(\eta, 0, v_\xi); \eta \geq 0\}$$





References

- *Positive Equilibrium Solutions for Age and Spatially Structured Population Models*, SIAM J. Math. Anal. **41** (2009), 1366-1387.
- *Global Bifurcation of Positive Equilibria in Nonlinear Population Models*, J. Differential Equations **248** (2010), 1756-1776.
- *On Positive Solutions of Some System of Reaction-Diffusion Equations with Nonlocal Initial Conditions*, J. Reine Angew. Math., to appear.