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 (\( \mu \) smooth)

\[ \beta(u, a) \geq 0 \]

birth rate (\( \beta \) smooth)

\[ \text{div}_x (D(u)\nabla_x u) \]

nonlinear diffusion (\( D(u) \geq d_0 > 0 \))
Nonlinear Age-Structured Models with Diffusion

balance equation

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

age boundary condition

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

initial condition

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

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

$$\delta u(t, a, x) + (1 - \delta)\partial_{\nu} u(t, a, x) = 0 , \quad t > 0, \ a \in (0, a_m), \ x \in \partial\Omega$$
Nonlinear Age-Structured Models with Diffusion

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literature: DiBlasio '78-, Webb '82-, Iannelli & Busenberg '83-, Langlais '85-, Thieme '91-, Rhandi & Schnaubelt '95-,
Nonlinear Age-Structured Models with Diffusion

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aim: positive time-independent solutions
For $q$ large let $L_q := L_q(\Omega)$ and $W_{q,B}^2 := W_{q,B}^2(\Omega)$.

For $(u, a)$ fixed define

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

to obtain an unbounded linear operator

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

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

$$\partial_a u + A(u, a) u = 0 \quad \text{in } L_q, \quad a \in (0, a_m),$$

$$u(0) = \int_0^{a_m} \beta(u, a) u(a) \, da \quad \text{in } L_q,$$

**literature** (for $A = \mu$): Prüß ’81-, Cushing ’84-, Webb ’85,...

**literature** (for $A = -\Delta_x + \mu$): Langlais ’85, Delgado & Molina & Suarez ’06, ’08
Equilibrium Solutions

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

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$$A(u, a) : W_{q,B}^2 \subset L_q \rightarrow L_q.$$

time-independent solutions $u : [0, a_m) \rightarrow W_{q,B}^2$ with $u(a) \geq 0$:

$$\partial_a u + A(u, a)u = 0 \quad \text{in } L_q, \quad a \in (0, a_m),$$
$$u(0) = \int_0^{a_m} \beta(u, a) u(a) \, da \quad \text{in } L_q,$$

problem: $u \equiv 0$ is a solution
For $u$ fixed, let

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

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

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

is the unique strong solution to the linear problem

$$\partial_a v + A(u, a)v = 0, \quad a \in (\sigma, a_m)$$

$$v(\sigma) = \phi, \quad \phi \in L_q \text{ and } \sigma \in (0, a_m).$$

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

For $u$ fixed, let

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

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

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

is the unique strong solution to the linear problem

$$\partial_a v + A(u, a)v = 0 , \quad a \in (\sigma, a_m)$$

$$v(\sigma) = \varphi ,$$

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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Reformulation

For $u$ fixed, let

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

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

$$\partial_a u + A(u, a)u = 0 \ , \ a \in (0, a_m)$$

$$u(0) = \int_0^{a_m} \beta(u, a) u(a) \, da$$

is equivalent to

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

with “spatial reproduction number”

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

Note:

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

means that \((u, \phi)\) with \(\phi := u(0)\) is a fixed point of the map

\[ (u, \phi) \mapsto (\Pi_u(\cdot, 0)\phi, Q(u)\phi) \ . \]
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Growth conditions, e.g. on spectral radius \(r(Q(u))\)

\[ \implies \text{nontrivial positive solutions by a fixed point method in 'conical shells'} \]
Let $\beta(u, a) := nb(u, a)$.

$n$ bifurcation parameter (intensity of fertility)

Consider

$$\partial_a u + A(u, a) u = 0, \quad a \in (0, a_m)$$

$$u(0) = n \int_0^{a_m} b(u, a) u(a) \, da,$$
Bifurcation Approach

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$n$ bifurcation parameter (intensity of fertility)

Consider

$$\partial_a u + A(u, a) u = 0 , \quad a \in (0, a_m)$$

$$u(0) = n \int_0^{a_m} b(u, a) u(a) \, da ,$$

where $b$ is normalized such that $r(Q_0) = 1$ for

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

Krein-Rutman: $r(Q_0)$ simple eigenvalue with eigenvector

$$B \in \text{int}(W^{2-2/q}_{q, B, +})$$
Local Bifurcation

Theorem

Let

\[ W_q := W^1_q((0, a_m), L_q) \cap L_q((0, a_m), W^2_{q,B}) . \]

Then the problem

\[ \partial_a u + A(u, a)u = 0 , \quad a \in (0, a_m) \]
\[ u(0) = n \int_0^{a_m} b(u, a)u(a) \, da \]

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

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

with \( n_0 = 1, z_0 = 0, \) and \( [\varepsilon \mapsto z_\varepsilon] \in C([0, \varepsilon_0), W_q) . \)
Lemma

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

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

Then

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

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

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

Proof.

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

\[ \Rightarrow \exists (n_\varepsilon, u_\varepsilon) \text{ with} \]

\[ u_\varepsilon = \varepsilon(\Pi_0(\cdot, 0)B + z_\varepsilon) . \]
Existence: The problem is equivalent to

\[ L u = T(n, u), \]

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

Then: Crandall & Rabinowitz

\[ \implies \exists (n_\varepsilon, u_\varepsilon) \text{ with } u_\varepsilon = \varepsilon (\Pi_0 (\cdot, 0) B + z_\varepsilon). \]

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

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

(i) **Extensions:**

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

(ii) **Direction of bifurcation:**

$$n \varepsilon = 1 + \varepsilon \zeta + o(\varepsilon) \quad (\zeta \text{ known})$$

Simpler in some cases:

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

Ex.:

$$\mu(u, a) \geq \mu(0, a), \quad b(u, a) \leq b(0, a)$$

$\Rightarrow$ supercritical bifurcation

(iii) **Conjecture:**

$u \equiv 0$ loses stability when the bifurcation parameter $n$ passes through the critical value $n = 1$. 
Remarks

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

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

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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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\[ n_\varepsilon = 1 + \zeta \varepsilon + o(\varepsilon) \quad (\zeta \text{ known}) \]

Simpler in some cases:
\[ n r(Q(u)) = 1 \quad \forall (n, u) \]

Ex.: $\mu(u, a) \geq \mu(0, a), b(u, a) \leq b(0, a)$
\[ \implies \text{supercritical bifurcation} \]

(iii) ‘Conjecture’: $u \equiv 0$ loses stability when the bifurcation parameter $n$ passes through the critical value $n = 1$. 
(iv) Varying mortality intensity:

\[ \mu(u, a) = n m(u, a) \]

\[ \Rightarrow \text{local bifurcation, subcritical} \]
Remarks (cont.)

(iv) Varying mortality intensity:

\[ \mu(u, a) = n m(u, a) \]

\[ \Rightarrow \text{local bifurcation, subcritical} \]

(v) Global bifurcation:

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

\[ \Rightarrow \text{there is an unbounded continuum of nontrivial positive solutions} \]

\[ (n, u) \text{ in } \mathbb{R}^+ \times \mathbb{W}^+_q \]

Proof: unilateral global bifurcation results of López-Gómez and Rabinowitz.
An Age-Structured Predator-Prey Model

\( u = u(a, x) \): prey, \quad \nu = \nu(a, x) \): predator

\[
\partial_a u - \Delta_D u = -u^2 - uv \quad \text{in } (0, a_m) \times \Omega,
\]

\[
u(0, x) = \eta \int_0^{a_m} b_1(a) u(a, x) \, da \quad \text{in } \Omega,
\]

\[
\partial_a \nu - \Delta_D \nu = -\nu^2 + uv \quad \text{in } (0, a_m) \times \Omega,
\]

\[
u(0, x) = \xi \int_0^{a_m} b_2(a) \nu(a, x) \, da \quad \text{in } \Omega.
\]

**coexistence solutions** \((u, \nu)\) with \(u > 0\) and \(\nu > 0\)

**literature** (elliptic case): Dancer ’84-; Cosner & Lazer ’84-; Blat & Brown ’84-; López-Gómez ’93-;...
An Age-Structured Predator-Prey Model

\[ u = u(a, x): \text{prey, \ } v = v(a, x): \text{predator} \]

\[ \partial_a u - \Delta_D u = -u^2 - uv \quad \text{in } (0, a_m) \times \Omega , \]

\[ u(0, x) = \eta \int_0^{a_m} b_1(a)u(a, x)\,da \quad \text{in } \Omega , \]

\[ \partial_a v - \Delta_D v = -v^2 + uv \quad \text{in } (0, a_m) \times \Omega , \]

\[ v(0, x) = \xi \int_0^{a_m} b_2(a)v(a, x)\,da \quad \text{in } \Omega . \]

assumptions: \[ b_j > 0, \int_0^{a_m} b_j(a)e^{-\lambda_1a}\,da = 1. \]

solution space: \[ \mathbb{W}_q := W^1_q(J, L_q(\Omega)) \cap L_q(J, W^2_{q,D}(\Omega)) \]
An Age-Structured Predator-Prey Model

\[ u = u(a, x): \text{prey}, \quad v = v(a, x): \text{predator} \]

\[ \partial_a u - \Delta_D u = -u^2 \quad \text{in } (0, a_m) \times \Omega, \]

\[ u(0, x) = \eta \int_0^{a_m} b_1(a)u(a, x) \, da \quad \text{in } \Omega, \]

**assumptions:** \( b_j > 0, \int_0^{a_m} b_j(a)e^{-\lambda_1 a} \, da = 1. \)

**solution space:** \( W_q := W^1_q(J, L_q(\Omega)) \cap L_q(J, W^2_{q,D}(\Omega)) \)
Semi-Trivial Branches

Proposition

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

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

The solution $u_\eta$ depends smoothly and increasingly on $\eta$ 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, $\xi$ parameter)

\[ B_1 := \{ (\xi, 0, v_\xi); \xi > 1 \} , \quad B_2 := \{ (\xi, u_\eta, 0); \xi \geq 0 \} \]
Coexistence Steady-States for Parameter $\xi$

**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) $B_3$ joins $B_2$ with $B_1$, or

(ii) $B_3$ is unbounded.

If, in addition,

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

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

Ch. Walker (LUH)
Coexistence Steady-States for Parameter $\xi$
Coexistence Steady-States for Parameter $\eta$

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

