A nonlinear age-structured model of semelparous species.

Radosław Wieczorek

University of Silesia
Katowice, Poland

Micro and Macro Systems in Life Sciences,
June, 8–13, 2015.

What is a semelparous species?

- an organism reproduces only once in its lifetime,
- usually dies afterwards,

What is a semelparous species?

- an organism reproduces only once in its lifetime,
- usually dies afterwards,
- we consider only species with lifespan of fixed length.

What is a semelparous species?

- cereals and grasses,

- an organism reproduces only once in its lifetime,
- usually dies afterwards,
- we consider only species with lifespan of fixed length.

What is a semelparous species?

- cereals and grasses,
- beet, carrot, cabbage, onion, lettuce

What is a semelparous species?

- cereals and grasses,
- beet, carrot, cabbage, onion, lettuce
- agave,

What is a semelparous species?

- cereals and grasses,
- beet, carrot, cabbage, onion, lettuce
- agave,
- bamboo,

What is a semelparous species?

- cereals and grasses,
- beet, carrot, cabbage, onion, lettuce
- agave,
- bamboo,
- arachnids and insects: magicicada

Age-structured models

Discrete-time model:

$x(t,a)$ — number of individuals of age a at time t.
$\mathbf{x}(t) = [x(t,1),\ldots,x(t,n)]$ — vector of subpopulation sizes.

Nonlinear Leslie model: $\mathbf{x}(t+1) = A(\mathbf{x})\,\mathbf{x}(t)$

Continues-time model:

$u(t,a)$ — age distribution of population at time t.
Evolution of population described by McKendricka-type system

$$\text{Evolution eqaution:} \begin{cases} \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu u(t,a) \\ u(t,0) = \beta(u) \\ u(0,a) = u_0(a) \end{cases}$$

Discrete-time model of n-years semelparous species

only speciments at age n can proliferate

$x(t, a)$ — number of individuals of age a at time t

Equations:

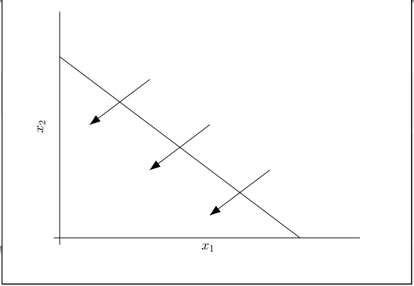
$$\begin{cases} x(t+1, a+1) = [1 - \mu(a, N(t))]x(t, a), \\ x(t+1, 1) = b(N(t))x(t, n), \end{cases}$$

- $N(t) = \sum_{a=1}^{n} x(t, a)$ — size of population at t
- μ — mortality rate,
- b — birth rate (average number of offspring)
  b is a positive decreasing function of N:

Stationary states

Trajectories are bounded

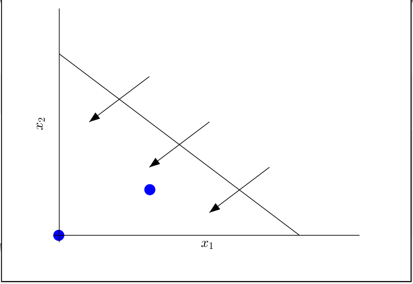
— there exists a compact positively invariant set



Stationary states

Trajectories are bounded

— there exists a compact positively invariant set

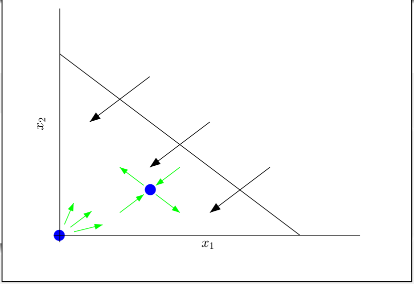


There exist exactly two stationary states:

- $x = 0$ — a trivial one
- $$\begin{cases} x_1^* = \frac{N_0}{\sum_{i=1}^{n} r(i)} \\ x_2^* = r(2) x_1^*, \\ \vdots \\ x_n^* = r(n) x_1^* \end{cases}$$ where $r(1) = 1$ and $r(i) = q(1) \cdots q(i-1)$, and $N_0 \in (0, N_{max})$ such that $r(n) b(N_0) = 1$

Stationary states

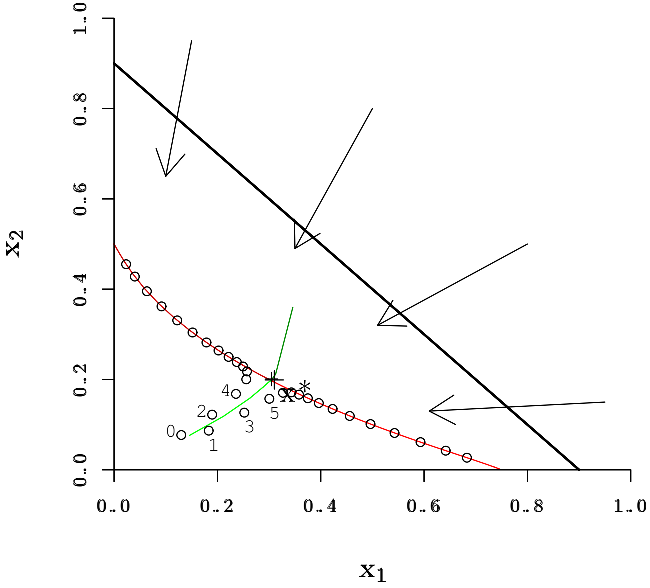
Trajectories are bounded
— there exists a compact positively invariant set



There exist exactly two stationary states:

- $x = 0$ — always repulsive

- $$\begin{cases} x_1^* = \frac{N_0}{\sum_{i=1}^{n} r(i)} \\ x_2^* = r(2) x_1^*, \\ \vdots \\ x_n^* = r(n) x_1^* \end{cases}$$ — unstable if n is even (and most often for odd n)



Two-year species: x_1, x_2 — age 1 and 2. x^* — steady state.

The competition between different age-classes results in the extinction of all but one age-classes.

age-class - speciments in the same age

Asymptoticaly, the behaviour of the population resembles the behaviour of a population consisted of one-year class only, described by a one-dimentional dynamical system g:

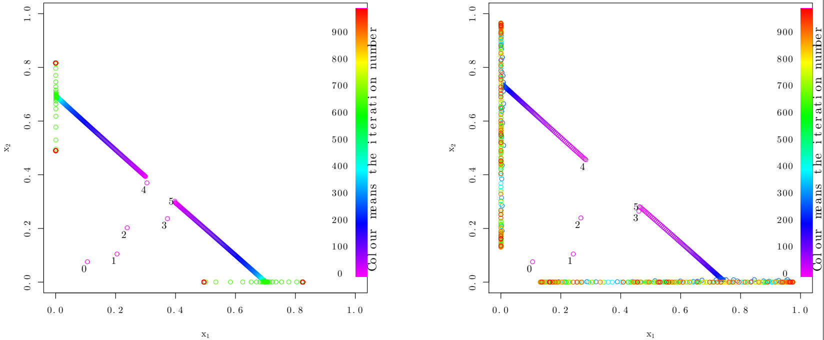
$$g(x) = b(r(n)x)\, r(n)\, x$$

$$\begin{bmatrix} x_1 \\ 0 \\ \vdots \\ 0 \end{bmatrix} \xrightarrow{\text{after } n \text{ steps}} \begin{bmatrix} g(x_1) \\ 0 \\ \vdots \\ 0 \end{bmatrix}$$

- stable point of g becomes a stable n-periodic orbit of the model,
- (stable) k-periodic orbit of transfomation g becomes a (stable) kn-periodic orbit of the model.

The competition between different age-classes results in the extinction of all but one age-classes.

age-class - speciments in the same age



periodic g with period 2

chaotic g

Transition to the continuous-time model

$x(t, a)$ – vector of numbers	step: 1	n– max. age
$\downarrow$	$\downarrow$	$\downarrow$
$u(t, a)$ – population density	step: $\Delta t \ll 1$	$m = n\Delta t$

$$x(t+1, a+1) = [1 - \mu(a, N(t))]x(t, a), \quad a = 2, ..., n$$

$$x(t+1, 1) = b(N(t))x(t, n),$$

Transition to the continuous-time model

$x(t,a)$ – vector of numbers	step: 1	n– max. age
$\downarrow$	$\downarrow$	$\downarrow$
$u(t,a)$ – population density	step: $\Delta t \ll 1$	$m = n\Delta t$

$$x(t+1, a+1) = [1-\mu(a, N(t))]x(t,a), \quad a = 2, ..., n$$

$$u(t+\Delta t, a+\Delta t) - u(t,a) = -\Delta t \mu(a) u(t,a) + o(\Delta t)$$

$$\downarrow \qquad \downarrow$$

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu(a)u$$

$$x(t+1, 1) = b(N(t))x(t,n),$$

$$u(t+\Delta t, \Delta t) = b(N(t))u(t, n\Delta t),$$

$$\downarrow \qquad \downarrow$$

$$u(t,0) = \beta(N(t))u(t,m)$$

Continuous-time model

We consider the McKendrick-type equation of the form:

$$(MK) \qquad \begin{cases} \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu(a)\, u(t,a), \\ u(t,0) = \beta(N(t))u(t,m), \end{cases}$$

where:

- $N(t) = \int_0^a u(t,a)\, da,$ — total mass of population
- m — maximal age of the specimen and age of reproduction
- μ — mortality rate
- β — birth rate

Assumptions:

- μ, β — continuous and positive functions
- β — decreasing
- $\beta(0)\phi(m) > 1$ (persistence)
- $\beta(\infty)\phi(m) < 1$ (boundedness)

Continuous-time model

$\left[u(t,a) \text{ — distribution of the population in time and age} \right]$

We consider the McKendrick-type equation of the form:

$$(MK) \qquad \begin{cases} \frac{\partial u(t,a)}{\partial t} + \frac{\partial u(t,a)}{\partial a} = -\mu(a)\, u(t,a), \\ u(t,0) = \beta(N(t))u(t,1), \end{cases}$$

where:

- $N(t) = \int_0^a u(t,a)\, da$, — total mass of population
- 1 — maximal age of the specimen and age of reproduction
- μ — mortality rate
- β — birth rate

Assumptions:

- μ, β — continuous and positive functions
- β — decreasing
- $\beta(0)\phi(1) > 1$ (persistence)
- $\beta(\infty)\phi(1) < 1$ (boundedness)

The renewal equation [the standard method of investigating McKendrick equation]

solving along the characteristics:

$$(\star) \qquad u(t,a) = \phi(a)u(t-a,0),$$

[where $\phi(a) = e^{-\int_0^a \mu(s)ds}$ is a survivorship function]

plus

$$u(t,0) = \beta(N(t))u(t,1),$$

[boundary condition]

give the so-called renewal equation:

$$(\star\star) \qquad u(t,0) = \beta\left(\int_0^1 \phi(a)u(t-a,0)\,da\right)\phi(1)u(t-1,0).$$

Having the solution of $(\star\star)$ we can use $(\star)$ to reconstruct the solution of the McKendrick equation (MK).

The renewal equation

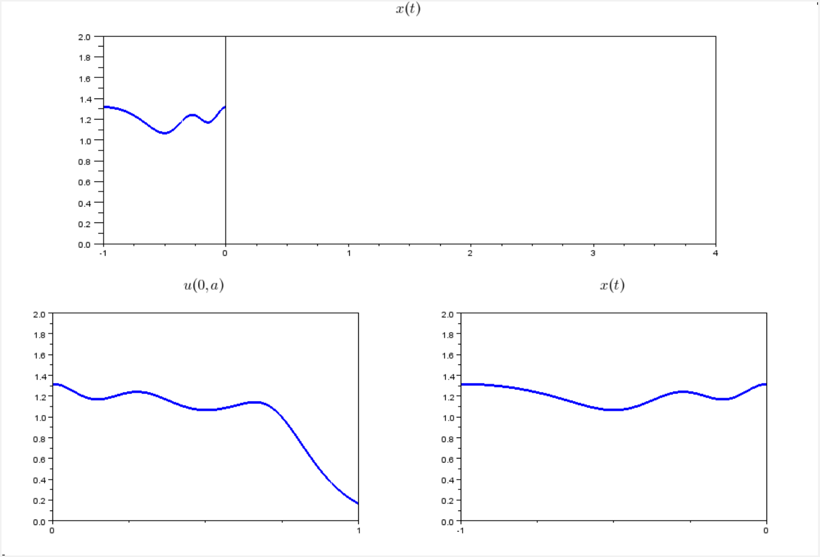
$$u(t,0) = \phi(1)\beta\left(\int_0^1 \phi(a)u(t-a,0)\,da\right)u(t-1,0)$$

Denote $x(t) = u(t,0)$ and $f(y) = \phi(1)\beta(y)$.
So, we consider the equation of the form

$$(RE)\quad \begin{cases} x(t) = f\left(\int_0^1 \phi(a)x(t-a)\,da\right)x(t-1), & t \geqslant 0, \\ x(t) = x_0(t), t \in [-1,0), & \text{[initial condition]} \end{cases}$$

with assumptions:

- ϕ — continuously differentiable, positive and strictly decreasing with $\phi(0) = 1$.
- f — decreasing, $f(0) > 1$ and $f(1) = 1$.


$x(t)$
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-1
0
1
2
3
4
$u(0,a)$
0
1
$x(t)$
-1
0

Stationary solutions

of the equation:

$$(RE) \qquad x(t) = f\left(\int_0^1 \phi(a)x(t-a)\,da \right) x(t-1), \quad t \geqslant 0,$$

- a trivial stationary solution $x(t) = 0$
- a positive one: $x^* = 1/\overline{\phi}$, where $\overline{\phi} = \int_0^1 \phi(a)\,da$.

These solutions give the only two stationary solutions of (MK), namely:

$$u(t,a) = 0 \qquad \text{[repulsive]}$$

and

$$u(t,a) = \phi(a)/\overline{\phi}. \qquad \text{[not stable]}$$

Periodic solutions with period = lifespan

For x to be an 1-periodic solution of (RE), we need

$$x(t) = f\left(\int_0^1 \phi(a)x(t-a)\,da \right) x(t),$$

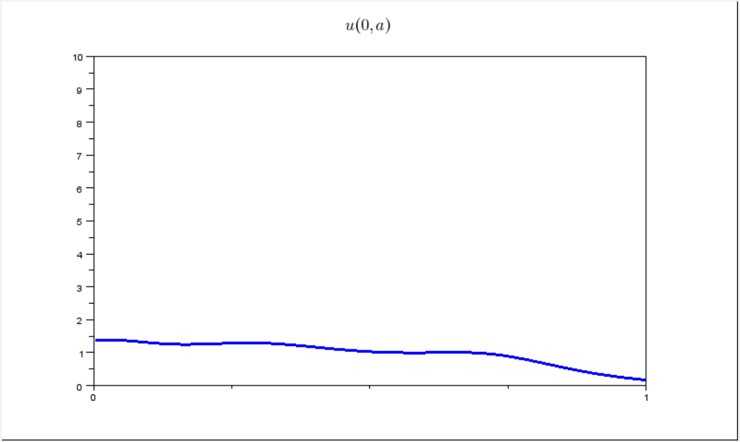
which is satisfied if for each $t \geqslant 0$ we have

$$\text{either} \quad \int_0^1 \phi(a)x(t-a)\,da = 1 \quad \text{or} \quad x(t) = 0$$

Theorem

The only two 1-periodic non-negative classical (L^1_{loc}) solutions of the renewal equation (RE) are the stationary ones, namely, 0 and x^* (given before).

Why to investigate measure-valued solutions?



Measure solutions

A measure x on $[-1,\infty)$ is called a measure solution of the renewal equation if

$$(\star) \qquad x(t) = f\Big(\phi * x\,(t)\Big)x(t-1), \quad t \geqslant 0,$$

where

$$\phi * x\,(t) = \int_{[t-1,t)} \phi(t-a)x(da), \quad t \geqslant 0.$$

By $(\star)$ we mean

$$x\Big([0,t)\Big) = \int_{[-1,t-1)} f\Big(\phi * x\,(s+1)\Big)x(ds), \text{ for all } t \geqslant 0.$$

Theorem

The only atomless measures that are 1-periodic solutions of $(\star)$ are the stationary ones (0 and x^*).

Purely atomic solutions with period = lifespan

Take some (finite or infinite) sequence $t_n \in [0,1)$. There exists a sequence of coefficients $\alpha_n > 0$ satisfying a system

$$\sum_i \alpha_i \phi(\lfloor t_n - t_i \rceil) = C_0, \text{ for all } n, \quad \text{where } \lfloor s \rceil = \begin{cases} s, & \text{if } s > 0, \\ s+1, & \text{if } s \leqslant 0. \end{cases}$$

such that a 1-periodic measure defined on $[0,1)$ by

$$x\Big|_{[0,1)} = \sum_n \alpha_n \delta_{t_n} \quad \text{satisfies } (RE).$$

[δ_t — Dirac measure at t]

One age-class solution — single Dirac delta

$\displaystyle\sum_{k=1}^{\infty} \frac{1}{\phi(1)} \delta_k$ is a 1-periodic solution of (RE)

$u(t) = \frac{\phi(t - \lfloor t \rfloor)}{\phi(1)} \delta_{t - \lfloor t \rfloor}$ is a 1-periodic solution of (MK)

Convergence to delta

If the initial function is supported on a small interval,
then the solution of (MK) converges to
a periodic solution consisted of a travelling Dirac delta:

Theorem

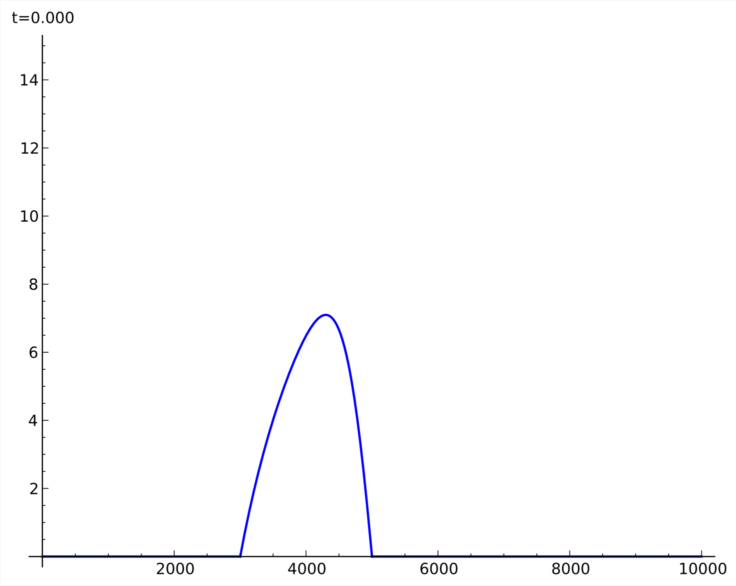
There exists $\rho > 0$ (depending on f and ϕ) such that if the initial function $u(0, a)$ is coutinuous and supported on the interval $(\alpha, 1)$ shorter than ρ then

$$u(t, a) \xrightarrow{t\to\infty} \tilde{u}_t = \alpha_0 \phi(t - \lfloor t \rfloor)\delta_{t-\lfloor t \rfloor}(s) \qquad \left[\begin{smallmatrix}\text{travelling} \\ \text{delta}\end{smallmatrix}\right]$$

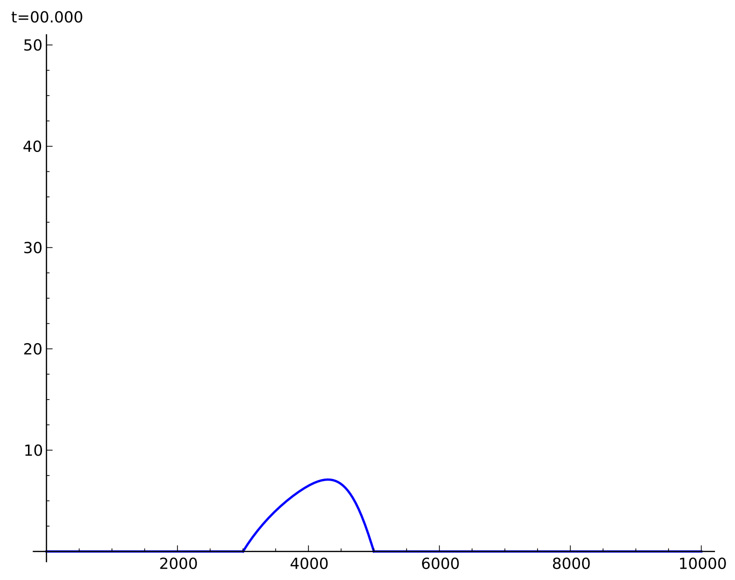
where α_0 is the uniquely defined by ϕ and f.

Precisely,
$\int_k^{k+1} x(s)ds \to \alpha_0$ and $\int_{k+\delta}^{k+1} x(s)ds \to 0$ for any $\delta > 0$
It's equivalent to the weak/weak*/flat convergence of measures: $u_t - \tilde{u}_t \xrightarrow{w} 0$, where $u_t(da) = u(t, a)da$

Convergence to delta



Convergence to delta



Convergence to delta?

Remark

The limit solution for a continues initial state:

$$\alpha_0 \phi(t - \lfloor t \rfloor)\delta_{t-\lfloor t \rfloor}$$

differs from the travelling delta measure solution:

$$\frac{1}{\phi(1)}\phi(t - \lfloor t \rfloor)\delta_{t-\lfloor t \rfloor}$$

The convergence depends on the initial condition:

Theorem

There exists $0 < \rho_1 < 1 - \rho$ such that if the gap in the support of the initial function is shorter then ρ_1 then the convergence to a traveling delta is impossible.

Some bibliography

[1] Odo Diekmann, Natalia Davydova, and Stephan van Gils, *On a boom and bust year class cycle*, J. Difference Equ. Appl. (2005)

[2] Rui Dilão and Abdelkader Lakmeche, *On the weak solutions of the McKendrick equation: existence of demography cycles*, Math. Model. Nat. Phenom. **1** (2006)

[3] Ryszard Rudnicki and Radosław Wieczorek, *Asymptotic analysis of a semelparous species model*, Fund. Informaticae (2010)

[4] Ryszard Rudnicki and Radosław Wieczorek, *A nonlinear age-structured model of semelparous species*, Discr. Cont. Dynamical Systems-B (2014)