Age-dependent single-species population dynamics with delayed argument

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Outline

History of applications of mathematics in biology and medicine

1202	Fibonacci sequence ("*Liber Abaci*")
1798	Malthus equation
1838	Verhulst equation
1926	Classical von Foerster model
1974	Gurtin and MacCamy model

von Foerster model

The first model applicable to age-dependent population dynamics was proposed by von Foerster in 1926.

$u(x, t)$ denote the density of a decomposition of the individuals in age x at time t;

$z(t)$ the total population at time t denoted by the formula:

$$z(t) = \int_0^\infty u(x, t)dx$$

von Foerster model

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial x} = -\lambda(x)u(x,t)$$

$$u(x,0) = v(x)$$

$$u(0,t) = \int_0^\infty \beta(x)u(x,t)dx$$

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The equation called in the literature as *McKendrick equation* or, more often, as *von Foerster equation*.

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The model considers mortality.

$\lambda(x)$ is called the *death-modulus* and describes the mortality per unit time individuals of age x

von Foerster model

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Initial condition

von Foerster model

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial x} = -\lambda(x)u(x,t)$$

$$u(x,0) = v(x)$$

$$u(0,t) = \int_0^\infty \beta(x)u(x,t)dx$$

The birth process is described by the *renewal equation*.

$\beta(x)$ — *birth-modulus*, it is the average number of offsprings produced (per unit time) by an individual of age x

Gurtin and MacCamy model

The model proposed by Gurtin and MacCamy (1974) was based on the assumption that the progress of the population depends on its number

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial x} = -\lambda(x, z(t))u(x,t)$$

$$u(x,0) = v(x)$$

$$u(0,t) = \int_0^\infty \beta(x, z(t))u(x,t)dx$$

$$z(t) = \int_0^\infty u(x,t)dx$$

Age-dependent model with delayed argument

Our theory is based on the following system of the equations

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial x} = -\lambda(x, z_t)u(x,t)$$

$$z(t) = \int_0^\infty u(x,t)dx$$

$$u(0,t) = \int_0^\infty \beta(x, z_t)u(x,t)dx$$

$$u(x,0) = v(x),$$

where

$$z_t : [-r, 0] \to [0, \infty), \quad r \geqslant 0, \quad z_t = z(t+s)$$

Biological justification

It is common knowledge that other factors can have an influence on the reproduction, for example:

- a period of gestation;
- a period of response of a system to stimulus.

These examples suggest the necessity to consider the descriptions with delayed parameter. The delay is natural assumption in every biological models, concerning for example problems of epidemiology and immunology.

Global assumptions

(H_1) $\varphi \in L^1(\mathbb{R}_+)$ is piecewise continuous;

(H_2) $\lambda, \beta \in C\left(\mathbb{R}_+ \times C([-r,0])\right)$; the Fréchet derivatives $D\lambda$ of $\lambda(x,\psi)$ and $D\beta$ of $\beta(x,\psi)$ with respect to ψ exist for all $x \geqslant 0$ and $\psi \geqslant 0$;

(H_3) The functions $\lambda(\cdot,\psi)$, $\beta(\cdot,\psi)$ belong to $C\left(C([-r,0]); L^\infty(\mathbb{R}_+)\right)$;

(H_4) The Fréchet derivatives $D_{\psi_0}\lambda$ and $D_{\psi_0}\beta$ in the point ψ_0 as a function of ψ_0 belong to $C\left(C([-r,0]); \mathcal{L}\left(C([-r,0]); L^\infty(\mathbb{R}_+)\right)\right)$, where $\mathcal{L}(X,Y)$ denotes the Banach space of all bounded linear operators from X to Y;

(H_5) $\varphi \geqslant 0$, $\lambda \geqslant 0$, $\beta \geqslant 0$.

Generalization and precursor

The elements which distinguish the model with delayed argument from Gurtin nad MacCamy's one:

- the reproduction as the death depend on the population in any preceding period of time;
- the dependence of λ and β on the variable z is functional one;
- we consider the Fréchet derivatives of the functions λ and β instead of their partial derivatives.

Main results

Equivalent expression of the problem

Let u be a solution of the age-dependent population problem up to time $T > 0$. Then the population z_t and the birth-rate B satisfy on $[0, T]$ the operator equations

$$z_t(s) = \int_0^{t+s} B(x)e^{-\int_x^{t+s} \lambda(\tau-x,z_\tau)d\tau} dx + \int_0^{\infty} \varphi(x)e^{-\int_0^{t+s} \lambda(x,z_\tau)d\tau} dx \qquad (1)$$

and

$$B(t) = \int_0^{t} \beta(t-x, z_t)B(x)e^{-\int_x^{t} \lambda(\tau-x,z_\tau)d\tau} dx + \int_0^{\infty} \beta(x+t, z_t)\varphi(x)e^{-\int_0^{t} \lambda(x+\tau,z_\tau)d\tau} dx. \qquad (2)$$

Main results

Equivalent expression of the problem, continuation

Conversely, if z_t and B are non-negative continuous functions satisfying (1) and (2) on $[0, T]$, and if u is defined on $\mathbb{R}_+ \times [0, T]$ by the formula

$$u(x,t) = \begin{cases} \varphi(x-t)e^{-\int_0^t \lambda(x-t+\tau, z_\tau)d\tau} & \text{for} \quad x \geqslant t \\ B(t-x)e^{-\int_0^x \lambda(\alpha, z_{t-x+\alpha})d\alpha} & \text{for} \quad t > x \end{cases},$$

then u is a solution of the age-dependent population problem up to time T.

Main results

$$B(t) = \int_0^t \beta(t-x, z_t) B(x) e^{-\int_x^t \lambda(\tau - x, z_\tau) d\tau} dx + \int_0^\infty \beta(x+t, z_t) \varphi(x) e^{-\int_0^t \lambda(x+\tau, z_\tau) d\tau} dx.$$

$$\mathcal{Z}_T(z)(s) = \int_0^{t+s} \mathcal{B}_T(z)(x) e^{-\int_x^{t+s} \lambda(\tau - x, z_\tau) d\tau} dx + \int_0^\infty \varphi(a) e^{-\int_0^{t+s} \lambda(a+\tau, z_\tau) d\tau} da.$$

Main results

$$B(t) = \mathcal{B}_T(z)(t)$$

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Main results

Lemma

There exists $T > 0$ such that the operator $\mathcal{Z}_T : C^+[-r,T] \to C^+[-r,T]$ defined by

$$\begin{aligned}\mathcal{Z}_T(z)(s) &= \int_0^{t+s} \mathcal{B}_T(z)(x) e^{-\int_x^{t+s} \lambda(\tau - x, z_\tau) d\tau} dx \\ &+ \int_0^{\infty} \varphi(a) e^{-\int_0^{t+s} \lambda(a+\tau, z_\tau) d\tau} da.\end{aligned}$$

has a unique fixed point.

Main results

Local existence of the solution

There exists $T > 0$ such that the population problem has a unique solution up to time T.

Global existence of the solution

If the average number of offsprings (per unit time) $\beta(x, z_t)$ is uniformly bounded for all x and z_t, i.e. $\overline{\beta} = \sup_{\substack{x \geqslant 0 \\ z_t \geqslant 0}} \beta(x, z_t) < \infty$, then the age-dependent population problem has a unique solution for all time.

Stability of the equilibrium age distribution

Conclusions

Von Foerster model	the dependence of the population dynamics on age;
Gurtin-MacCamy model	the reproduction as the death depend on the number of the population;
The above model	functional dependence of the birth and death moduli on the population in any preceding period of time.