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Asymptotic behaviour of a structured population model☆

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ABSTRACT

We consider a first order partial differential equation with a transformed argument which describes a model of the maturity-structured cell population. A new criterion for an asynchronous exponential growth of the solution to such an equation is given.

1. Introduction

In this paper we study a general maturity-structured population model described by the following equation:

$$\frac{\partial N(t,m)}{\partial t}+\frac{\partial (g(m)N(t,m))}{\partial m}=-\mu(m)N(t,m)+PN(t,m). \tag{1}$$

We consider Eq. (1) with the boundary condition

$$g(a)N(t,a)=\int_a^1 b^a(m)N(t,m)\,dm \tag{2}$$

appearing frequently in age-structured models. The variable m, called maturity, describes a state of a cell and is a number from the interval $[a,1]$. We denote by $\mu(m)$ the rate of loss of individuals by death and division. The maturity changes according to the equation

$$\frac{dm}{dt}=g(m). \tag{3}$$

In models similar to (1), assumptions that guarantee the boundedness of cell maturity, play an important role. Here we assume, as in [1], that $g(1)=0$. This condition guarantees that the maturity variable cannot exceed 1. Note that models of cellular replication studied in [2–5] are based on a different biological assumption expressed as $\int_a^1 \mu(m)\,dm=\infty$ which means that the death rate is unbounded at $m=1$. An advantage of our approach is that both the birth and death rates can be bounded.

Structured population models have a long history [6–11]. Generally, one can consider two types of structured models: with equal [1,3,4,12,13] and unequal fission [14–18]. Moreover, there are also a few models of both types of binary fission,

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see e.g. [5]. In a recent paper [2] the authors consider a model with general division processes including age-structured models. The division operator in our model is the same as in [2]. To keep the paper self contained we recall assumptions concerning the replication process. We assume that a cell with maturity m produces k individuals and that a transition probability function $\mathcal{P}_k(m, A)$ is the probability that any of its descendants has the maturity in the set A, where $A \in \Sigma$ and Σ is the σ-algebra of Borel subsets of $[a, 1]$. A cell with a maturity m has

$$\mathcal{P}(m, A) = \sum_{k=1}^{\infty} k b_k(m) \mathcal{P}_k(m, A) \tag{4}$$

descendants with parameters in the set A in a unit of time, where $b_k(m)$ denotes the rate at which a cell with maturity m produces k individuals. By

$$b(m) = \sum_{k=1}^{\infty} k b_k(m) \tag{5}$$

we denote the mean number of its descendants in a unit of time. Let $b^a(m) = \mathcal{P}(m, \{a\})$ and $b^r(m) = \mathcal{P}^r(m, [a, 1])$, where

$$\mathcal{P}^r(m, A) = \mathcal{P}(m, A \setminus \{a\}). \tag{6}$$

We assume that for each m the measure $\mathcal{P}^r(m, \cdot)$ is absolutely continuous with respect to the Lebesgue measure for a.e. m. Then, by the Radon–Nikodym theorem, there exists a unique operator P defined on the space $L^1[a, 1]$ such that for each nonnegative function $f \in L^1[a, 1]$ and each set $A \in \Sigma$ we have

$$\int_A Pf(m)\, dm = \int_a^1 \mathcal{P}^r(m, A) f(m)\, dm. \tag{7}$$

The main result of this paper (Theorem 1) gives sufficient conditions for solutions of Eq. (1) to have asynchronous exponential growth (AEG), i.e.

$$N(m, t) \sim C e^{\lambda t} v(m) \quad \text{if } t \to \infty, \tag{8}$$

where $v(m)$ is a stationary maturity profile. The proof of the main result uses techniques of stochastic semigroups [5,19–22] and it mainly relies on a theorem concerning asymptotic stability of partially integral stochastic semigroups [21]. The AEG property is usually verified by methods from spectral theory of positive semigroups [23] which are technically difficult. Our approach does not require the analysis of the whole spectrum of the generator of the semigroup. The novelty of our methods is the application of Proposition 5 from [21], which states that a partially integral stochastic semigroup is asymptotically stable iff it has a unique and positive invariant density.

The outline of the paper is as follows. The main result is formulated in Section 2. In Section 3 we show that an operator which appears in the dual equation has a positive eigenvector. In Section 4 we show that Eq. (1) generates a semigroup $\{T(t)\}_{t\ge 0}$ of nonnegative operators and, by making a change of variables, we replace Eq. (1) with another one which generates a stochastic semigroup $\{S(t)\}_{t\ge 0}$. In Section 5 we construct the unique invariant positive density for the stochastic semigroup $\{S(t)\}_{t\ge 0}$. Section 6 contains the proof of the main result. We show that the semigroup $\{S(t)\}_{t\ge 0}$ is asymptotically stable, which implies that semigroup $\{T(t)\}_{t\ge 0}$ has asynchronous exponential growth.

2. Formulation of the result

Let $N(t, m)$ be the density of individuals with maturity m at time t. Then $\int_{m_1}^{m_2} N(t, m)\, dm$ denotes the number of cells at time t with the parameter m from the interval $[m_1, m_2]$. We study Eq. (1) with boundary condition (2) and with the initial condition

$$N(0, m) = N_0(m) \quad \text{for } m \in [a, 1]. \tag{9}$$

We assume that $g\colon [a, 1] \to [0, \infty)$ is a continuously differentiable function satisfying $g(m) > 0$ for $m \in [a, 1)$ with $g(1) = 0$ and that the functions $\mu, b^a, b^r, b\colon [a, 1) \to [0, \infty)$ are bounded, continuous, and measurable. We additionally assume that the derivatives $\mu'(1), g'(1)$ exist with $g'(1) < 0$ and that for every $\overline{m} \in (a, 1)$

$$\int_{\overline{m}}^1 \mathcal{P}(m, [a, \overline{m}))\, dm > 0. \tag{10}$$

One can interpret (10) as follows: for every $\overline{m} \in (a, 1)$ a cell with parameter less than $\overline{m}$ can be a daughter of a cell with parameter greater than $\overline{m}$. We also assume that a mother cell with parameter m cannot have daughters with parameter greater than $m - h$ which can be stated as

$$\mathcal{P}_k(m, [a, m - h]) = 1 \quad \text{for all } m \in [a, 1],\ k \ge 1. \tag{11}$$