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Delay equation models for populations that experience competition at immature life stages

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Abstract

We consider stage-structured population models of intra- and inter-specific competition at immature life stages. A prototype delay model is derived for a single species that experiences larval competition. Its solutions are bounded for any birth function. Other ways of modelling the birth rate can lead to nonlinear integral equations. In some situations the technique of reducing an age-structured model to a system of delay equations applies. In the case of immature competition the delay equations cannot always be written down explicitly because their right hand sides depend on the solutions of the nonlinear ordinary differential equations that arise when one solves the nonlinear age-structured equations that determine the maturation rates in terms of the birth rates. This situation arises in the case of competition between two strains or species. However, in our two-strain competition model, vital properties of those right hand sides can be indirectly inferred using monotone systems theory.

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1. Introduction

Stage structured models of populations commonly divide the population into immature and mature individuals. Immature individuals are often defined as those of age less than some fixed threshold age τ, and mature individuals are those of age exceeding τ. We usually consider τ to be the age at which sexual activity begins. In the case of a single species, with a denoting age it is common practice to work with a variable $u(t,a)$ defined as the age density of the species at time t, and to start with the McKendrick–von Foerster equation

$$\left(\frac{\partial}{\partial t}+\frac{\partial}{\partial a}\right)u(t,a)=\begin{cases}-\mu_l\,u(t,a), & 0<a<\tau,\\ -\mu_m\,u(t,a), & a>\tau,\end{cases}$$

subject to the birth law $u(t,0)=b(A(t))$, where $A(t)=\int_\tau^\infty u(t,a)\,da$ is the total number of sexually mature adults. This is a particular case of a model we present in Section 2, and one can reformulate as the following delay differential equation for $A(t)$:

$$\frac{dA(t)}{dt}=e^{-\mu_l\tau}b(A(t-\tau))-\mu_m A(t) \tag{1.1}$$

which is Eq. (2.11) of this paper, in the case $k_l=0$. A significant problem with this approach is that it presumes that competitive effects occur only among the adults. The competition effect is modelled solely by the way we choose the function $b(\cdot)$. This function might level off or even decrease at large densities due to competition among the adults for space or resources, and in this way we reason that their egg laying rate is affected by this competition. Competition enters the model in no other way, and in particular it is assumed that there is no competition among immature individuals who simply experience a density-independent per-capita death rate μ_l throughout their development.

However, there is plenty of evidence that strong intra- or inter-specific competition can occur at the immature life stage as well. Gilpin [5] discusses larval competition as a growth-regulating mechanism in *Drosophila*. Prado et al. [12] present evidence of intra-specific competition among the larvae of pit-trapping antlions in Brazil. Armistead et al. [2] describe inter-specific competition between the larvae of two mosquito species in the USA, *Aedes albopictus* and *Aedes japonicus*, suggesting that *Ae. albopictus* larvae have a competitive advantage over those of *Ae. japonicus*. Blanchard et al. [3] describe competition between the larvae of the American slipper limpet *Crepidula fornicata* and the Japanese oyster *Crassostrea gigas*, and report results which suggest that limpet larvae compete with oyster larvae by depleting phytoplankton concentrations. In the disease modelling context, the need for mathematical models of mosquito-borne diseases that incorporate competition among the larvae will be important because this kind of competition can affect susceptibility of adult mosquitoes to dengue infection (Alto et al. [1]).

In Section 2 we derive simple scalar delay differential equations that can be used as models for a single species that experiences intra-specific competition at the immature (e.g. larval) life stage. Competition may or may not occur among adults. We particularly draw attention to Eq. (2.11) which we want to propose as a simple single-species model, analogous to the logistic equation, that may be suitable as a starting point for populations that experience immature life stage competition. It has similarities to the well known Nicholson's blowflies equation [8], but with a more complicated maturation rate incorporating a parameter k_l that quantifies immature competition. The proposed model (2.11) also allows us to model competition among adults