

Oscillations induced by size-structured populations with saturating food dependent reproduction rate

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ABSTRACT

We study a size-structured population model represented by delay equations with infinite delay. The population is split into two stages according to their maturity which is determined by their size. In this paper, we investigate the occurrence of population cycles by implementing numerical simulations with EBT-methods.

Key words: size-structure; resource-consumer model; delay equations with infinite delay; state dependent delay; EBT-method;

1 Introduction

Individuals differ from each other in terms of size and age etc.. These physiological differences affect the vital rates such as growth, survival, development and reproduction rates. The growth in age or size is often coupled to maturation so that reproduction takes place only after individuals have reached a certain age or size. The importance of body size is related to the fact that 80% of all species grow and develop throughout their entire life (Werner [8]). Therefore size is one of the most important individual physiological traits which would affect to the population-level phenomena. Practically, it is often the case that one distinguishes individuals into several discrete stages in terms of age or size. In continuous time models described by delay differential equations, development or transition to the next stage is described by the maturation delay (see Cooke et al. [1], Gourley and Kuang [5] etc.). Recently, de Roos and Persson [7] studied a size structured population model in which two size

classes, juveniles and adults, are distinguished. The model considered in [7] is described by a system of delay differential equations with state dependent delay. By means of numerical analysis of steady state and numerical simulations, they showed that three types of population cycles can occur depending on the nature of competition among individuals. Motivated by the paper [7], we study a mathematical model which describes the population dynamics of size structured population of the form:

$$\begin{aligned}
 b(t) &= \beta_A(F(t))A(t), \\
 \frac{dF}{dt}(t) &= D - \gamma_J(F(t))J(t) - \gamma_A(F(t))A(t), \\
 J(t) &= \int_{t-\tau(t)}^t b(\alpha) e^{-\int_{\alpha}^t \mu_J(F(\sigma)) d\sigma} d\alpha, \\
 A(t) &= \int_{-\infty}^{t-\tau(t)} b(\alpha) e^{-\int_{\alpha}^{t+\tilde{\tau}(\alpha)} \mu_J(F(\sigma)) d\sigma - \int_{\alpha+\tilde{\tau}(\alpha)}^t \mu_A(F(\sigma)) d\sigma} d\alpha, \\
 s_m - s_b &= \int_{t-\tau(t)}^t g(F(\sigma)) d\sigma = \int_t^{t+\tilde{\tau}(t)} g(F(\sigma)) d\sigma.
 \end{aligned} \tag{DE}$$

Here $b(t)$ denotes the population birth rate, while $F(t)$ denotes the food density at time t . $J(t)$ and $A(t)$ denote the population sizes of juveniles and adults at time t , respectively. Two types of time delay $\tau = \tau(t)$ and $\tau = \tilde{\tau}(t)$ are implicitly defined by the forth equation of (DE). Note that individuals that mature at time t were born at time $t - \tau$, while individuals that are born at time t mature at time $t + \tilde{\tau}$. The functions $g(F)$, $\mu_J(F)$, $\mu_A(F)$, $\beta_A(F)$, $\gamma_J(F)$ and $\gamma_A(F)$ represent the rates for individual growth, death of juveniles and adults, reproduction and consumption of juveniles and adults, respectively. We assume that the size-at-birth of individuals is fixed at s_b . We further assume that the maturation size of juveniles is also fixed at $s_m > s_b$. D is the constant rate at which food is provided in the environment.

System (DE) can be derived from a size-structured resource-consumer model described by partial differential equations as a special case (see for example, [4]). Note that system (DE) includes the equations (3a) and (3b) considered in [7] as a special case. In fact, equations (3a) and (3b) correspond to (DE) if $\gamma_J(F) = aF$, $\gamma_A(F) = qaF$, $g(F) = \varepsilon_g aF$, $\mu_J(F) = \mu/(aF)$, $\mu_A(F) = \mu/(qaF)$ and $\beta_A(F) = \varepsilon_b qaF$ (for details, see [7]). It is also natural to assume that

these functions are saturating with respect to the food density. The purpose of this paper is to investigate the occurrence of population cycles induced by (DE) with saturating reproduction rate by implementing numerical simulations with “Escalator Boxcar Train” method [6] (hereafter we use the abbreviation “EBT”). Although it is difficult to study partial differential equations both analytically and numerically, the EBT-method offers a way to implement numerical simulations easier. The implementation of numerical simulations with the EBT-method is also possible for a system of delay differential equations (see de Roos [7]). The organization is as follows. In the next section, we show the condition for the existence of an interior equilibrium of system (DE). Finally, we discuss our results.

2 Saturating reproduction rate

2.1 Interior equilibrium

It follows from the fourth equation of (DE), we infer that in steady state

$$\tilde{\tau} = \tau = \frac{s_m - s_b}{g(F)}. \quad (2.1)$$

For $b \neq 0$, the steady state version of (DE) reduces to a condition on F , viz.

$$\beta_A(F)e^{-\tau\mu_J(F)}\frac{1}{\mu_A(F)} = 1. \quad (2.2)$$

The left hand side is easily interpreted as the basic reproduction number $R_0(F)$. Note that one should use (2.1) to make it into a condition involving only F . We assume that all $\beta_A(F)$, $g(F)$, $\mu_J(F)$ and $\mu_A(F)$ are smooth functions of F . For $\beta_A(F)$ and $g(F)$, we further assume that $\beta'_A(F) > 0$ and $g'(F) > 0$ for all $F \in [0, \infty)$. While for $\mu_J(F)$ and $\mu_A(F)$, we further assume that $\mu'_J(F) \leq 0$ and $\mu'_A(F) \leq 0$. Then equation (2.2) has exactly one root whenever the left hand side exceeds 1 for large F .

2.2 Numerical simulations

In this subsection, we implement numerical simulations with EBT-method to investigate whether population cycles can occur. We specify functions $\gamma_J(F)$,

$\gamma_A(F)$ and $g(F)$ as

$$\gamma_J(F) = F, \quad \gamma_A(F) = F, \quad g(F) = F, \quad (2.3)$$

The death rates for juveniles μ_J and for adults μ_A are given by $\mu_J = \mu$ and $\mu_A = q\mu$, respectively. The reproduction rate β_A is given by

$$\beta_A(F) = \frac{MF}{a + F}. \quad (2.4)$$

Parameter values are fixed as $\mu = 1.0$, $q = 0.5$, $a = 1$, $M = 100$ and $D = 8$. We examined two cases in one of which we set $\ell = 2$ while in the other of which we set $\ell = 4$. The left panels of Figure 1 present time evolution of the food density (top) and the total population (bottom) for $\ell = 2$. We observe damped oscillations and the convergence to the equilibrium. This implies that the occurrence of population cycles is not expected. On the other hand, the right panels of Figure 1 present time evolution of the food density (top) and the total population (bottom) for $\ell = 4$. In this case, population cycles are observed. Thus we conclude that nonlinearity, in particular, the boundedness of reproduction rate in food density can be a driving factor to induce population cycles.

3 Discussion

We studied delay equations with infinite delay describing the population dynamics of size-structured population which is feeding on some food as a resource. We showed the condition for the existence of the interior equilibrium and implemented numerical simulations with EBT-method to investigate the occurrence of population cycles. We showed that population cycles can be observed for bounded reproduction rate with respect to the food density when the death rate for juveniles is lower than that of for adults. Further investigation remains as our future work.

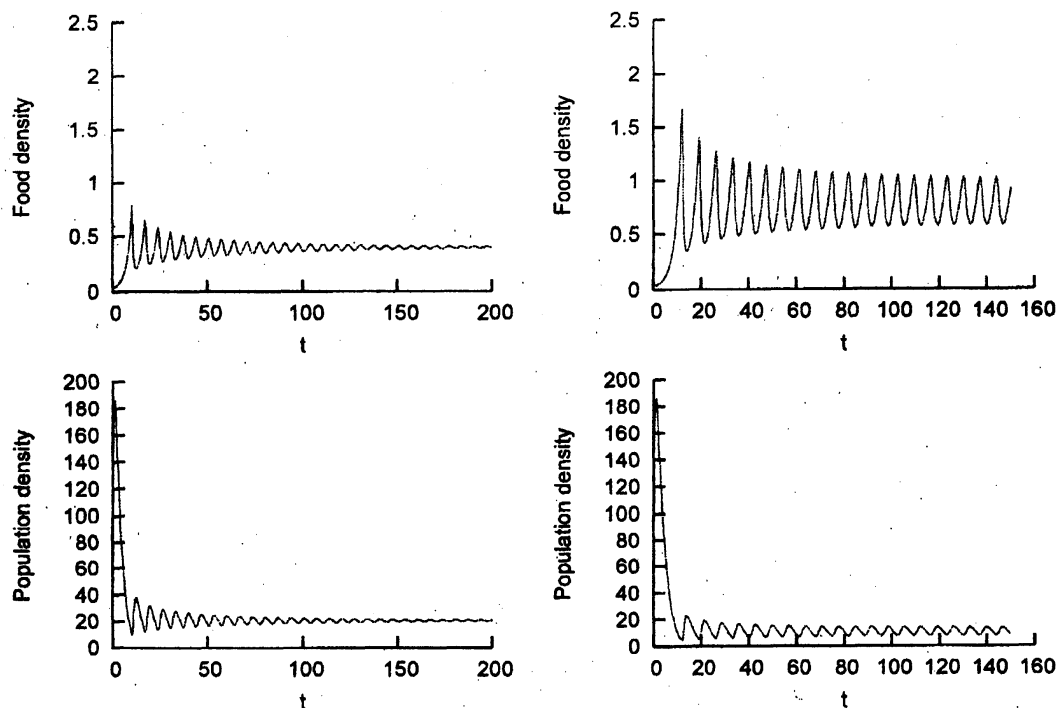


Figure 1: $\ell = 2.0$ (left: convergence) and $\ell = 4.0$ (right: oscillation)

References

- [1] Cooke, K.L., van den Driessche, P., Zou, X., Interaction of maturation delay and nonlinear birth in population and epidemic models. *J. Math. Biol.* **39**, 332–352 (1999)
- [2] Diekmann O., van Gilis, S.A., Lunel, S.M.V., Walther, H.-O., Delay Equations: Functional, Complex, and Nonlinear Analysis, volume 110 of Applied Mathematical Sciences. Springer-Verlag, 1995.
- [3] Diekmann, O., Getto, Ph., Gyllenberg, M., Stability and bifurcation analysis of Volterra functional equations in the light of suns and stars, submitted.
- [4] Diekmann, Gyllenberg, M., Abstract delay equations inspired by population dynamics, submitted.
- [5] Gourley, S.A. and Kuang, Y, A stage structured predator-prey model and its dependence on maturation delay and death rate. *J. Math. Biol.* **49**, 188–200 (2004)

- [6] A.M. de Roos, A gentle introduction to models of physiologically structured populations. In Structured-population models in marine, terrestrial, and freshwater systems. (S. Tuljapurkar & H. Caswell, Eds.), pp. 119-204, Chapman & Hall, New York. 1997.
- [7] de Roos, A.M. and Persson, L., Competition in size-structured populations: mechanisms inducing cohort formation and population cycles. *Theor. Pop. Biol.* **63**, 1-16 (2003)
- [8] Werner, E. E., Size, scaling and the evolution of complex life cycles. In Ebenman, B., and Persson, L., editors, *Size-structured Populations - Ecology and Evolution*, pp 60-81, Springer Verlag, Berlin. 1988.