

## Steady state analysis for some delay equations

中岡慎治 (Shinji Nakaoka)

静岡大学大学院理工学研究科

Graduate school of Science and Technology, Shizuoka University

### ABSTRACT

We study the dynamics of size-structured population model represented by delay equations with infinite delay. The population is split into two groups according to their maturity which is determined by their size. Delay equations consist of a Volterra functional equation coupled with a delay differential equation which describe the time evolution of population birth rate and the food density, respectively. In this paper, steady state analysis for the interior equilibrium of delay equations is carried out in order to address questions under what conditions population cycles can occur.

**Key words:** size-structure; resource-consumer model; delay equations with infinite delay; state dependent delay; steady-state analysis;

## 1 Introduction

Individuals differ from each other in terms of size and age etc.. These physiological differences affect the vital rates such as survival, development and reproduction rate. The growth in age and 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 [7]). Therefore size is one of the most important individual physiological traits which would affect to the population-level phenomena. Practically, in particular it is natural for insects which typically go through several stages during their life, 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 sojourn time (see Cooke et al. [1], Gourley and Kuang [5] etc.). Recently, de Roos and Persson [6] studied a size structured population model in which two size classes, juveniles and adults, are distinguished. The model considered in [6] is described by a system of delay differential equations with state dependent delay. By means of numerical analysis of steady state and numerical simulations with the EBT-method, they showed that three types of population cycles can occur depending on the nature of competition among individuals. In this paper, we study a mathematical model which describes the population dynamics of size structured population of the form:

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

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 size 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 [6] 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  $\beta_A(F) = \varepsilon_b qaF$ . The purpose of this paper is to investigate under what conditions population cycles can occur by analyzing a characteristic equation associated with the linearized equations of system (DE) around an interior equilibrium. The organization is as follows. In the next section, we show the condition for the existence of an interior equilibrium of system (DE). Then we derive a linearized equations of system (DE) around the interior equilibrium. A characteristic equation is defined from the linearized equations. Then we look for the existence of a complex conjugate of pure imaginary roots for the characteristic equation to examine whether Hopf bifurcation occurs or not. In the last section, we discuss our results.

## 2 Steady state analysis

### 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 Linearized equations

Throughout the remainder of this paper, we assume that the interior equilibrium uniquely exists. In this subsection, we derive linearized equations for system (DE) around the interior equilibrium  $\bar{F}$  and  $\bar{b}$ . We do not write calculations for deriving the linearized equations. We shall only show the results.

Define

$$\theta_J(\bar{F}) := \bar{b}\mu_J(\bar{F}) \left\{ \frac{g'(\bar{F})}{g(\bar{F})} - \frac{\mu'_J(\bar{F})}{\mu_J(\bar{F})} \right\}, \quad \theta_A(\bar{F}) := \bar{b}\mu_A(\bar{F}) \left\{ \frac{g'(\bar{F})}{g(\bar{F})} - \frac{\mu'_A(\bar{F})}{\mu_A(\bar{F})} \right\}.$$

$$k_{10} = \bar{b} \frac{\beta'_A(\bar{F})}{\beta_A(\bar{F})}, \quad k_{11}(\sigma) = H(\sigma - \bar{\tau}) \mu_A(\bar{F}) e^{\mu_A(\bar{F})(\bar{\tau} - \sigma)},$$

where  $H$  is the Heaviside function,

$$k_{12}(\sigma) = \begin{cases} \theta_J(\bar{F}) + (\theta_A(\bar{F}) - \theta_J(\bar{F})) e^{-\mu_A(\bar{F})\sigma} & \text{for } \sigma \leq \bar{\tau} \\ \theta_J(\bar{F}) - \bar{b}\mu_A(\bar{F}) \frac{g'(\bar{F})}{g(\bar{F})} + (\theta_A(\bar{F}) - \theta_J(\bar{F})) e^{-\mu_A(\bar{F})\sigma} & \text{for } \sigma > \bar{\tau}, \end{cases}$$

$$k_{20} = -\bar{b} \left\{ \frac{\gamma'_A(\bar{F})}{\mu_A(\bar{F})} e^{-\mu_J(\bar{F})\bar{\tau}} + \frac{\gamma'_J(\bar{F})}{\mu_J(\bar{F})} (1 - e^{-\mu_J(\bar{F})\bar{\tau}}) \right\},$$

$$k_{21}(\sigma) = \begin{cases} -\gamma_J(\bar{F}) e^{-\mu_J(\bar{F})\sigma} & \text{for } \sigma \leq \bar{\tau} \\ -\gamma_A(\bar{F}) e^{-\mu_J(\bar{F})\bar{\tau}} e^{\mu_A(\bar{F})(\bar{\tau} - \sigma)} & \text{for } \sigma > \bar{\tau} \end{cases}$$

$$k_{22}(\sigma) = -\frac{\gamma_A(\bar{F})}{\beta_A(\bar{F})} k_{12}(\sigma) + \gamma_J(\bar{F}) \bar{b} e^{-\mu_J(\bar{F})\bar{\tau}} \varphi(\sigma),$$

$$\varphi(\sigma) = \begin{cases} \frac{g'(\bar{F})}{g(\bar{F})} - \frac{\mu'_J(\bar{F})}{\mu_J(\bar{F})} \left\{ 1 - e^{-\mu_J(\bar{F})(\sigma - \bar{\tau})} \right\} & \text{for } \sigma \leq \bar{\tau} \\ 0 & \text{for } \sigma > \bar{\tau}. \end{cases}$$

The linearized system is given by

$$x(t) = k_{10}y(t) + \int_0^\infty (k_{11}(\sigma)x(t - \sigma) + k_{12}(\sigma)y(t - \sigma)) d\sigma, \quad (2.3)$$

$$\frac{dy}{dt}(t) = k_{20}y(t) + \int_0^\infty (k_{21}(\sigma)x(t - \sigma) + k_{22}(\sigma)y(t - \sigma)) d\sigma. \quad (2.4)$$

### 2.3 Characteristic equation

The characteristic equation for (2.3) and (2.4) is given by

$$\left\{1 - \tilde{k}_{11}(\lambda)\right\} \left\{\lambda - k_{20} - \tilde{k}_{22}(\lambda)\right\} - \tilde{k}_{21}(\lambda) \left\{k_{10} + \tilde{k}_{12}(\lambda)\right\} = 0, \quad (2.5)$$

where

$$\tilde{k}_{mn}(\lambda) = \int_0^\infty k_{mn}(\sigma) e^{-\lambda\sigma} d\sigma, \quad (m, n = 1, 2). \quad (2.6)$$

To check whether equations (DE) undergoes a Hopf bifurcation, we look for a complex conjugate of pure imaginary root of (2.5). System (DE) defines non-sun-reflexive dual semigroups in a non-reflexive Banach space, so the theory on sun-reflexive dual semigroups has supposed not to work if one only refers the book for delay equations [2]. However, recently Diekmann and Gyllenberg have shown that delay equations can be reformulated as abstract weak\*-integral equations involving dual semigroups when the solution take values in a non-reflexive Banach space [4]. Then the theory, methods and results such as linearized stability, center manifold theory and Hopf bifurcation theory developed in [2] are applicable to our delay equations (see also [2], [3], [4]). Hereafter we suppress to write the argument and simply write  $\beta_A$ ,  $\gamma_A$ ,  $\gamma_J$ ,  $g$ ,  $\mu_J$  and  $\mu_A$ . For  $\omega \neq 0$ ,

$$\begin{aligned} \tilde{k}_{mn}(i\omega) &= c_{mn}(\omega) - is_{mn}(\omega) \\ &:= \int_0^\infty k_{mn}(\sigma) \cos(\omega\sigma) d\sigma - i \int_0^\infty k_{mn}(\sigma) \sin(\omega\sigma) d\sigma, \quad (m, n = 1, 2). \end{aligned}$$

Define  $\varphi_A(\omega) \in (0, \pi/2)$  and  $\varphi_J(\omega) \in (0, \pi/2)$  by

$$\cos \varphi_A(\omega) = \frac{\mu_A}{\sqrt{\mu_A^2 + \omega^2}} \text{ and } \sin \varphi_A(\omega) = \frac{\omega}{\sqrt{\mu_A^2 + \omega^2}}, \quad (2.7)$$

$$\cos \varphi_J(\omega) = \frac{\mu_J}{\sqrt{\mu_J^2 + \omega^2}} \text{ and } \sin \varphi_J(\omega) = \frac{\omega}{\sqrt{\mu_J^2 + \omega^2}}. \quad (2.8)$$

We simply write  $\varphi_A(\omega)$  and  $\varphi_J(\omega)$  as  $\varphi_A$  and  $\varphi_J$ , respectively. Note that

$$\frac{\cos \varphi_A}{\mu_A} = \frac{\sin \varphi_A}{\omega} \text{ and } \frac{\cos \varphi_J}{\mu_J} = \frac{\sin \varphi_J}{\omega}. \quad (2.9)$$

Direct calculation yields that

$$c_{11} = \cos \varphi_A \cos(\omega\tau + \varphi_A), \quad s_{11} = \cos \varphi_A \sin(\omega\tau + \varphi_A),$$

$$\begin{aligned}
c_{12} &= \theta_J \frac{\sin \omega \tau}{\omega} + \frac{\sin \varphi_A}{\omega} \left[ (\theta_A - \theta_J) \cos \varphi_A + \left( \theta_J - b \mu_A \frac{g'}{g} \right) \cos (\omega \tau + \varphi_A) \right], \\
s_{12} &= \theta_J \frac{1 - \cos \omega \tau}{\omega} + \frac{\sin \varphi_A}{\omega} \left[ (\theta_A - \theta_J) \sin \varphi_A + \left( \theta_J - b \mu_A \frac{g'}{g} \right) \sin (\omega \tau + \varphi_A) \right], \\
c_{21} &= -\frac{\gamma_A}{\mu_A} e^{-\mu_J \tau} \cos \varphi_A \cos (\omega \tau + \varphi_A) - \frac{\gamma_J}{\mu_J} \cos \varphi_J [\cos \varphi_J - e^{-\mu_J \tau} \cos (\omega \tau + \varphi_J)], \\
s_{21} &= -\frac{\gamma_A}{\mu_A} e^{-\mu_J \tau} \cos \varphi_A \sin (\omega \tau + \varphi_A) - \frac{\gamma_J}{\mu_J} \cos \varphi_J [\sin \varphi_J - e^{-\mu_J \tau} \sin (\omega \tau + \varphi_J)], \\
c_{22} &= \left( \frac{\gamma_J}{\mu_J} - \frac{\gamma_A}{\mu_A} \right) e^{-\mu_J \tau} \theta_J \frac{\sin \omega \tau}{\omega} + b \frac{\mu'_J \gamma_J}{\mu_J \mu_J} \cos \varphi_J [\cos \varphi_J - e^{-\mu_J \tau} \cos (\omega \tau + \varphi_J)] \\
&\quad - \frac{\gamma_A}{\mu_A} e^{-\mu_J \tau} \frac{\sin \varphi_A}{\omega} \left[ (\theta_A - \theta_J) \cos \varphi_A + \left( \theta_J - b \mu_A \frac{g'}{g} \right) \cos (\omega \tau + \varphi_A) \right], \\
s_{22} &= \left( \frac{\gamma_J}{\mu_J} - \frac{\gamma_A}{\mu_A} \right) e^{-\mu_J \tau} \theta_J \frac{1 - \cos \omega \tau}{\omega} + b \frac{\mu'_J \gamma_J}{\mu_J \mu_J} \cos \varphi_J [\sin \varphi_J - e^{-\mu_J \tau} \sin (\omega \tau + \varphi_J)] \\
&\quad - \frac{\gamma_A}{\mu_A} e^{-\mu_J \tau} \frac{\sin \varphi_A}{\omega} \left[ (\theta_A - \theta_J) \sin \varphi_A + \left( \theta_J - b \mu_A \frac{g'}{g} \right) \sin (\omega \tau + \varphi_A) \right].
\end{aligned}$$

Here we exploited relations

$$\begin{aligned}
\int_0^\tau e^{-\mu \sigma} \cos \omega \sigma d\sigma &= \frac{\mu - e^{-\mu \tau} (\mu \cos \omega \tau - \omega \sin \omega \tau)}{\mu^2 + \omega^2}, \\
\int_0^\tau e^{-\mu \sigma} \sin \omega \sigma d\sigma &= \frac{\omega - e^{-\mu \tau} (\omega \cos \omega \tau + \mu \sin \omega \tau)}{\mu^2 + \omega^2}, \\
\int_\tau^\infty e^{-\mu \sigma} \cos \omega \sigma d\sigma &= \frac{e^{-\mu \tau} (\mu \cos \omega \tau - \omega \sin \omega \tau)}{\mu^2 + \omega^2}, \\
\int_\tau^\infty e^{-\mu \sigma} \sin \omega \sigma d\sigma &= \frac{e^{-\mu \tau} (\omega \cos \omega \tau + \mu \sin \omega \tau)}{\mu^2 + \omega^2}.
\end{aligned}$$

and  $e^{-\mu_J \tau} = \mu_A / \beta_A$ . Introducing complex variables

$$z_{mn} := c_{mn} + i s_{mn}, \quad (m, n = 1, 2) \quad (2.10)$$

gives

$$\begin{aligned}
z_{11} &= \cos \varphi_A e^{i(\omega \tau + \varphi_A)}, \\
z_{12} &= \frac{\theta_J}{\omega} 2 \sin \left( \frac{\omega \tau}{2} \right) e^{i \frac{\omega \tau}{2}} + \frac{\sin \varphi_A}{\omega} e^{i \varphi_A} \left\{ (\theta_A - \theta_J) + \left( \theta_J - b \mu_A \frac{g'}{g} \right) e^{i \omega \tau} \right\}, \\
z_{21} &= -\frac{\gamma_A}{\mu_A} e^{-\mu_J \tau} \cos \varphi_A e^{i(\omega \tau + \varphi_A)} - \frac{\gamma_J}{\mu_J} \cos \varphi_J e^{i \varphi_J} (1 - e^{-\mu_J \tau} e^{i \omega \tau}), \\
z_{22} &= \frac{\theta_J}{\omega} \left( \frac{\gamma_J}{\mu_J} - \frac{\gamma_A}{\mu_A} \right) e^{-\mu_J \tau} 2 \sin \left( \frac{\omega \tau}{2} \right) e^{i \frac{\omega \tau}{2}} + b \frac{\mu'_J \gamma_J}{\mu_J \mu_J} \cos \varphi_J e^{i \varphi_J} (1 - e^{-\mu_J \tau} e^{i \omega \tau}) \\
&\quad - \frac{\gamma_A}{\mu_A} e^{-\mu_J \tau} \frac{\sin \varphi_A}{\omega} e^{i \varphi_A} \left\{ (\theta_A - \theta_J) + \left( \theta_J - b \mu_A \frac{g'}{g} \right) e^{i \omega \tau} \right\}.
\end{aligned}$$

Note that

$$\begin{aligned} z_{12}z_{21} - z_{11}z_{22} = & \{-(c_{11}c_{22} - s_{11}s_{22}) + c_{12}c_{21} - s_{12}s_{21}\} \\ & + i\{-(s_{11}c_{22} + c_{11}s_{22}) + (s_{12}c_{21} + c_{12}s_{21})\}. \end{aligned}$$

Therefore, characteristic equation (2.5) with  $\lambda = i\omega$  can be rewritten as

$$k_{20} + i\omega - (k_{20} + i\omega)z_{11} + k_{10}z_{21} + z_{22} + z_{12}z_{21} - z_{11}z_{22} = 0. \quad (2.11)$$

## 2.4 Food dependent uptake rate

In this subsection, we suppose that only uptake rates  $\gamma_J$  and  $\gamma_A$  depend on the food density. Then it immediately follows that  $\mu'_J = \mu'_A = \beta'_A = g' = 0$ . Note that  $k_{10} = \theta_A = \theta_J = 0$ .  $z_{11}$ ,  $z_{12}$ ,  $z_{21}$  and  $z_{22}$  are reduced to

$$\begin{aligned} z_{11} &= \cos \varphi_A e^{i(\omega\tau + \varphi_A)}, \quad z_{12} = z_{22} = 0, \\ z_{21} &= -\frac{\gamma_A}{\mu_A} e^{-\mu_J\tau} \cos \varphi_A e^{i(\omega\tau + \varphi_A)} - \frac{\gamma_J}{\mu_J} \cos \varphi_J e^{i\varphi_J} (1 - e^{-\mu_J\tau} e^{i\omega\tau}). \end{aligned}$$

Thus  $z_{12}z_{21} - z_{11}z_{22} = 0$ . (2.11) is reduced to

$$k_{20} + i\omega - (k_{20} + i\omega)z_{11} = 0. \quad (2.12)$$

Substituting  $z_{11}$  and  $z_{21}$  into (2.12) gives

$$(k_{20} + i\omega) \cos \varphi_A e^{i\varphi_A} e^{i\omega\tau} = k_{20} + i\omega, \quad (2.13)$$

Since  $|e^{i\omega\tau}| = 1$ ,

$$|(k_{20} + i\omega) \cos \varphi_A e^{i\varphi_A}| = |k_{20} + i\omega|. \quad (2.14)$$

It follows from (2.14) that

$$|\cos \varphi_A e^{i\varphi_A}| = \frac{\mu_A}{\mu_A^2 + \omega^2} = 1.$$

Now we are assuming that  $\omega \neq 0$ . This is a contradiction. Hence there are no pure imaginary roots of the characteristic equation.

### 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 derived the linearized equations for system (DE) around the interior equilibrium. The characteristic equation is defined for the linearized system. We focused on a particular case to investigate the occurrence of population cycle via Hopf bifurcation. In a particular case, the rates for growth  $g$ , reproduction  $\beta_A$ , death of juveniles  $\mu_J$  and death of adults  $\mu_A$  are independent functions of the food density, while consumption rates for juveniles and adults are functions of the food density. In this case, we showed that no occurrence of Hopf bifurcation is expected. This finding suggests that for the occurrence of Hopf bifurcation, we should impose that at least one physiological rates  $\beta_A$ ,  $g$ ,  $\mu_J$  or  $\mu_A$  depends on the food density  $F$ . If we do not assume that  $\beta_A$ ,  $g$ ,  $\mu_J$  and  $\mu_A$  are independent functions of the food density, we may expect there exists a pair of complex conjugate of pure imaginary roots of characteristic equation. Actually, extensive numerical computations and numerical simulations implemented in [6] showed the occurrence of sustained population cycles. Mathematical analysis to show the existence of pure imaginary roots of the characteristic equation for general case is left for our future work.

### 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] 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)
- [7] 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.