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Modelling and Analysis of Stage-Structured Population Model with State-Dependent Maturation Delay and Harvesting

J. F. M. Al-Omari¹

Basic Science Department
Faculty of Engineering Technology
Al-Balqa' Applied University, Amman 11134, Jordan
jfmalomari@fet.edu.jo

A. Tallafha

Department of Mathematics
University of Jordan, Amman, Jordan

Abstract

In 1992, Aiello, Freedman and Wu proposed a mathematical model of certain marine population in which the time from birth to maturity is directly related to the number of individuals present. In this paper we derive an alternative model where the immature birth rate is taken to be a non-monotone birth function in the kind seen in other frequently studied population model, the death rate for the matures is taken to be a general function, and with harvesting of the mature and immature populations. We study the dynamics of our model analytically, and we present results on positivity and boundedness. We also carry out a linearised analysis on the equilibria, which is algebraically very complicated in the case of the non-trivial equilibrium. We prove that the zero steady state is globally asymptotically stable in the situation when the positive equilibrium does not exist.

Keywords: Population model; Stage structure; State-dependent; Globally stable; time delay; Harvesting; Equilibrium

¹Corresponding author

1 Introduction

It has been noticed over the years by many authors that time delays have come to play an important role in almost all branches of science, for example, ecology and biology. This importance derives from the fact that many of the phenomena around us do not act instantaneously from the moment of their occurrence. For example, a change in the resources or environment does not affect the birth rate of a single population immediately. There may be some time afterwards to take account of the time to reach maturity. In ecology, realistic models often need to incorporate a time lag between the moment an action takes place and the moment its effect is observed. Many species go through two or more life stages as they proceed from birth to death. Most population models in the literature ignore such reality and assume that all individuals are identical and do not take into account any age structure. However, in many situations age structure can influence population size and growth in a major way. It has been recognized that mortality and fertility depend on an individual's age and even sometimes on the size of the individuals.

In the 1980's Gurney, Nisbet and others have proposed and analysed various models known as 'stage-structure' models. See, for example, Gurney and Nisbet [8], Gurney et al [9] and Nisbet and Gurney [12]. These authors were particularly concerned with the need for a systematic approach to model formulation, and with the need for models containing parameters measured by ecologists.

Of special relevance to the present paper, we will consider the following system first introduced by Aiello and Freedman [1]

$$\begin{aligned} u_i'(t) &= \alpha u_m(t) - \gamma u_i(t) - \alpha e^{-\gamma\tau} u_m(t - \tau), \\ u_m'(t) &= \alpha e^{-\gamma\tau} u_m(t - \tau) - \beta u_m^2(t), \end{aligned} \quad (1.1)$$

where α, β, γ and the delay τ (the time from birth to maturity) are positive constants. In this system u_i and u_m denote the numbers of immature (juvenile) and mature (adult) members of a single-species population respectively. System (1.1) has received much attention in the literature. Their model predicts a positive steady state as the global attractor, thereby suggesting that stage structure does not generate the sustained oscillations frequently observed in nature in single populations. It provides an alternative, and arguably more realistic, model for a single population than the well known logistic equation $u' = u(1 - u)$ by recognising that individuals cannot reproduce right from birth but only after they have become mature, which takes time τ .

The model assumes that all juveniles mature at exactly the same age τ . This is an approximation which will not always be realistic. An alternative is to use a distributed delay term to allow for the possibility that individuals may take different amounts of time to mature, for more information, see, Al-Omari and

Gourley [4], Gourley and Kuang [7].

Unharvested systems with time delay have been studied by many others. See, for example, Gopalsamy [6] and Al-Omari and Gourley [3]. But with harvesting, see, for example, Song and Chen [13], Al-Omari [5].

Generally the equilibria of this kind of equations show a dependence on the time delay. The analysis of such models (even the linearised analysis) is very complicated.

A subsequent paper of Aiello et al [1] modified system (1.1) to allow the time delay to be state dependent, that is, the time delay is taken to be an increasing function of the total population $u_i + u_m$. They proposed the following system, in which $u = u_i + u_m$:

$$\begin{aligned} u_i'(t) &= \alpha u_m(t) - \gamma u_i(t) - \alpha e^{-\gamma\tau(u)} u_m(t - \tau(u)), \\ u_m'(t) &= \alpha e^{-\gamma\tau(u)} u_m(t - \tau(u)) - d u_m^2(t). \end{aligned} \quad (1.2)$$

2 The Model

The main purpose of the present paper is to study an alternative model of (1.2) allowing a non-monotone birth function rather than a linear one as in (1.2) which is relevant in modelling some insect populations, in which the birth rate is approximately proportional to the number of adults if the number of them is small, but is effectively zero if there are many adults, since the adults may have to devote some of their energy to finding food for their own survival that reproduction does not happen. See, for example, Gurney et al [10] where this point is discussed in relation to populations of blowflies. Also in our model we shall leave the death rate for the immature as a linear one, but the death rate for the matures we have aimed to replace quadratic function by more general death rate function $D(M(t))$ that satisfies some qualitative assumptions those are dictated by the need for biological realism, such as, $D(0) = 0$, $D''(0) > 0$ and differentiable, strictly increasing for all $M > 0$. We also modify system (1.2) to have constant harvesting of the mature and immature populations. Hence our analysis in this paper is more complicated than in (1.2). Therefore, we propose the following system

$$\begin{aligned} I'(t) &= \alpha M(t) e^{-aM(t)} - \gamma I(t) - \alpha e^{-(\gamma+E_1)T(P)} M(t - T(P)) e^{-aM(t-T(P))} - E_1 I(t), \\ M'(t) &= \alpha e^{-(\gamma+E_1)T(P)} M(t - T(P)) e^{-aM(t-T(P))} - D(M(t)) - E_2 M(t), \end{aligned} \quad (2.1)$$

where $P = I + M$, and α , a and γ are positive constants. In this system $I(t)$ and $M(t)$ denote, respectively, the number of immature and mature populations. The parameters E_1 and E_2 denote, respectively, the harvesting effort of the

immature and mature population. It is assumed that the birth rate at any time is a non-monotone function, where we choose it to be of the form $\alpha M(t)e^{-aM(t)}$. The term $\alpha e^{-(\gamma+E_1)T(P)} M(t - T(P)) e^{-aM(t-T(P))}$ that appears in the first and second equations represents the rate at time t at which individuals leave the immature and enter the mature class, having just reached maturity. These are individuals who were born at time $t - T(P)$. Therefore, the rate of entering the mature class is $\alpha M(t - T(P)) e^{-aM(t-T(P))}$ times the fraction of those born at time $t - T(P)$ who are still alive now and are not harvested. That is, this fraction is $e^{-(\gamma+E_1)T(P)}$, which accounts for mortality and harvesting during the juvenile phase, follows from the assumption that the death and harvesting of the immature are following a linear law given by $-\gamma I(t)$ and $-E_1 I(t)$, (on the basis of such a law, if $N(t)$ is any population, then the number that survive from $t - T$ to t is $e^{-\gamma T} N(t - T)$). The state-dependent time delay $T(P)$ is taken to be an increasing differentiable bounded function of the total population $P = I + M$, so that $T'(P) \geq 0$, and we shall also assume that $T_0 \leq T(P) \leq T_1$, where $T_0 = T(0)$ and $T_1 = T(\infty)$. The initial conditions for (2.1) are

$$\begin{aligned} M(\theta) &= \phi_1(\theta) \geq 0, \quad \text{for all } \theta \in [-T_1, 0] \quad \text{and} \\ I(0) &= \phi_2(0) \geq 0, \quad \text{with} \\ \phi_2(0) &= \int_{-T_\theta}^0 \alpha e^{(\gamma+E_1)\xi} M(\xi) e^{-aM(\xi)} d\xi, \end{aligned} \tag{2.2}$$

which is the number of immatures that have survived to time $t = 0$. Here, T_θ is the maturation time at $t = 0$, and the lower limit on the integral is $-T_\theta$ because anyone born before that time will have matured before time $t = 0$, where $T_\theta = T(M(0) + I(0))$.

For our model to make sense we need

$$T'(P) < \frac{ae}{\alpha},$$

where $\frac{\alpha}{ae}$ is the maximum value of $\alpha M e^{-aM}$. This means that the function $t - T(P)$ must be an increasing function of t as t increases, because otherwise we could find two different times at which the same individuals become adults twice at the same instant of time, which is absurd.

3 Positivity and Boundedness

In this section we address positivity and boundedness of the solution of system (2.1). This is important since the solutions of our system represent populations, and because we anticipate that limited resources will place a natural restriction to how many individuals can survive.

First we show that $M(t) > 0$ and $I(t) > 0$ for all $t > 0$.

Theorem 1 *In system (2.1), assume that $D(0) = 0$ and $D(M) > 0$ when $M > 0$. Assume also that $\phi_1(t) > 0$ for $-T_\theta \leq t \leq 0$, and if the initial data (2.2) holds. Then $M(t) > 0$ and $I(t) > 0$ for all $t > 0$.*

Proof: First we show that $M(t) > 0$ for all $t > 0$. Assume that there exists $t_0 = \inf\{t > 0 : M(t) = 0\}$, noticing that $M(t) > 0$ for $-T_\theta \leq t \leq 0$. Evaluating the second equation of (2.1) at time t_0 , we obtain

$$M'(t_0) = \begin{cases} \alpha e^{-(\gamma+E_1)T(P(t_0))} \phi_1(t_0 - T(P(t_0))) e^{-a\phi_1(t_0 - T(P(t_0)))} > 0 & \text{for } 0 \leq t_0 \leq T_\theta, \\ \alpha e^{-(\gamma+E_1)T(P(t_0))} M(t_0 - T(P(t_0))) e^{-aM(t_0 - T(P(t_0)))} > 0 & \text{for } t_0 > T_\theta. \end{cases}$$

Then $M'(t_0) > 0$. But by the definition of t_0 , $M'(t_0) = 0$, this is a contradiction. Hence $M(t) > 0$ for all $t \geq 0$.

Next, we shall show that $I(t) > 0$ for all $t > 0$.

Consider now the equation

$$u'(t) = -\gamma u(t) - \alpha e^{-(\gamma+E_1)T(P)} M(t-T(P)) e^{-aM(t-T(P))} - E_1 u(t), \quad u(0) = \phi_2(0) > 0.$$

By positivity of $M(t)$, then we have $I(t) > u(t)$ on $0 < t \leq T_\theta$. But

$$u(t) = e^{-(\gamma+E_1)t} u(0) + \alpha e^{-(\gamma+E_1)t} \int_0^t e^{(\gamma+E_1)\theta} e^{-(\gamma+E_1)T(P(\theta))} M(t - T(\theta)) e^{-aM(t-T(\theta))} d\theta.$$

Hence by (2.2), we have

$$u(T_\theta) = e^{-(\gamma+E_1)T_\theta} \int_{-T_\theta}^0 \alpha e^{(\gamma+E_1)\xi} M(\xi) e^{-aM(\xi)} d\xi + \alpha e^{-(\gamma+E_1)T_\theta} \int_0^{T_\theta} e^{(\gamma+E_1)\theta} e^{-(\gamma+E_1)T(P(\theta))} M(\theta - T(\theta)) e^{-aM(\theta-T(\theta))} d\theta.$$

This implies that $u(T_\theta) = 0$, and therefore, $I(t) > 0$ for $t \in [0, T_\theta]$. By repeating this arguments to include all positive times, we can show that $I(t) > 0$ for all $t > 0$.

We can further prove the following results regarding boundedness of the positive solution of systemt (2.1).

Theorem 2 *Assume that M is any positive constant such that*

$$\frac{\alpha}{ae\mu} < M,$$

where $\mu = \min\{\gamma + E_1, E_2\}$. Assume further that $\phi_1(t) > 0$ for $-T_\theta \leq t \leq 0$, and if the initial data (2.2), holds. Then the solution of (2.1) is bounded.

Proof: Define

$$W(t) = I(t) + M(t), \quad t \in [0, \infty).$$

By positivity of solutions, $W(t) > 0$. Then calculating the derivative of $W(t)$ along the solution of system (2.1), we have

$$\begin{aligned} W'(t) &= \alpha M(t)e^{-aM(t)} - (\gamma + E_1)I(t) - D(M(t)) - E_2M(t) \\ &\leq \frac{\alpha}{ae} - (\gamma + E_1)I(t) - E_2M(t) \\ &< \frac{\alpha}{ae} - \mu W. \end{aligned}$$

Therefore, this implies that

$$\limsup_{t \rightarrow \infty} W(t) \leq \frac{\alpha}{ae\mu} < M.$$

This proves the theorem.

4 Existence and feasibility of positive equilibria

Now, we carry out existence and feasibility of the equilibria of system (2.1), and we interested in the nonnegative equilibria, the equilibria which are the solutions of

$$\begin{aligned} \alpha M(t)e^{-aM(t)} - \gamma I(t) - \alpha e^{-(\gamma+E_1)T(P)} M(t)e^{-aM(t)} - E_1 I(t) &= 0, \\ \alpha e^{-(\gamma+E_1)T(P)} M(t)e^{-aM(t)} - D(M(t)) - E_2 M(t) &= 0. \end{aligned} \tag{4.1}$$

It is clear that the origin $E_0 := (0, 0)$ is an equilibrium of system (4.1). Note that, it is not possible for system (2.1) to have an equilibrium of the form $(0, m)$ or $(m, 0)$ where $m > 0$. This is biologically reasonable since the the two species cannot survive at an equilibrium level in the absence of the other, because they depend on each other. It is clear that as $M \rightarrow \infty$, in the first equation of (4.1), then

$$I = \frac{\alpha}{\gamma + E_1} \left(1 - e^{-(\gamma+E_1)T_1}\right) M e^{-aM}.$$

Therefore, in particular, $I \rightarrow 0$ as $M \rightarrow \infty$. Also we know that since $M e^{-aM}$ is bounded, then $I \not\rightarrow \infty$. We also know that $(0, 0)$ belongs to the first equation of (4.1). What we can conclude now, if there exists a positive root μ to the equation

$$\alpha e^{-(\gamma+E_1)T(\mu)} \mu e^{-a\mu} = D(\mu) + E_2 \mu, \tag{4.2}$$

then the curve defined by the second equation passes through $(0, \mu)$ in the (I, M) -plane and decreases and either meets the I -axis at a finite value, or tends to it as $I \rightarrow \infty$. Therefore if condition (4.2) satisfies, then system (2.1) has a positive equilibrium $\hat{E} = (\hat{I}, \hat{M})$, and otherwise the system will have only the zero solution. We shall show later that if (4.2) holds for all $\mu > 0$, then $(I(t), M(t)) \rightarrow (0, 0)$ as $t \rightarrow \infty$. Suppose that K_1 and K_2 denote the slope of the LHS and RHS of equation (4.2) respectively, at the origin. Clearly $K_1 = \alpha e^{-(\gamma+E_1)T_1}$ and $K_2 = D'(0) + E_2$. Now, if $K_1 \leq K_2$, then system (2.1) does not have a positive equilibrium, that is to say, the unique nonnegative equilibrium is $E_0 := (0, 0)$. But if

$$K_1 = \alpha e^{-(\gamma+E_1)T_1} > K_2 = D'(0) + E_2, \tag{4.3}$$

then there will be a positive root μ of equation (4.2).

We may observe that one situation in which (4.3) will not hold is if there is significant juvenile mortality (large γ). Another situation in which (4.2) will not hold if the harvesting effort of the mature or immature populations is large enough (E_1 or E_2 is large). Where we shall concentrate in this paper on the value of the harvesting effort of the immature population. Also, a root will not exist if T_0 is large, (i.e., the minimum maturation time is too large). So that the feasibility of the positive equilibrium depends on the value of the parameters. As we will see later, if we increase one of the above parameters, say, E_1 , then this will lead to make the root μ smaller, which in turn, makes the positive equilibrium components both get smaller, where the equilibrium $\hat{E} := (\hat{I}, \hat{M})$ vanishes at a finite value of E_1 . So far, we have shown that a positive equilibrium $\hat{E} := (\hat{I}, \hat{M})$ exists if and only if there exists a real positive root μ of equation (4.2).

We shall now study the linearised stability of the two equilibria E_0 and \hat{E} by linearising system (2.1).

5 Linearised stability

We shall carry out the linearised stability of the two equilibria E_0 and \hat{E} by linearising system (2.1) about them. We will begin by examining the linear stability about an arbitrary equilibrium $E^* = (I^*, M^*)$. Setting $I = I^* + u$ and $M = M^* + v$ where u and v are small. We linearise the first equation of system (2.1), and linearising the second one will be by similar ideas. Using Taylor expansions, and neglecting all nonlinear terms in u any v , the first equation is linearised as follows:

$$\begin{aligned} u'(t) &= \alpha(M^* + v)e^{-a(M^*+v)} - (\gamma + E_1)(I^* + u) \\ &\quad - \alpha e^{-(\gamma+E_1)T(P^*+u+v)}(M^* + v(t - T(P^* + u + v)))e^{-a(M^*+v(t-T(P^*+u+v)))} \\ &= \left(\alpha M^* e^{-aM^*} + \alpha v e^{-aM^*} \right) (1 - av) - (\gamma + E_1)I^* - (\gamma + E_1)u \end{aligned}$$

$$\begin{aligned}
& -\alpha e^{-(\gamma+E_1)T(P^*)} e^{-(\gamma+E_1)(u+v)T'(P^*)} [M^* + v(t - T(P^*))] e^{-aM^*} e^{-av(t-T(P^*))} \\
= & \alpha M^* e^{-aM^*} - \alpha av M^* e^{-aM^*} + \alpha v e^{-aM^*} - (\gamma + E_1) I^* - (\gamma + E_1) u \\
& -\alpha e^{-(\gamma+E_1)T(P^*)} (1 - (\gamma + E_1)(u + v)T'(P^*)) [M^* \\
& + v(t - T(P^*))] e^{-aM^*} (1 - av(t - T(P^*))) \\
= & -\alpha av M^* e^{-aM^*} + \alpha v e^{-aM^*} - (\gamma + E_1) u \\
& + \alpha a M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} v(t - T(P^*)) - \alpha e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} v(t - T(P^*)) \\
& + \alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} u(t) \\
& + \alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} v(t) \\
= & \left[\alpha e^{-aM^*} - \alpha a M^* e^{-aM^*} + \alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} \right] v(t) \\
& + \left[\alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} - (\gamma + E_1) \right] u(t) \\
& + \left[\alpha a M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} - \alpha e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} \right] v(t - T(P^*)),
\end{aligned}$$

where $P^* = I^* + M^*$. Similarly, the second equation of system (2.1) becomes

$$\begin{aligned}
v'(t) = & \left[\alpha e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} - \alpha a M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} \right] v(t - T(P^*)) \\
& - \alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} u(t) \\
& - \left[\alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} + D'(M^*) + E_2 \right] v(t).
\end{aligned}$$

Therefore the linearised system will be, after resubstituting I for u and M for v ,

$$\begin{aligned}
I'(t) = & \left[\alpha e^{-aM^*} - \alpha a M^* e^{-aM^*} + \alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} \right] M \\
& + \left[\alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} - (\gamma + E_1) \right] I \\
& + \left[\alpha a M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} - \alpha e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} \right] M(t - T(P^*)), \\
M'(t) = & \left[\alpha e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} - \alpha a M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} \right] M(t - T(P^*)) \\
& - \alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} I(t) \\
& - \left[\alpha(\gamma + E_1)T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} + D'(M^*) + E_2 \right] M(t).
\end{aligned} \tag{5.1}$$

Non-trivial solutions of the form $(I, M) = (c_1, c_2) \exp(\lambda t)$ exist if and only if the characteristic equation

$$\lambda^2 + p\lambda + r + (s\lambda + q)e^{-\lambda T(P^*)} = 0, \tag{5.2}$$

where

$$\begin{aligned}
p &= D'(M^*) + E_2 + \gamma + E_1, \\
r &= (\gamma + E_1) \left[D'(M^*) + E_2 + \left(\alpha T'(P^*)M^* e^{-(\gamma+E_1)T(P^*)} e^{-aM^*} \right) (\gamma + E_1 \right. \\
&\quad \left. - D'(M^*) - E_2 + e^{-aM^*} (\alpha - \alpha a M^*) \right), \\
s &= -e^{-aM^*} (\alpha - \alpha a M^*) e^{-T(P^*)(\gamma+E_1)}, \\
q &= -e^{-aM^*} (\alpha - \alpha a M^*) e^{-T(P^*)(\gamma+E_1)} (\gamma + E_1).
\end{aligned}$$

Next, we will evaluate the characteristic equation (5.2) about the trivial equilibrium $E_0 = (0, 0)$. It is clear that, at E_0 ,

$$\begin{aligned} p &= D'(0) + E_2 + \gamma + E_1, \\ r &= (\gamma + E_1)(D'(0) + E_2) \\ s &= -\alpha e^{-T_0(\gamma + E_1)}, \\ q &= -\alpha e^{-T_0(\gamma + E_1)}(\gamma + E_1). \end{aligned}$$

Then, after substituting the last expressions of p , r , s , and q in (5.2), it reduces to

$$\begin{aligned} \lambda^2 + (D'(0) + E_2 - \alpha e^{-T_0(\gamma + E_1 + \lambda)} + \gamma + E_1) \lambda \\ + (\gamma + E_1) (D'(0) + E_2 - \alpha e^{-T_0(\gamma + E_1 + \lambda)}) = 0, \end{aligned}$$

which can be simplified to

$$(\lambda + \gamma + E_1) (\lambda + D'(0) + E_2 - \alpha e^{-T_0(\gamma + E_1 + \lambda)}) = 0.$$

The roots λ of the above equation are $\lambda = -\gamma - E_1 < 0$ and the roots of the equation

$$\lambda + D'(0) + E_2 = \alpha e^{-T_0(\gamma + E_1 + \lambda)}.$$

We shall now find the condition which determine that all roots of the above equation satisfy $Re\lambda < 0$. Assume for contradiction that there exists a root λ^* such that $Re\lambda^* \leq 0$. Then

$$\begin{aligned} |\lambda^* + D'(0) + E_2| &= |\alpha e^{-T_0(\gamma + E_1 + \lambda^*)}| \\ &\leq \alpha e^{-T_0(\gamma + E_1)} |e^{-T_0\lambda^*}| \\ &= \alpha e^{-T_0(\gamma + E_1)} e^{-T_0 Re\lambda^*} \\ &\leq \alpha e^{-T_0(\gamma + E_1)}, \end{aligned}$$

since $Re\lambda^* \leq 0$. This implies that λ^* is in the circle in the complex λ plane centered at $\lambda = -D'(0) - E_2$ and of radius $\alpha e^{-T_0(\gamma + E_1)}$. Accordingly, we shall have a contradiction if (4.3) holds (i.e. if the nontrivial equilibrium exists). Thus, if the non-trivial equilibrium exists then the trivial equilibrium $(0, 0)$ must be linearly unstable. However if (4.3) does not exist (i.e. the non-trivial equilibrium \hat{E} does not exist) then $E_0 = (0, 0)$ is linearly stable.

For the nontrivial equilibrium \hat{E} , it is not completely straightforward to carry on a linearised stability analysis, mainly because of the delay is a function depending on the state variables I and M . This is different from the situation in Aiello et al [2] since they can find an equilibrium for any value of their parameters. Therefore, we need first to make an approximation to the expressions for the equilibrium components \hat{I} and \hat{M} .

5.1 Linearised stability of the the nontrivial equilibrium

Let us turn now to the linearisation about the equilibrium $\hat{E} = (\hat{I}, \hat{M})$, As we have mentioned before that, if the harvesting effort of the immature population is large enough then a positive equilibrium will not exist, but one must remember that the feasibility of the positive equilibrium \hat{E} (i.e., strict positivity of \hat{I} and \hat{M}) depends on E_1 . We can show that \hat{I} and \hat{M} decrease as E_1 increases and that \hat{E} may lose feasibility at a finite value of E_1 , (say E_{1c}) such that it exists whenever $E_1 < E_{1c}$, or may remain feasible for all E_1 (e.g. if the birth function is linear and the death function quadratic at a small M as in (1.2)). Note that the critical value E_{1c} can be computed by

$$\alpha e^{-(\gamma+E_{1c})T_0} = D'(0) + E_1.$$

Where it is used in the expression of \hat{M} and \hat{I} below. Therefore,

$$E_{1c} = \frac{1}{T_0} \ln \left(\frac{\alpha e^{-\gamma T_0}}{D'(0) + E_2} \right) > 0.$$

Now, we let $E_1 = E_{1c} - \delta$ with $\delta > 0$ being small, where in this situation the linearisation about \hat{E} can be studied analytically. The equilibrium components \hat{I} and \hat{M} cannot be computed explicitly, from (4.1) but we can compute an approximation of them in the case for small δ , using the fact that the equilibrium we are seeking will be near the origin. Using Taylor expansions, of

$$e^{-a\hat{M}} = 1 - a\hat{M},$$

$$T(\hat{P}) = T_0 + T'(0)\hat{P},$$

and

$$e^{-(\gamma+E_{1c}-\delta)(T_0+T'(0)\hat{P})} = e^{-(\gamma+E_{1c})T_0} (1 - (\gamma + E_{1c} - \delta)\hat{P}T'(0)),$$

then, system (4.1) at \hat{I} and \hat{M} becomes

$$\begin{aligned} \alpha\hat{M} - (\gamma + E_{1c})\hat{I} - \alpha e^{-(\gamma+E_{1c})T_0}\hat{M} &= 0, \\ -(\gamma + E_{1c})T'(0)(\hat{I} + \hat{M}) + \delta T_0 &= 0. \end{aligned} \quad (5.3)$$

If we solve the approximating equations (5.3) for the equilibrium component \hat{M} and \hat{I} gives (to order δ)

$$\hat{M} = \frac{\delta T_0}{T'(0)(\alpha + \gamma + E_{1c} - D'(0) - E_2)}, \quad (5.4)$$

and,

$$\hat{I} = \frac{\delta T_0 (\alpha - \alpha e^{-(\gamma+E_{1c})T_0})}{(\gamma + E_{1c})T'(0)(\alpha + \gamma + E_{1c} - D'(0) - E_2)}. \quad (5.5)$$

Note that, the expressions for the equilibrium components \hat{I} and \hat{M} depends on the critical value of E_{1c} , where we can see that as E_1 increases \hat{I} and \hat{M} decrease until reach zero at the critical harvest rate E_{1c} which indicates that the harvesting rate has an effect on the dynamics of the model.

We now evaluate the characteristic equation (5.2) at the interior equilibrium $\hat{E} = (\hat{I}, \hat{M})$ with its components \hat{M} and \hat{I} given by (5.4) and (5.5) respectively. The characteristic equation (5.2) at \hat{E} , becomes

$$\lambda^2 + \hat{p}\lambda + \hat{r} + (\hat{s}\lambda + \hat{q})e^{-\lambda T(\hat{P})} = 0, \tag{5.6}$$

where

$$\begin{aligned} \hat{p} &= D'(\hat{M}) + E_2 + \gamma + E_{1c} - \delta, \\ \hat{r} &= (\gamma + E_{1c} - \delta) \left[D'(\hat{M}) + E_2 + \left(T'(\hat{P})\hat{M}(D'(0) + E_2) \right) (\gamma + E_{1c} - \delta \right. \\ &\quad \left. - D'(0) - E_2 + \alpha) \right], \\ \hat{s} &= - \left(\alpha - 2\alpha a \hat{M} \right) e^{-T(\hat{P})(\gamma + E_{1c} - \delta)}, \\ \hat{q} &= - \left(\alpha - 2\alpha a \hat{M} \right) e^{-T(\hat{P})(\gamma + E_{1c} - \delta)} (\gamma + E_{1c} - \delta). \end{aligned} \tag{5.7}$$

Next, we want to investigate the possibility if there is any condition for stability of \hat{E} when $T'(\hat{P}) = 0$, and then investigate whether instability could occur as we increase the value of $T'(\hat{P})$ from zero. That is, we want to think of $T'(\hat{P})$ as a bifurcation parameter.

For $T'(\hat{P}) = 0$, then it is clear that $\hat{r} = (\gamma + E_{1c} - \delta)(D'(\hat{M}) + E_2)$. Substituting the other expressions in (5.7) into the characteristic equation (5.6), which can be simplified as

$$(\lambda + \gamma + E_{1c} - \delta) \left(\lambda + D'(\hat{M}) + E_2 - (\alpha - 2\alpha a \hat{M})e^{-T(\hat{P})(\gamma + E_{1c} - \delta + \lambda)} \right) = 0.$$

There is a negative eigenvalue $\lambda = -(\gamma + E_{1c} - \delta)$, and the other eigenvalues will be the roots of the equation

$$\lambda + D'(\hat{M}) + E_2 = (\alpha - 2\alpha a \hat{M})e^{-T(\hat{P})(\gamma + E_{1c} - \delta + \lambda)}. \tag{5.8}$$

Substituting the expression (5.4) for \hat{M} into the equation (5.8) and expand $T(\hat{P})$ and $D'(\hat{M})$ in Taylor series we have

$$\begin{aligned} \lambda + D'(0) + E_2 &\leq \lambda + D'(0) + D''(0)\hat{M} + E_2 \\ &= \left(\alpha - 2\alpha a \hat{M} \right) e^{-(\gamma + E_{1c} - \delta)T(\hat{P})} e^{-T(\hat{P})\lambda} \\ &= \left[\alpha - 2\alpha a \hat{M} \right] e^{-(\gamma + E_{1c})T(\hat{P})} \left(1 + \delta T(\hat{P}) \right) e^{-T(\hat{P})\lambda} \end{aligned}$$

$$\begin{aligned}
 &= \left[\alpha - 2\alpha a \hat{M} + \alpha \delta T(\hat{P}) \right] e^{-(\gamma + E_{1c})T(\hat{P})} e^{-T(\hat{P})\lambda} \\
 &= \left[\alpha - 2\alpha a \hat{M} + \alpha \delta T_0 \right] e^{-(\gamma + E_{1c})T_0} \left(1 - (\gamma + E_{1c}) \hat{P} T'(0) \right) e^{-T(\hat{P})\lambda} \\
 &= \left[\alpha - 2\alpha a \hat{M} + \alpha \delta T_0 - \alpha (\gamma + E_{1c}) \hat{P} T'(0) \right] e^{-(\gamma + E_{1c})T_0} e^{-T(\hat{P})\lambda} \\
 &= \left[\alpha - \frac{2\alpha a T_0 \delta}{T'(0)(\alpha + \gamma + E_{1c} - D'(0) - E_2)} \right] e^{-(\gamma + E_{1c})T_0} e^{-T(\hat{P})\lambda},
 \end{aligned}$$

where we have retained terms up to and including order δ . In carrying out the above calculation, we have used $D''(0) > 0$, $\alpha e^{-(\gamma + E_{1c})T_0} = D'(0) + E_2$, and

$$\alpha \delta T_0 - \alpha (\gamma + E_{1c}) \hat{P} T'(0) = 0$$

to order δ , which can be easily done, by substituting the expression (5.4) and (5.5) for \hat{M} and \hat{I} into \hat{P} . Therefore for $\delta > 0$ small the eigenvalue equation is approximately

$$\begin{aligned}
 &\lambda + D'(0) + D''(0)\hat{M} + E_2 \\
 &= \left[\alpha - \frac{2\alpha a T_0 \delta}{T'(0)(\alpha + \gamma + E_{1c} - \alpha e^{-(\gamma + E_{1c})T_0})} \right] e^{-(\gamma + E_{1c})T_0} e^{-T(\hat{P})\lambda}. \tag{5.9}
 \end{aligned}$$

We will now show that all roots of equation (5.9) satisfy $\text{Re } \lambda < 0$ when δ is sufficiently small. We assume, for contradiction, that there exists a root λ^* such that $\text{Re } \lambda^* \geq 0$. Then

$$\begin{aligned}
 |\lambda^* + D'(0) + E_2| &\leq \left| \lambda^* + D'(0) + D''(0)\hat{M} + E_2 \right| \\
 &= \left| \left[\alpha - \frac{2\alpha a T_0 \delta}{T'(0)(\alpha + \gamma + E_{1c} - D'(0) - E_2)} \right] e^{-(\gamma + E_{1c})T_0} \right| \left| e^{-T(\hat{P})\lambda^*} \right| \\
 &\leq \left[\alpha - \frac{2\alpha a T_0 \delta}{T'(0)(\alpha + \gamma + E_{1c} - D'(0) - E_2)} \right] e^{-(\gamma + E_{1c})T_0} \quad \text{since } \text{Re } \lambda^* \geq 0 \\
 &< \alpha e^{-(\gamma + E_{1c})T_0} = D'(0) + E_2.
 \end{aligned}$$

This means that λ^* is strictly within the circle centred at $-(D'(0) + E_2)$ and of radius $D'(0) + E_2$, which is impossible since $\text{Re } \lambda^* \geq 0$. Therefore, all roots of equation (5.9) satisfy $\text{Re } \lambda < 0$. Consequently if $T'(\hat{P}) = 0$ then \hat{E} is linearly asymptotically stable.

Now suppose we start to increase the value of $T'(\hat{P})$ from the value zero, to see if there will appear new roots of the characteristic equation (5.6) in the far left of the complex plane and as $T'(\hat{P})$ is further increased these roots may cross the imaginary axis, giving rise to an instability. That is, the question is: can we find a critical value of $T'(\hat{P})$ at which the equilibrium lose its stability? Suppose that there is a critical value of $T'(\hat{P})$ at which the equation (5.6) has a pair of complex conjugate roots on the imaginary axis. Therefore, for $T'(\hat{P}) \neq 0$, let $\lambda = \omega i$. Then (5.6), after seperating into real and imaginary parts, becomes

$$\begin{aligned}
 -\omega^2 + \hat{r} &= (\alpha - 2\alpha a \hat{M}) e^{-(\gamma + E_{1c} - \delta)T(\hat{P})} \left[(\gamma + E_{1c} - \delta) \cos(T(\hat{P})\omega) + \omega \sin(T(\hat{P})\omega) \right], \\
 \hat{p}\omega &= (\alpha - 2\alpha a \hat{M}) e^{-(\gamma + E_{1c} - \delta)T(\hat{P})} \left[\omega \cos(T(\hat{P})\omega) - (\gamma + E_{1c} - \delta) \sin(T(\hat{P})\omega) \right].
 \end{aligned}$$

Then upon squaring and adding the last two equations, we get

$$\omega^4 + (\hat{p}^2 - \hat{s}^2 - 2\hat{r})\omega^2 + \hat{r}^2 - \hat{q}^2 = 0, \tag{5.10}$$

It follows that if

$$\hat{p}^2 - \hat{s}^2 - 2\hat{r} > 0 \text{ and } \hat{r}^2 - \hat{q}^2 > 0 \tag{5.11}$$

are satisfied, then the equation (5.10) does not have positive solutions; that is the characteristic equation (5.6) does not have purely imaginary roots, where we will get a contradiction.

Now, to see if the two inequalities in (5.11) are satisfied we need to make further approximation for the expressions in (5.7) using Taylor expansions, and note that \hat{M} and \hat{I} both depend on δ , we have

$$\begin{aligned} \hat{p}^2 &= \left(D'(0) + D''(0)\hat{M} + E_2\right)^2 + 2(D'(0) + D''(0)\hat{M} + E_2)(\gamma + E_{1c} - \delta) + (\gamma + E_{1c} - \delta)^2 \\ &= (D'(0) + E_2)^2 + 2D''(0)\hat{M}(D'(0) + E_2) + 2(D'(0) + E_2)(\gamma + E_{1c} - \delta) \\ &\quad + 2D''(0)\hat{M}(\gamma + E_{1c} - \delta) + (\gamma + E_{1c} - \delta)^2 \\ \hat{r}^2 &= (\gamma + E_{1c} - \delta)^2 \left[D'(0) + D''(0)\hat{M} + E_2 + \delta T_0(D'(0) + E_2)\right]^2 \\ &= (\gamma + E_{1c} - \delta)^2 \left[(D'(0) + E_2)^2 + 2D''(0)\hat{M}(D'(0) + E_2) + 2\delta T_0(D'(0) + E_2)^2\right] \\ \hat{s}^2 &= (\alpha - 2\alpha a\hat{M})^2 e^{-2T(\hat{P})(\gamma + E_{1c} - \delta)} \\ &= (\alpha^2 - 4\alpha^2 a\hat{M})e^{-2(\gamma + E_{1c})(T_0 + T'(0)\hat{P})}(1 + 2\delta T(\hat{P})) \\ &= (\alpha^2 - 4\alpha^2 a\hat{M} + 2\alpha^2\delta T(\hat{P}))e^{-2(\gamma + E_{1c})T_0}(1 - 2(\gamma + E_{1c})T'(0)\hat{P}) \\ &= (D'(0) + E_2)^2 - 4a\hat{M}(D'(0) + E_2) \\ \hat{q} &= (\gamma + E_{1c} - \delta)^2 \left[(D'(0) + E_2)^2 - 4a\hat{M}(D'(0) + E_2)\right]. \end{aligned}$$

By substituting these expressions in the first and second inequalities of (5.11), the second inequality is trivially satisfied, because it add up to a positive quantity. The first inequality can be made positive by taking δ to be small. Therefore, we have proved the following theorem on the stability of \hat{E} .

Theorem 3 *The equilibrium $\hat{E} = (\hat{I}, \hat{M})$, where \hat{I} and \hat{M} are given by (5.5) and (5.4) respectively, is linearly asymptotically stable for $\delta > 0$ sufficiently small.*

6 Global stability of the trivial equilibrium

We will prove that the trivial equilibrium $E_0 = (0, 0)$ is globally asymptotically stable for the case when a non-trivial equilibrium $\hat{E} = (\hat{I}, \hat{M})$ does not exist.

Theorem 4 *Assume that $\alpha e^{-(\gamma+E_1)T(\mu)} \mu e^{-a\mu} < D(\mu) + E_2\mu$ for all $\mu > 0$. Then the equilibrium $E_0 = (0, 0)$ is globally asymptotically stable, that is $(I(t), M(t)) \rightarrow (0, 0)$ as $t \rightarrow \infty$.*

Proof: First we show that $M(t) \rightarrow 0$. Clearly E_0 is the unique equilibrium of system (2.1) under the hypothesis of the theorem. We already know that $M(t)$ is bounded and positive for all $t > 0$. The prove of this theorem is in several stages. First we deal with the cases when $M(t)$ is eventually monotonically decreasing or increasing, i.e., monotone for all t sufficiently large. But, by positivity of solutions, $M(t)$ is not eventually monotonically decreasing because if so, then $M(t)$ must approach some limit $\hat{M} \geq 0$. This limit must be an equilibrium of the second equation of (2.1). Therefore, this limit must be zero, because otherwise we will have a contradiction to the hypothesis of the theorem. Now assume, for contradiction, that $M(t)$ is eventually monotonic increasing. By boundedness of $M(t)$, then $\lim_{t \rightarrow \infty} M(t)$ exists. Let $L = \lim_{t \rightarrow \infty} M(t)$, then $L \geq 0$, now we show that $L = 0$. Otherwise if $L > 0$, then, from the second equation of system (2.1), we have

$$\begin{aligned} M'(t) &= \alpha e^{-(\gamma+E_1)T(I(t)+M(t))} M(t - T(P)) e^{-aM(t-T(P))} \\ &\quad - D(M(t)) - E_2 M(t) \\ &\leq \alpha e^{-(\gamma+E_1)T(M(t))} M(t - T(P)) e^{-aM(t-T(P))} - D(M(t)) - E_2 M(t), \end{aligned}$$

since $T(P)$ is bounded. Letting $t \rightarrow \infty$, gives

$$0 \leq \alpha e^{-(\gamma+E_1)T(L)} L e^{-aL} - D(L) - E_2 L,$$

where, we conclude that

$$\alpha e^{-(\gamma+E_1)T(L)} L e^{-aL} \geq D(L) + E_2 L,$$

since $L > 0$. Which contradicts the hypothesis of the theorem.

Now suppose that $M(t)$ is not eventually monotonic, we show that

$L = \limsup_{t \rightarrow \infty} M(t) = 0$, otherwise, if $L > 0$, then there exists a sequence t_i ($t_i > t_{i-1}$, $\lim_{i \rightarrow \infty} t_i = \infty$) such that $M'(t_i) = 0$ and $\lim_{i \rightarrow \infty} M(t_i) = L$. It is clear to show that $L < \frac{1}{a}$, where $\frac{1}{a}$ is the value of μ where $\alpha \mu e^{-a\mu}$ achieves its maximum, because otherwise we will have a contradiction with the hypothesis of the theorem.

Let $\varepsilon > 0$ be sufficiently small such that $L + \varepsilon < \frac{1}{a}$. Then for this ε , there exists $t_1 > 0$ such that for $t > t_1$ we have

$$M(t) \leq L + \varepsilon.$$

Also, since $T(P)$ is bounded, we can find i_1 such that if $i \geq i_1$ we have

$$M(t_i - T(I(t_i) + M(t_i))) \leq L + \varepsilon.$$

Since $L + \varepsilon < \frac{1}{a}$ and $\alpha M e^{-aM}$ is increasing for values up to $\frac{1}{a}$, therefore, applying the second equation of system (2.1) when $t = t_i$ where $i \geq i_1$, we have

$$\begin{aligned} 0 = M'(t_i) &\leq \alpha e^{-(\gamma+E_1)T(M(t_i))} M(t_i - T(I(t_i) + M(t_i))) e^{-aM(t_i - T(I(t_i) + M(t_i)))} \\ &\quad - D(M(t_i)) - E_2 M(t_i). \\ &\leq \alpha e^{-(\gamma+E_1)T(M(t_i))} (L + \varepsilon) e^{-a(L+\varepsilon)} - D(M(t_i)) - E_2 M(t_i). \end{aligned}$$

Letting $i \rightarrow \infty$,

$$0 \leq \alpha e^{-(\gamma+E_1)T(L)} (L + \varepsilon) e^{-a(L+\varepsilon)} - D(L) - E_2 L.$$

This is true for all $\varepsilon > 0$ sufficiently small. Thus

$$\alpha e^{-(\gamma+E_1)T(L)} L e^{-aL} \geq D(L) + E_2 L.$$

This contradicts the hypothesis of the theorem unless $L = 0$

To complete the proof of the theorem we need to show that $I(t) \rightarrow 0$ as $t \rightarrow \infty$.

By the first equation of system (2.1), we have

$$I'(t) = \alpha M(t) e^{-aM(t)} - \gamma I(t) - \alpha e^{-(\gamma+E_1)T(P)} M(t - T(P)) e^{-aM(t - T(P))} - E_1 I(t).$$

Since $I(t)$ is bounded, now suppose that $\lim_{t \rightarrow \infty} I(t)$ does not exist, then there must exist two sequences t_i^n and t_i^m such that

$$\lim_{i \rightarrow \infty} I(t_i^n) = I_n, \quad I'(t_i^n) = 0, \quad \lim_{i \rightarrow \infty} I(t_i^m) = I_m, \quad I'(t_i^m) = 0,$$

$$I_n < I_m, \quad I(t_i^n) \neq 0, \quad I(t_i^m) \neq 0,$$

Applying the first equation of system (2.1) at t_i^n and t_i^m yields

$$\begin{aligned} 0 = I'(t_i^n) &= \alpha M(t_i^n) e^{-aM(t_i^n)} - \gamma I(t_i^n) \\ &\quad - \alpha e^{-(\gamma+E_1)T(P)} M(t_i^n - T(P)) e^{-aM(t_i^n - T(P))} - E_1 I(t_i^n), \\ 0 = I'(t_i^m) &= \alpha M(t_i^m) e^{-aM(t_i^m)} - \gamma I(t_i^m) \\ &\quad - \alpha e^{-(\gamma+E_1)T(P)} M(t_i^m - T(P)) e^{-aM(t_i^m - T(P))} - E_1 I(t_i^m). \end{aligned} \tag{6.1}$$

Since $\lim_{t \rightarrow \infty} M(t) = 0$, then by (6.1) we have

$$I_n = \lim_{i \rightarrow \infty} I(t_i^n) = \lim_{i \rightarrow \infty} I(t_i^m) = I_m,$$

a contradiction. Hence $\lim_{t \rightarrow \infty} I(t)$ exists. But since $I(t)$ is bounded, then $\lim_{t \rightarrow \infty} I'(t) = 0$, and hence

$$\lim_{t \rightarrow \infty} I(t) = 0.$$

This complete the proof of the theorem.

7 Discussion

So far in this paper we have shown that when the non-trivial equilibrium \hat{E} does not exist, the zero equilibrium $(0, 0)$ is globally asymptotically stable. We proved that the solutions of the mature and immature equations are always positive and bounded. We have also, investigated the situation when \hat{E} does exist, but only just, showing that it is linearly stable when it is close to zero equilibrium with the later being linearly unstable.

This leaves open the question of whether other dynamical behaviour in model (2.1) might occur, in parameter regimes for which \hat{E} is not close to the zero equilibrium. In principle, \hat{E} could become unstable leading to oscillatory behaviour. Investigating this possibility is, unfortunately, not algebraically feasible. Indeed, as the analysis of section 5.1 made clear, the algebra involved in the linearised analysis is extremely complicated even when \hat{E} is close to $(0, 0)$. The reasons for this are mainly concerned with the fact that the model involves state-dependent delay. We leave this problem to future investigation.

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