

ANALYSIS OF A MODEL REPRESENTING STAGE-STRUCTURED POPULATION GROWTH WITH STATE-DEPENDENT TIME DELAY*

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Abstract. A stage-structured model of population growth is proposed, where the time to maturity is itself state dependent. It is shown that under appropriate assumptions, all solutions are positive and bounded. Criteria for the existence of positive equilibria, and further conditions for the uniqueness of the equilibria are given. The stability of the equilibria are also discussed. In addition, an attracting region is determined for solutions, such that this region collapses to the unique positive equilibrium in the state-independent case.

Key words. attractor, bounded, equilibrium, positivity, single-species, stability, stage structure, time delay

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1. Introduction. In [2], a stage-structured model of population growth consisting of immature and mature individuals was analyzed, where the stage-structure was modeled by the introduction of a constant time delay. Previously, other models of population growth with time delays were considered in the literature [1], [7], [8], [10], [11], [14], [16], [17], [20]. Age- and stage-structured models of various types (discrete and distributed time delays, stochastic, etc.) have also been utilized [4], [12], [15], [18], [21].

In [9], it was observed that for Antarctic whale and seal populations, the length of time to maturity is a function of the amount of food (mostly krill) available. Prior to World War II, it was observed that individual seals took five years to mature, small whales took seven to ten years, and large whale species took twelve to fifteen years to reach maturity. Subsequent to the introduction of factory ships after the war, and with it a depletion of the large whale populations, there was an increase in the krill available for the seals and the remaining whales. It was then noted that seals took three to four years to mature and small whales now only took five years. Maturation time for large whales also significantly decreased.

Since the amount of food available per biomass for a fixed food supply in a closed environment is a function of the total consumer biomass, we modify the model considered in [2] to include a monotonically decreasing, state-dependent time delay. The existence of a such monotonically increasing time to maturity has been observed in other contexts as well. For example, Andrewartha and Birch [3, p. 370] describe how the duration of larval development of flies is a nonlinear increasing function of larval density. We believe that this is the first time such a population model has

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appeared in the literature. It is the purpose of this paper to analyze as best we can the proposed model.

In the next section, we propose our model. In §3, we obtain positivity and boundedness results. An equilibrium analysis will follow in §4. In particular, we show that multiple positive equilibria can exist (where the constant time delay case only allows at most one), and we obtain criteria for the uniqueness of an equilibrium and for its asymptotic stability. In §5, we examine the global behavior of solutions. Such behavior has been considered important in the literature [5]. A brief discussion follows in §6.

2. The model. In [2], we utilize the system

$$(2.1) \quad \begin{aligned} \dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t - \tau), \\ \dot{x}_m(t) &= \alpha e^{-\gamma\tau} x_m(t - \tau) - \beta x_m^2(t), \end{aligned}$$

where $x_i(t)$ and $x_m(t)$ represent the immature and mature populations densities respectively to model stage-structured population growth. There, τ represents a constant time to maturity. α, β , and γ are positive constants.

Here we modify system (2.1) to account for the observed dependence of τ on the population density. Hence we consider the system, where $z = x_i + x_m$,

$$(2.2) \quad \begin{aligned} \dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau(z)} x_m(t - \tau(z)), \\ \dot{x}_m(t) &= \alpha e^{-\gamma\tau(z)} x_m(t - \tau(z)) - \beta x_m^2(t), \\ x_i(t) &= \varphi_i(t) \geq 0, \quad x_m(t) = \varphi_m(t) \geq 0, \quad -\tau_M \leq t \leq 0, \end{aligned}$$

where $\cdot = d/dt$, $\alpha > 0$, $\beta > 0$, $\gamma > 0$, $\tau_m \leq \tau(z) \leq \tau_M$, (τ_m and τ_M are defined in (2.3) below), $\varphi_m(t)$ is the given initial mature population, and $\varphi_i(t)$ is the derived immature population (as explained in what follows) on $-\tau_M \leq t \leq 0$. Since $\tau(z)$ is observed to be an increasing function of population density with a lower limit, we further assume that $\tau'(z)$ exists ($t = d/dz$), so that

$$(2.3) \quad \tau'(z) \geq 0, \quad 0 < \tau_m \leq \tau(z) \leq \tau_M,$$

with $\lim_{z \rightarrow 0^+} \tau(z) = \tau_m$ and $\lim_{z \rightarrow \infty} \tau(z) = \tau_M$.

Now, for the model to make sense, i.e., so as to exclude the possibility of adults becoming immatures except by birth, we must impose conditions on $\tau(z(t))$ so that $t - \tau(z(t))$ is a strictly increasing function of t . Thus we need $(d/dt)\tau(z) = \tau'(z)\dot{z}(t) < 1$. This is equivalent to

$$\tau'(z)(\dot{x}_i(t) + \dot{x}_m(t)) < 1 \quad \text{or} \quad \tau'(z)(\alpha x_m(t) - \gamma x_i(t) - \beta x_m^2(t)) < 1.$$

We know that $\tau'(z) \geq 0$ is true. Now, if $\tau'(z) = 0$, we have a constant delay and, clearly, $t - \tau(z(t))$ is strictly increasing. Hence we assume $\tau'(z) > 0$, in which case

$$\tau'(z)(\alpha x_m(t) - \gamma x_i(t) - \beta x_m^2(t)) \leq \tau'(z)(\alpha x_m(t) - \beta x_m^2(t)),$$

provided that $x_i(t) \geq 0$. Thus if $\tau'(z)(\alpha x_m(t) - \beta x_m^2(t)) < 1$, $t - \tau(z(t))$ is strictly increasing. However, $(\alpha x_m(t) - \beta x_m^2(t))$ attains its maximum value of $\alpha^2/4\beta$ when $x_m = \alpha/2\beta$. Thus if

$$(2.4) \quad \tau'(z) < 4\beta/\alpha^2,$$

$t - \tau(z(t))$ will be strictly increasing. Thus we have proved the following theorem.

THEOREM 2.1. *Let (2.3), (2.4), and $x_i(t) \geq 0$ when $t \geq 0$ hold. Then $t - \tau(z(t))$ is a strictly increasing function of t .*

Now, let τ_u be defined so that

$$(2.5) \quad \tau_u = \tau \left(\varphi_m(0) + \int_{-\tau_u}^0 \alpha \varphi_m(s) e^{\gamma s} ds \right).$$

Such a τ_u exists, since if we regard (2.5) as an expression in which τ_u is a variable, as the left-hand side increases from zero to infinity, the right-hand side will increase, but is bounded below by τ_m and above by τ_M . The value τ_u so defined may not be unique, so we set

$$\tau_s = \inf \left\{ \tau_u : \tau_u = \tau \left(\varphi_m(0) + \int_{-\tau_u}^0 \alpha \varphi_m(s) e^{\gamma s} ds \right) \right\}.$$

We then define $\varphi_i(0) = \int_{-\tau_s}^0 \alpha \varphi_m(s) e^{\gamma s} ds$, which by the change of variable $r = s + \tau_s$ and then resubstituting s for r becomes

$$(2.6) \quad \varphi_i(0) = \int_0^{\tau_s} \alpha \varphi_m(s - \tau_s) e^{\gamma(s - \tau_s)} ds.$$

In this manner, $\varphi_i(0)$ represents the accumulated survivors of those members of the immature population born between time $-\tau_s$ and 0.

For values of t , $-\tau_s \leq t \leq 0$ we understand that $x_m(t) = \varphi_m(t)$, and that $x_i(0) = \varphi_i(0)$. Note also that $\tau(z(0)) = \tau_s$.

3. Positivity and boundedness. Since the solutions of system (2.2) represent populations, it is important to show positivity and boundedness. Positivity implies that the system persists, i.e., the populations survive. Boundedness may be interpreted as a natural restriction to growth as a consequence of limited resources. We develop these considerations in the following theorems.

THEOREM 3.1. *Let $\varphi_m(t) > 0$ for $-\tau_M \leq t \leq 0$. Then $x_m(t) > 0$ for $t > 0$.*

Proof. Suppose that $x_m(t) = 0$ for some value of t . Since $x_m(0) > 0$, by continuity of solutions, such a value of t must be strictly greater than zero. Let $t^* = \inf \{t : t > 0, x_m(t) = 0\}$. Then from system (2.2) $\dot{x}_m(t^*) = \alpha e^{-\gamma \tau(z(t^*))} (x_m(t^* - \tau(z(t^*)))$. Since $\tau(z) > 0$, $t^* - \tau(z(t^*)) < t^*$, implying that $x_m(t^* - \tau(z(t^*))) > 0$ by definition of t^* . This, in turn, implies that $\dot{x}_m(t^*) > 0$, giving us a contradiction. Therefore no such t^* exists, and the theorem is proved.

The next theorem shows that for a given positive initial function, $x_m(t)$ is uniformly bounded away from zero.

THEOREM 3.2. *Let $\varphi_m(t) > 0$ for $-\tau_M \leq t \leq 0$. Then there exists a $\delta_m = \delta_m(\varphi_m) > 0$ such that $x_m(t) > \delta_m$ for all $t \geq 0$.*

Proof. Let $\delta_m(\varphi_m) = \frac{1}{2} \min \{ \inf_{-\tau_M \leq t \leq 0} \varphi_m(t), \alpha \beta^{-1} e^{-\gamma \tau_M} \}$. Assume that there exists a t^* such that $t^* = \inf \{t : t \geq 0, x_m(t) = \delta_m\}$. Since $x_m(0) = \varphi_m(0)$, and $\varphi_m(0) \geq 2\delta_m$, by continuity it follows that $t^* > 0$. Hence

$$\begin{aligned} \dot{x}_m(t^*) &= \alpha e^{-\gamma \tau(z(t^*))} x_m(t^* - \tau(z(t^*))) - \beta x_m^2(t^*) \\ &> \alpha e^{-\gamma \tau_M} \delta_m - \beta \delta_m^2 \\ &\geq \alpha e^{-\gamma \tau_M} \delta_m - \frac{1}{2} \alpha e^{-\gamma \tau_M} \delta_m = \frac{1}{2} \alpha e^{-\gamma \tau_M} \delta_m > 0. \end{aligned}$$

Since $\dot{x}_m(t^*) > 0$ is impossible by definition of t^* , we have a contradiction. Therefore no such t^* exists and $x_m(t) > \delta_m(\varphi_m)$ for all $t > 0$. This proves the theorem.

We now show that the mature population is bounded.

THEOREM 3.3. *Let $\varphi_m(t) > 0$ for $-\tau_M \leq t \leq 0$. Then there exists $\Delta_m = \Delta_m(\varphi_m) > 0$ such that $x_m(t) \leq \Delta_m$ for $t \geq 0$.*

Proof. Our proof is split into two cases. (a) First, suppose that $\dot{x}_m(t) \geq 0$ for all $t > T$ for some $T \geq 0$. Then for $t > T + \tau_M$,

$$\begin{aligned} 0 \leq \dot{x}_m(t) &= \alpha e^{-\gamma\tau(z(t))} x_m(t - \tau(z(t))) - \beta x_m^2(t) \\ &\leq \alpha e^{-\gamma\tau(z(t))} x_m(t) - \beta x_m^2(t), \end{aligned}$$

since $x_m(t - \tau(z(t))) \leq x_m(t)$. This, in turn, implies that

$$x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau(z(t))} \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$$

for $t > T$, since $x_m(t) > 0$, giving us our desired result.

(b) Now assume that there exists a sequence $\{t_n\}_{n=1}^\infty$ such that $\dot{x}_m(t_n) = 0$, and such that $x_m(t_n)$ is a local maximum, where $x_m(t) \leq x_m(t_n)$, $0 < t < t_n$, for all n . Then by a similar analysis at $t = t_n$, the result follows.

Thus, choosing $\Delta_m(\varphi_m) = \max\{\sup_{-\tau_M \leq t \leq 0} \varphi_m(t), \alpha\beta^{-1}e^{-\gamma\tau_m}\}$, proves the theorem.

Now, Theorems 3.2 and 3.3 show that, given an admissible set of initial conditions, solutions $x_m(t)$ to system (2.2) will remain positive and will be bounded. We now prove that solutions $x_i(t)$ will be bounded above by a bound that depends on initial conditions.

THEOREM 3.4. *Let $\varphi_m(t) > 0$ for $-\tau_m \leq t \leq 0$. Then there exists a $\Delta_i(\varphi_m) = x_i(0) + \alpha\gamma^{-1}\Delta_m$ such that $x_i(t) < \Delta_i$ for all t .*

Proof. First, we observe that since $x_i(0) = \int_{-\tau_s}^0 \alpha\varphi_m(s)e^{\gamma s} ds$, Δ_i is indeed a functional depending only on $\varphi_m(t)$. Then from system (2.2),

$$\dot{x}_i(t) = \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau(z(t))} x_m(t - \tau(z(t))).$$

Integrating this expression we get, for $t > 0$,

$$\begin{aligned} x_i(t) &= e^{-\gamma t} x_i(0) + \alpha e^{-\gamma t} \int_0^t e^{\gamma s} x_m(s) ds \\ &\quad - \alpha e^{-\gamma t} \int_0^t e^{\gamma s} e^{-\gamma\tau(z(s))} x_m(s - \tau(z(s))) ds. \end{aligned}$$

Hence

$$\begin{aligned} x_i(t) &< e^{-\gamma t} x_i(0) + \alpha e^{-\gamma t} \int_0^t e^{\gamma s} x_m(s) ds \\ &\leq e^{-\gamma t} x_i(0) + \alpha e^{-\gamma t} \int_0^t \Delta_m e^{\gamma s} ds \\ &= e^{-\gamma t} x_i(0) + \alpha e^{-\gamma t} \gamma^{-1} \Delta_m (e^{\gamma t} - 1) \\ &= e^{-\gamma t} x_i(0) + \alpha \gamma^{-1} \Delta_m (1 - e^{-\gamma t}) \\ &< x_i(0) + \alpha \gamma^{-1} \Delta_m, \end{aligned}$$

proving the theorem.

Finally, we would like to prove that $x_i(t) > 0$ for all values of t . However, this does not seem to be possible without placing additional restrictions on either the initial conditions or on the delay function $\tau(z)$. For example, if we assume that $\tau'(z) \equiv 0$, then we have shown in [2] that $x_i(t)$ remains positive for all t , but, of course, there we had no state dependence of the time delay.

However, it is possible to state conditions on $\tau'(z)$ that for a given set of initial conditions will give us the positivity of $x_i(t)$, while at the same time maintaining the essential character of the state-dependent time delay.

THEOREM 3.5. *Suppose that (2.4) is satisfied and that $\tau'(z) > 0$ is small enough so that the inequality*

$$(3.1) \quad \delta_m \int_{t-\tau_m}^t e^{\gamma s} ds > \Delta_m \int_{-\tau_s}^{t-\tau_m} \frac{\alpha^2 \tau'(z)}{4\beta - \alpha^2 \tau'(z)} e^{\gamma s} ds$$

holds for all values of t . Then $x_i(t) > 0$ for all $t \geq 0$.

Proof. Suppose that $x_i(t) = 0$ for some value of t . Define

$$t^* = \inf\{t > 0 : x_i(t) = 0\}.$$

Since $x_i(0) > 0$, $t^* > 0$ by continuity. Then integrating the first equation of (2.2), we get

$$\begin{aligned} x_i(t^*) &= e^{-\gamma t^*} x_i(0) + \alpha e^{-\gamma t^*} \int_0^{t^*} e^{\gamma s} x_m(s) ds \\ &\quad - \alpha e^{-\gamma t^*} \int_0^{t^*} e^{\gamma s} e^{-\tau(z(s))} x_m(s - \tau(z(s))) ds. \end{aligned}$$

Since $x_i(t^*) = 0$ and since $x_i(0) = \int_{-\tau_s}^0 \alpha e^{\gamma s} x_m(s) ds$, this is equivalent to

$$(3.2) \quad \int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s) ds = \int_0^{t^*} e^{\gamma(s-\tau(z(s)))} x_m(s - \tau(z(s))) ds.$$

Substituting $r = s - \tau(z(s))$ into the right-hand side of (3.2) and then resubstituting r for s we get,

$$\int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s) ds = \int_{-\tau_s}^{t^* - \tau(z(t^*))} \frac{e^{\gamma s} x_m(s)}{1 - \tau'(z)\dot{z}(s)} ds.$$

Now, since $x_i(t) > 0$ for $t < t^*$, by Theorem 2.1 we have that $t - \tau(z(t))$ is an increasing function of t for $t \leq t^*$, so that $1 - \tau'(z)\dot{z}(t) > 0$ holds for $-\tau_s \leq t \leq t^* - \tau(z(t^*))$. Since $x_m(t) > 0$ as well, we get the inequality

$$\int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s) ds \leq \int_{-\tau_s}^{t^* - \tau_m} \frac{e^{\gamma s} x_m(s)}{1 - \tau'(z)\dot{z}(s)} ds.$$

This gives us

$$\begin{aligned} (3.3) \quad \int_{t^* - \tau_m}^{t^*} e^{\gamma s} x_m(s) ds &\leq \int_{-\tau_s}^{t^* - \tau_m} \left(\frac{1}{1 - \tau'(z)\dot{z}(s)} - 1 \right) e^{\gamma s} x_m(s) ds \\ &= \int_{-\tau_s}^{t^* - \tau_m} \frac{\tau'(z)\dot{z}(s)}{1 - \tau'(z)\dot{z}(s)} e^{\gamma s} x_m(s) ds \end{aligned}$$

Now the left-hand side of inequality (3.3) satisfies

$$(3.4) \quad \int_{t^*-\tau_m}^{t^*} e^{\gamma s} x_m(s) ds \geq \delta_m \int_{t^*-\tau_m}^{t^*} e^{\gamma s} ds.$$

The right-hand side satisfies

$$\int_{-\tau_s}^{t^*-\tau_m} \frac{\tau'(z)\dot{z}(s)}{1-\tau'(z)\dot{z}(s)} e^{\gamma s} x_m(s) ds \leq \int_{-\tau_s}^{t^*-\tau_m} \Delta_m \frac{\tau'(z)\dot{z}(s)}{1-\tau'(z)\dot{z}(s)} e^{\gamma s} ds.$$

However, $\tau'(z) > 0$ and $\tau'(z)\dot{z}(t) < 1$, so, since $x/(1-x)$ is an increasing function for $0 < x < 1$. Furthermore, for fixed $\tau'(z)$, $\tau'(z)\dot{z}(t)/(1-\tau'(z)\dot{z}(t))$ is maximized when $\dot{z}(t)$ is at its maximum value, which, as we saw in the previous section, is $\dot{z}(t) = \alpha^2/4\beta$. So we have that

$$\int_{-\tau_s}^{t^*-\tau_m} \Delta_m \frac{\tau'(z)\dot{z}(s)}{1-\tau'(z)\dot{z}(s)} e^{\gamma s} ds \leq \Delta_m \int_{-\tau_s}^{t^*-\tau_m} \frac{\alpha^2 \tau'(z)}{4\beta - \alpha^2 \tau'(z)} e^{\gamma s} ds$$

is true. Thus we have the following inequality:

$$(3.5) \quad \int_{-\tau_s}^{t^*-\tau_m} \frac{\tau'(z)\dot{z}(s)}{1-\tau'(z)\dot{z}(s)} e^{\gamma s} x_m(s) ds \leq \Delta_m \int_{-\tau_s}^{t^*-\tau_m} \frac{\alpha^2 \tau'(z)}{4\beta - \alpha^2 \tau'(z)} e^{\gamma s} ds.$$

Finally, putting inequalities (3.3)–(3.5) together, we get that, at t^* ,

$$\delta_m \int_{t^*-\tau_m}^{t^*} e^{\gamma s} ds \leq \Delta_m \int_{-\tau_s}^{t^*-\tau_m} \frac{\alpha^2 \tau'(z)}{4\beta - \alpha^2 \tau'(z)} e^{\gamma s} ds$$

must be true. This contradicts the hypothesis of our theorem, so no such t^* can exist and $x_i(t) > 0$ for all $t > 0$. This proves the theorem.

Whether Theorem 3.5 imposes conditions on $\tau'(z)$ that are too stringent remains the subject of further research. For the remainder of this paper, however, we assume that $x_i(t)$ is positive for all t . In any case, since our conditions for $x_i(t)$ remaining positive depend in part on $\delta_m(\varphi_m)$ and on $\Delta_m(\varphi_m)$, a given set of initial conditions for system (2.2) may or may not be admissible, depending on the system parameters. Thus we achieve sufficient conditions for the positivity of $x_i(t)$ by placing restrictions on both $\tau'(z)$ and on the initial conditions.

However, noting that Theorem 3.5 gives only sufficient conditions for an initial function to give a meaningful solution, we can also state the following theorem.

THEOREM 3.6. *Suppose that $e^{-\gamma\tau_m} \leq \delta_m/\Delta_m$. Then $x_i(t) > 0$ for all $t \geq 0$.*

Proof. From the proof of Theorem 3.5, we know that if $t^* = \inf\{t > 0 : x_i(t) = 0\} < \infty$, then (3.2) is true. The left-hand side of (3.2) satisfies

$$(3.6) \quad \delta_m \gamma^{-1} (e^{\gamma t^*} - e^{-\gamma\tau_s}) \leq \int_{-\tau_s}^{t^*} e^{\gamma s} x_m(s) ds$$

by substituting the lower bound δ_m for the function $x_m(s)$ and integrating. In a similar manner, the right-hand side of (3.2) satisfies

$$(3.7) \quad \int_0^{t^*} e^{\gamma(s-\tau(z(s)))} x_m(s-\tau(z(s))) ds \leq \Delta_m \gamma^{-1} e^{-\gamma\tau_m} (e^{\gamma t^*} - 1).$$

Now, let

$$f_1(t) = \delta_m \gamma^{-1} (e^{\gamma t} - e^{-\gamma\tau_s}) \quad \text{and} \quad f_2(t) = \Delta_m \gamma^{-1} e^{-\gamma\tau_m} (e^{\gamma t} - 1).$$

Also, $f_1'(t) = \delta_m e^{\gamma t}$ and $f_2'(t) = \Delta_m e^{-\gamma\tau_m} e^{\gamma t}$. Hence, if $e^{-\gamma\tau_m} \leq \delta_m/\Delta_m$ were true, then $f_2'(t) \leq f_1'(t)$ would be true for all t . Since $f_2(0) < f_1(0)$ is true, then it would be necessary that $f_2(t) < f_1(t)$ be true for all t if $e^{-\gamma\tau_m} < \delta_m/\Delta_m$ were to hold. However, (3.2) together with (3.6) and (3.7), implies that $f_1(t^*) \leq f_2(t^*)$. Therefore if $e^{-\gamma\tau_m} < \delta_m/\Delta_m$ then no such t^* could exist, and $x_i(t) = 0$ would be impossible for any t . This proves the theorem.

Theorem 3.5 seems to imply that as $\tau'(z)$ gets larger, the more restricted the set of admissible initial functions becomes, and that if $\tau'(z)$ approaches the value $4\beta/\alpha^2$ for some value of $z(t)$, that the set of admissible functions approaches the null set. Theorem 3.6, however, seems to imply that there will always be some initial function that gives a solution to the system where $x_i(t)$ remains positive, independent of any behaviour of $\tau(z)$.

We are not able, however, to bound $x_i(t)$ below by any value strictly greater than zero. The conditions we must impose on the system and its initial conditions to get such a strictly positive lower bound for $x_i(t)$ remain a subject for further study. However, in §5 we will see that the limit as t approaches infinity of $x_i(t)$ is strictly positive given some simple assumptions on $\tau(z)$.

4. Equilibria: Existence and local stability. There are only two types of equilibria, namely, the origin (denoted by $E_0(0, 0)$) and one or more interior equilibria (denoted by $\hat{E}(\hat{x}_i, \hat{x}_m)$).

Clearly, there are no axial equilibria other than E_0 . This is obvious biologically as well, since the mature population cannot survive without the immatures, and vice versa.

Showing that \hat{E} always exists is equivalent to showing that the algebraic system

$$(4.1) \quad \alpha x_m - \gamma x_i - \alpha e^{-\gamma\tau(z)} x_m = 0,$$

$$(4.2) \quad \alpha e^{-\gamma\tau(z)} - \beta x_m = 0$$

always has at least one positive solution. Let Γ_1 be the solution curve for $x_i \geq 0$, $x_m \geq 0$ of (4.1) and let Γ_2 be the solution curve for (4.2).

Let us first consider the solution curve Γ_2 . This curve is strictly decreasing, passing through $(0, a)$ in the $x_i - x_m$ plane, where a is the unique positive root of $\beta a = \alpha e^{-\gamma\tau(a)}$. To show that Γ_2 is strictly decreasing, we compute dx_m/dx_i along Γ_2 . From (4.2), we have that $x_m = \alpha\beta^{-1}e^{-\gamma\tau(z)}$, so that differentiating (4.2) we get

$$\frac{dx_m}{dx_i} = -\frac{\alpha\gamma e^{-\gamma\tau(z)}\tau'(z)}{\beta + \alpha\gamma e^{-\gamma\tau(z)}\tau'(z)},$$

which is always less than zero since $\tau'(z) > 0$ is assumed. Furthermore, $\lim_{x_i \rightarrow \infty} x_m(x_i) = b$ along Γ_2 , where $b = \beta^{-1}\alpha e^{-\gamma\tau_M}$.

Γ_1 has the following properties: $(0, 0) \in \Gamma_1$. Furthermore, on $\Gamma_1, \lim_{x_i \rightarrow \infty} x_m(x_i) = \infty$. Hence Γ_1 and Γ_2 must intersect at positive values, establishing the existence of \hat{E} .

It is not necessarily the case that \hat{E} is unique, since Γ_1 and Γ_2 may intersect at more than one point. Such nonuniqueness of stable equilibria has also been observed in nature in the case of Antarctic whales (see [13]).

It is therefore desirable to obtain criteria for there to exist a unique equilibrium. Both Γ_1 and Γ_2 define x_m as a function of $x_i, x_m = g_1(x_i)$ and $x_m = g_2(x_i)$, respectively. Then \hat{E} will be unique, provided that $g'_1(\hat{x}_i) > g'_2(\hat{x}_i)$ for every such \hat{E} , since if there were more than one \hat{E} , the reverse inequality must hold for alternate equilibria.

Now from (4.1) we have that $\alpha x_m - \gamma x_i - \alpha e^{-\gamma\tau(z)} x_m = 0$ along Γ_1 . Hence, along this curve, $x_m(\alpha - \alpha e^{-\gamma\tau(z)}) = \gamma x_i$. Taking derivatives with respect to x_i gives us

$$(4.3) \quad g'_1(x_i) = \frac{\gamma(1 - \alpha x_m e^{-\gamma\tau(z)} \tau'(z))}{\alpha(1 - e^{-\gamma\tau(z)} + \gamma x_m e^{-\gamma\tau(z)} \tau'(z))}.$$

From (4.2), we see that

$$(4.4) \quad g'_2(x_i) = - \frac{\alpha \gamma e^{-\gamma\tau(z)} \tau'(z)}{\beta + \alpha \gamma e^{-\gamma\tau(z)} \tau'(z)},$$

where in (4.3) and (4.4), x_m is the appropriate function of x_i .

Now from (4.1) and (4.2) we get the relations

$$(4.5) \quad \begin{aligned} e^{-\gamma\tau(\hat{z})} &= \alpha^{-1} \beta \hat{x}_m, \\ \hat{x}_i &= \gamma^{-1}(\alpha - \beta \hat{x}_m) \hat{x}_m, \end{aligned}$$

and also

$$(4.6) \quad g'_1(\hat{x}_i) = \frac{\gamma[1 - \beta \hat{x}_m^2 \tau'(\hat{z})]}{\alpha - \beta \hat{x}_m + \beta \gamma \hat{x}_m^2 \tau'(\hat{z})},$$

$$g'_2(\hat{x}_i) = - \frac{\gamma \hat{x}_m \tau'(\hat{z})}{1 + \gamma \hat{x}_m \tau'(\hat{z})}.$$

Hence $g'_1(\hat{x}_i) > g'_2(\hat{x}_i)$, provided

$$(4.7) \quad \frac{\gamma[1 - \beta \hat{x}_m^2 \tau'(\hat{z})]}{\alpha - \beta \hat{x}_m + \beta \gamma \hat{x}_m^2 \tau'(\hat{z})} > - \frac{\gamma \hat{x}_m \tau'(\hat{z})}{1 + \gamma \hat{x}_m \tau'(\hat{z})}.$$

Now from (4.2), clearly $\hat{x}_m < \alpha\beta^{-1}$. Hence $\alpha - \beta \hat{x}_m + \beta \gamma \hat{x}_m^2 \tau'(\hat{z}) > \beta \gamma \hat{x}_m^2 \tau'(\hat{z}) \geq 0$. Hence inequality (4.7) is equivalent to

$$(1 + \gamma \hat{x}_m \tau'(\hat{z}))(1 - \beta \hat{x}_m^2 \tau'(\hat{z})) > \hat{x}_m \tau'(\hat{z})(-\alpha + \beta \hat{x}_m - \beta \gamma \hat{x}_m^2 \tau'(\hat{z})).$$

However, the left-hand side of this equality becomes

$$1 + \hat{x}_m \tau'(\hat{z})(\gamma - \beta \hat{x}_m) - \beta \gamma \hat{x}_m^3 \tau'(\hat{z})^2.$$

Thus the inequality becomes

$$1 + \hat{x}_m(\gamma - \beta \hat{x}_m) \tau'(\hat{z}) - \beta \gamma \hat{x}_m^3 \tau'(\hat{z})^2 > \hat{x}_m \tau'(\hat{z})(-\alpha + \beta \hat{x}_m - \beta \gamma \hat{x}_m^2 \tau'(\hat{z})),$$

which, by combining terms, gives us that $g'_1(\hat{x}_i) > g'_2(\hat{x}_i)$, provided

$$(4.8) \quad 1 + \hat{x}_m \tau'(\hat{z})(\alpha + \gamma - 2\beta \hat{x}_m) > 0.$$

We are now ready to state and prove a theorem giving criteria for uniqueness of \hat{E} .

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THEOREM 4.1. *If any one of (i) $\gamma > \alpha$; (ii) $\hat{x}_m < \frac{\alpha+\gamma}{2\beta}$ for all \hat{x}_m ; (iii) $\tau'(\hat{z}) < 1/(\hat{x}_m(2\beta\hat{x}_m - \alpha - \gamma))$ holds, then \hat{E} is unique.*

Proof. If (ii) holds, then inequality (4.8) is valid. Since $\hat{x}_m < \alpha\beta^{-1}$, then if (i) holds, (ii) also holds. Finally, it is clear that if (iii) holds, then inequality (4.8) is valid. This proves the theorem.

As much as possible, we carry out a stability analysis of the equilibria, noting that the linearized stability theory for state-dependent delays is not yet completely developed. The following analysis, which is only a local stability analysis, is only formal in nature.

Let $E^*(x_i^*, x_m^*)$ be an arbitrary equilibrium. Then the variational system of system (2.2) about E^* is given by

$$(4.9) \quad \begin{aligned} \frac{d}{dt} \begin{pmatrix} x_i(t) \\ x_m(t) \end{pmatrix} &= \begin{pmatrix} -\gamma + \xi^* & \alpha + \xi^* \\ -\xi^* & -2\beta x_m^* - \xi^* \end{pmatrix} \begin{pmatrix} x_i(t) \\ x_m(t) \end{pmatrix} \\ &+ \begin{pmatrix} 0 & -\alpha e^{-\gamma\tau(z^*)} \\ 0 & \alpha e^{-\gamma\tau(z^*)} \end{pmatrix} \begin{pmatrix} x_i(t - \tau(z^*)) \\ x_m(t - \tau(z^*)) \end{pmatrix}, \end{aligned}$$

where

$$(4.10) \quad \xi^* = \alpha\gamma e^{-\gamma\tau(z^*)}\tau'(z^*)x_m^*.$$

This leads to a characteristic equation given by

$$(4.11) \quad \det \begin{vmatrix} \lambda + \gamma - \xi^* & \alpha e^{-\tau(z^*)(\lambda+\gamma)} - \alpha - \xi^* \\ \xi^* & \lambda + 2\beta x_m^* + \xi^* - \alpha e^{-\tau(z^*)(\lambda+\gamma)} \end{vmatrix} = 0.$$

For the equilibrium $E_0(0, 0)$, clearly $\xi^* = 0$, and (4.11) reduces to

$$(\lambda + \gamma)(\lambda - \alpha e^{-\tau_m(\lambda+\gamma)}) = 0.$$

Clearly $\lambda = -\gamma$ is one of the eigenvalues. All other eigenvalues are given by solutions of

$$\lambda = \alpha e^{-\tau_m(\lambda+\gamma)},$$

which always has a real, positive solution. Hence E_0 is a saddle point.

For any interior equilibrium $\hat{E}(\hat{x}_i, \hat{x}_m)$, we set

$$\hat{\xi} = \alpha\gamma e^{-\gamma\tau(\hat{z})}\tau'(\hat{z})\hat{x}_m = \beta\gamma\hat{x}_m^2\tau'(\hat{z}).$$

Expanding the characteristic equation (4.11) gives us

$$\begin{aligned} &\lambda^2 + [\gamma + 2\beta\hat{x}_m - \alpha e^{-\tau(\hat{z})(\gamma+\lambda)}]\lambda \\ &+ \gamma(\hat{\xi} + 2\beta\hat{x}_m - \alpha e^{-\tau(\hat{z})(\gamma+\lambda)}) - \hat{\xi}(\hat{\xi} + 2\beta\hat{x}_m - \alpha e^{-\tau(\hat{z})(\gamma+\lambda)}) \\ &= \hat{\xi}(-\alpha - \hat{\xi} + \alpha e^{-\tau(\hat{z})(\gamma+\lambda)}), \end{aligned}$$

which is equivalent to

$$\lambda^2 + [\gamma + 2\beta\hat{x}_m - \alpha e^{-\tau(\hat{z})(\lambda+\gamma)}]\lambda + \gamma(\hat{\xi} + 2\beta\hat{x}_m - \alpha e^{-\tau(\hat{z})(\lambda+\gamma)}) - \hat{\xi}(2\beta\hat{x}_m) = -\alpha\hat{\xi}$$

so that

$$\lambda^2 + [\gamma + 2\beta\hat{x}_m]\lambda + \gamma(\hat{\xi} + 2\beta\hat{x}_m) - \hat{\xi}2\beta\hat{x}_m + \alpha\hat{\xi} = \alpha e^{-\tau(\hat{z})(\lambda+\gamma)}(\lambda + \gamma).$$

Then, since $\hat{\xi} = \alpha\gamma e^{-\gamma\tau(\hat{z})}\tau'(\hat{z})\hat{x}_m = \beta\gamma\hat{x}_m^2\tau'(\hat{z})$ we have

$$\lambda^2 + [\gamma + 2\beta\hat{x}_m]\lambda + \beta\gamma\hat{x}_m[\gamma\hat{x}_m\tau'(\hat{z}) + 2 - 2\beta\hat{x}_m^2\tau'(\hat{z}) + \alpha\hat{x}_m\tau'(\hat{z})] = \beta\hat{x}_m e^{-\gamma\tau(\hat{z})}(\lambda + \gamma),$$

which gives us

$$(4.12) \quad \lambda^2 + [2\beta\hat{x}_m + \gamma]\lambda + \beta\gamma\hat{x}_m[2 + \hat{x}_m(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z})] = \beta\hat{x}_m e^{-\gamma\tau(\hat{z})}(\lambda + \gamma)$$

as the characteristic equation. This characteristic equation is similar to one described in [19], but differs in the signs of some of the coefficients. Also see [6] for general theory in this regard.

In [2], where $\tau'(z) \equiv 0$, it was shown that \hat{E} is globally asymptotically stable. Our first stability result for a state-dependent time delay is that if $\tau'(\hat{z}) = 0$, local asymptotic stability holds.

THEOREM 4.2. *Let $\tau'(\hat{z}) = 0$. Then \hat{E} is locally asymptotically stable.*

Proof. If $\tau'(\hat{z}) = 0$, the characteristic equation (4.12) can be written as

$$(4.13) \quad (\lambda + \gamma)(\lambda + 2\beta\hat{x}_m - \beta\hat{x}_m e^{-\gamma\tau(\hat{z})}) = 0.$$

Again $\lambda = -\gamma$ is one eigenvalue, and the others are given by the equation

$$(4.14) \quad \lambda + 2\beta\hat{x}_m = \beta\hat{x}_m e^{-\gamma\tau(\hat{z})}.$$

Suppose that $\Re \lambda \geq 0$. Then from (4.14) we compute the real parts of λ and get

$$\begin{aligned} \Re \lambda + 2\beta\hat{x}_m &= \beta\hat{x}_m e^{-\gamma\tau(\hat{z})} \Re e^{\lambda} \cos(\gamma\tau(\hat{z}) \Im \lambda) \\ &\leq \beta\hat{x}_m. \end{aligned}$$

Hence $\Re \lambda \leq -\beta\hat{x}_m < 0$, a contradiction proving the theorem.

We now consider the case where $\tau'(\hat{z}) > 0$. We let $\lambda = \mu + i\nu$ and separate the characteristic equation (4.12) into real and imaginary parts, giving

$$(4.15) \quad \begin{aligned} \mu^2 - \nu^2 + (2\beta\hat{x}_m + \gamma)\mu + \eta &= \beta\hat{x}_m e^{-\hat{\tau}\mu}[(\gamma + \mu) \cos \hat{\tau}\nu + \nu \sin \hat{\tau}\nu], \\ 2\mu\nu + (2\beta\hat{x}_m + \gamma)\nu &= \beta\hat{x}_m e^{-\hat{\tau}\mu}[\nu \cos \hat{\tau}\nu - (\gamma + \mu) \sin \hat{\tau}\nu], \end{aligned}$$

where

$$\hat{\tau} = \gamma\tau(\hat{z}), \quad \eta = \beta\gamma\hat{x}_m[2 + \hat{x}_m(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z})].$$

We will think of η as a parameter that varies with $\tau'(\hat{z})$. When $\tau'(\hat{z}) = 0$, then $\eta = 2\beta\gamma\hat{x}_m$, and for this value of η , \hat{E} is asymptotically stable.

Suppose now that there is a first value of $\tau'(\hat{z}) > 0$ such that for this value $\eta = \bar{\eta}$ gives us that $\mu = 0$, so that \hat{E} loses its stability. Then (4.15) becomes

$$(4.16) \quad \begin{aligned} \nu^2 - \bar{\eta} &= -\beta\hat{x}_m[\gamma \cos \hat{\tau}\nu + \nu \sin \hat{\tau}\nu], \\ (2\beta\hat{x}_m + \gamma)\nu &= \beta\hat{x}_m[\nu \cos \hat{\tau}\nu - \gamma \sin \hat{\tau}\nu]. \end{aligned}$$

Squaring and adding (4.16) gives

$$(4.17) \quad \nu^4 + [3\beta^2\hat{x}_m^2 + 4\beta\gamma\hat{x}_m + \gamma^2 - 2\bar{\eta}]\nu^2 + [\bar{\eta}^2 - \beta^2\gamma^2\hat{x}_m^2] = 0.$$

For such $\bar{\eta}$ to exist, (4.17) must have real roots. Hence we can now prove the following theorem.

THEOREM 4.3. *If either (i) $\hat{x}_m \leq (\alpha + \gamma)/2\beta$ or (ii) $\hat{x}_m > (\alpha + \gamma)/2\beta$ and $\tau'(\hat{z}) \leq 3/(4\hat{x}_m(2\beta\hat{x}_m - \alpha - \gamma))$ holds, then \hat{E} is locally asymptotically stable.*

Proof. After substituting for $\bar{\eta}$, (4.17) becomes, after combining like terms and rearranging,

$$\nu^4 - 2\beta\gamma\hat{x}_m^2(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z})\nu^2 + \beta^2\gamma^2\hat{x}_m^4[(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z})]^2 + [3\beta^2\hat{x}_m^2 + \gamma^2]\nu^2 + 3\beta^2\gamma^2\hat{x}_m^2 + 4\beta^2\gamma^2\hat{x}_m^3(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z}) = 0.$$

Thus we get the relation

$$f(\nu^2) = [\nu^2 - \beta\gamma\hat{x}_m^2\tau'(\hat{z})(\alpha + \gamma - 2\beta\hat{x}_m)]^2 + [3\beta^2\hat{x}_m^2 + \gamma^2]\nu^2 + 3\beta^2\gamma^2\hat{x}_m^2 + 4\beta^2\gamma^2\hat{x}_m^3(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z}) = 0.$$

Observe that the first three expressions in $f(\nu^2)$ are always positive. So, if $x_m \leq (\alpha + \gamma)/2\beta$, the last expression is also positive since $\hat{x}_m > 0$, $\tau'(\hat{z}) > 0$ by assumption, and $(\alpha + \gamma - 2\beta\hat{x}_m) > 0$ will be true. Hence $f(\nu^2) > 0$, and no such $\hat{\eta}$ can exist.

Now, if $\hat{x}_m > (\alpha + \gamma)/2\beta$, then $(\alpha + \gamma - 2\beta\hat{x}_m) < 0$. Then if $\tau'(z) < \frac{3}{4}(\hat{x}_m(2\beta\hat{x}_m - \alpha - \gamma))$ we have

$$3\beta^2\gamma^2\hat{x}_m^2 + 4\beta^2\gamma^2\hat{x}_m^3(\alpha + \gamma - 2\beta\hat{x}_m)\tau'(\hat{z}) \geq 3\beta^2\gamma^2\hat{x}_m^2 - 4\beta^2\gamma^2\hat{x}_m^3 \cdot \frac{3}{4\hat{x}_m} = 0.$$

Since the first two terms of $f(\nu^2)$ are positive, then $f(\nu^2) > 0$ must hold. So if either (i) or (ii) holds, then $f(\nu^2) > 0$ for all $\nu^2 \geq 0$, and (4.17) has no real solution. Then for that value of $\tau'(\hat{z})$, $\mu = 0$ is impossible. Hence, since $\mu < 0$ when $\tau'(\hat{z}) = 0$, by continuity, $\mu < 0$ for that value of $\tau'(\hat{z})$, proving the theorem.

We note that in the case where \hat{E} is not unique, unstable (saddlepoint) equilibria must exist.

5. Global behavior of solutions. In this section we are interested in obtaining some global properties of the solutions of our model. In particular, we wish to ascertain that their behavior is reasonable, provided the initial inputs are reasonable.

The first results show that if the mature population remains below or above a certain value for length of time τ_M , it will do so from then on.

THEOREM 5.1. *Let $(x_i(t), x_m(t))$ be a solution of system (2.2).*

(i) *If there exists $t_1 \geq -\tau_m$ such that $x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$ for $t_1 \leq t \leq t_1 + \tau_M$, then $x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$ for all $t \geq t_1$.*

(ii) *If there exists $t_2 \geq -\tau_m$ such that $x_m(t) \geq \alpha\beta^{-1}e^{-\gamma\tau_m}$ for $t_2 \leq t \leq t_2 + \tau_M$, then $x_m(t) \geq \alpha\beta^{-1}e^{-\gamma\tau_m}$ for all $t \geq t_2$.*

Proof. We prove the result for case (i). The proof of case (ii) follows analogously. Suppose that there exists $t^* > t_1 + \tau_M$ such that $x_m(t^*) = \alpha\beta^{-1}e^{-\gamma\tau_m}$ and $x_m(t) < \alpha\beta^{-1}e^{-\gamma\tau_m}$ for $t_1 \leq t < t^*$, where $\dot{x}_m(t^*) \geq 0$. However, from system (2.2),

$$\begin{aligned} \dot{x}_m(t^*) &= \alpha e^{-\gamma\tau(z)}x_m(t^* - \tau(z)) - \beta x_m^2(t^*) \\ &= \alpha e^{-\gamma\tau(z)}x_m(t^* - \tau(z)) - \alpha^2\beta^{-1}e^{-2\gamma\tau_m} \\ &\leq \alpha e^{-\gamma\tau_m}[x_m(t^* - \tau(z)) - \alpha\beta^{-1}e^{-\gamma\tau_m}] < 0, \end{aligned}$$

a contradiction.

From this theorem, the following corollary follows immediately.

COROLLARY 5.2. (i) If $\varphi_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$, $-\tau_M \leq t \leq 0$, then $x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$ for all $t \geq 0$. (ii) If $\varphi_m(t) \geq \alpha\beta^{-1}e^{-\gamma\tau_M}$, $-\tau_M \leq t \leq 0$, then $x_m(t) \geq \alpha\beta^{-1}e^{-\gamma\tau_M}$ for all $t \geq 0$.

In the case where we know that $x_m(t)$ is monotone, then we can show that the limit as $t \rightarrow \infty$ of $x_m(t)$ lies in a certain bounded interval.

THEOREM 5.3. Suppose that $x_m(t)$ is eventually monotonic. Then $\alpha\beta^{-1}e^{-\gamma\tau_M} \leq \lim_{t \rightarrow \infty} x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$.

Proof. Since $x_m(t)$ is eventually monotonic and $x_m(t)$ is bounded, there exists $0 < \bar{x}_m < \infty$ such that $\lim_{t \rightarrow \infty} x_m(t) = \bar{x}_m$, $\lim_{t \rightarrow \infty} \dot{x}_m(t) = 0$. Hence from system (2.2), taking the limit superior as $t \rightarrow \infty$, we have that

$$0 = \bar{x}_m \left(\alpha e^{-\gamma\tau(\limsup_{t \rightarrow \infty} x_i(t) + \bar{x}_m)} - \beta \bar{x}_m \right).$$

Thus $\bar{x}_m = \alpha\beta^{-1}e^{-\gamma\tau(\limsup_{t \rightarrow \infty} x_i(t) + \bar{x}_m)}$, so that $\alpha\beta^{-1}e^{-\gamma\tau_M} \leq \bar{x}_m \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$, proving the theorem.

We can now state bounds on the eventual behaviour of $x_m(t)$, independent of admissible initial conditions.

THEOREM 5.4. Let $(x_i(t), x_m(t))$ be a solution of system (2.2). Then

$$(5.1) \quad \alpha\beta^{-1}e^{-\gamma\tau_M} \leq \liminf_{t \rightarrow \infty} x_m(t) \leq \limsup_{t \rightarrow \infty} x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}.$$

Proof. If $x_m(t)$ is eventually monotonic, the result follows from Theorem 5.3. Hence we assume that $x_m(t)$ is oscillatory. We prove that $\limsup_{t \rightarrow \infty} x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$. The other inequality follows analogously.

Define the sequence $\{t_k\}$ as those times for which $x_m(t)$ achieves a maximum, i.e., $\dot{x}_m(t_k) = 0$, $\ddot{x}_m(t_k) < 0$. Define

$$(5.2) \quad \tilde{x}_m = \limsup_{k \rightarrow \infty} \{x_m(t_k)\}.$$

Then $0 < \tilde{x}_m < \infty$ and $\limsup_{t \rightarrow \infty} x_m(t) = \tilde{x}_m$.

If $\tilde{x}_m \leq \alpha\beta^{-1}e^{-\gamma\tau_m}$, we are done. Hence assume that

$$(5.3) \quad \tilde{x}_m > \alpha\beta^{-1}e^{-\gamma\tau_m}.$$

Then from system (2.2), $0 = \dot{x}_m(t_k) = \alpha e^{-\gamma\tau(z_k)}x_m(t_k - \tau(z_k)) - \beta x_m^2(t_k)$, where $z_k = x_i(t_k) + x_m(t_k)$.

We now choose a subsequence of $\{t_k\}$, relabelled as $\{t_k\}$ so that $\lim_{k \rightarrow \infty} x_m(t_k) = \tilde{x}_m$ and $t_{k+1} \geq t_k + \tau_M$. We then choose a further subsequence of $\{t_k\}$, again relabelled $\{t_k\}$ so that $\lim_{k \rightarrow \infty} z_k = \tilde{z}$, where $\tilde{z} = \limsup_{k \rightarrow \infty} z_k$.

Now let $x_m^\# = \limsup_{k \rightarrow \infty} x_m(t_k - \tau(z_k))$ for this subsequence $\{t_k\}$. We choose a final subsequence of $\{t_k\}$, once again relabelled $\{t_k\}$, so that $\lim_{k \rightarrow \infty} x_m(t_k - \tau(z_k)) = x_m^\#$.

Now from the definition of τ_m and inequality (5.3), we get, taking the limit as $k \rightarrow \infty$,

$$0 = \alpha e^{-\gamma\tau(\tilde{z})}x_m^\# - \beta \tilde{x}_m^2 < \alpha e^{-\gamma\tau_m}(x_m^\# - \tilde{x}_m).$$

If $x_m^\# \leq \tilde{x}_m$, we have a contradiction.

Hence we assume that $x_m^\# > \tilde{x}_m$. Then we have that for each k , we can choose a value t_i such that $\dot{x}_m(t_i) = 0$, $\ddot{x}_m(t_i) < 0$, and $\limsup_{i \rightarrow \infty} x_m(t_i) \geq x_m^\# > \tilde{x}_m$. This, however, contradicts the definition of \tilde{x}_m in expression (5.2), so $x_m^\# > \tilde{x}_m$ cannot be true. This eliminates the last possibility and proves the theorem.

We can now use the above estimates to obtain estimates on the x_i . We first note that we can find $T(\varepsilon) > 0$ to large that

$$(5.4) \quad \alpha\beta^{-1}e^{-\gamma\tau_M} - \varepsilon < x_m(t) < \alpha\beta^{-1}e^{-\gamma\tau_m} + \varepsilon$$

for given $\varepsilon > 0$ whenever $t \geq T$. Then the first equation of (2.2) can be written in the integral equation form

$$(5.5) \quad x_i(t) = e^{-\gamma(t-T)}[x_i(T) + \alpha \int_T^t e^{\gamma(s-T)} (x_m(s) - e^{-\gamma\tau(z(s))}x_m(s - \tau(z(s)))) ds].$$

Although (5.5) is valid for all t , we will utilize it only for those $t \geq T + \tau_M$.

THEOREM 5.5. *Let $(x_i(t), x_m(t))$ be a solution of system (2.2). Then*

$$\limsup_{t \rightarrow \infty} x_i(t) \leq \alpha^2\beta^{-1}\gamma^{-1}(e^{-\gamma\tau_m} - e^{-2\gamma\tau_M}).$$

Proof. Utilizing (5.4) and (5.5), we get for $t \geq T + \tau_M$

$$(5.6) \quad x_i(t) \leq e^{-\gamma(t-T)}[x_i(T) + \alpha \int_T^t e^{\gamma(s-T)} (\alpha\beta^{-1}e^{-\gamma\tau_m} + \varepsilon - e^{-\gamma\tau_M}(\alpha\beta^{-1}e^{-\gamma\tau_M} - \varepsilon)) ds],$$

where $\varepsilon > 0$ is arbitrary. Hence from (5.6) we get that

$$\begin{aligned} \limsup_{t \rightarrow \infty} x_i(t) &\leq \limsup_{t \rightarrow \infty} e^{-\gamma(t-T)}x_i(T) \\ &\quad + \limsup_{t \rightarrow \infty} \alpha e^{-\gamma(t-T)}[\alpha\beta^{-1}e^{-\gamma\tau_m} - \alpha\beta^{-1}e^{-2\gamma\tau_M} \\ &\quad + \varepsilon(1 + e^{-\gamma\tau_M})] \int_T^t e^{\gamma(s-T)} ds \\ &= [\alpha^2\beta^{-1}(e^{-\gamma\tau_m} - e^{-2\gamma\tau_M}) \\ &\quad + \alpha\varepsilon(1 + e^{-\gamma\tau_M})] \limsup_{t \rightarrow \infty} e^{-\gamma(t-T)} \int_T^t e^{\gamma(s-T)} ds \\ &= \gamma^{-1}[\alpha^2\beta^{-1}(e^{-\gamma\tau_m} - e^{-2\gamma\tau_M}) + \alpha\varepsilon(1 + e^{-\gamma\tau_M})](1 - \lim_{t \rightarrow \infty} e^{-\gamma(t-T)}) \\ &= \alpha^2\beta^{-1}\gamma^{-1}(e^{-\gamma\tau_m} - e^{-2\gamma\tau_M}) + \alpha\gamma^{-1}\varepsilon(1 + e^{-\gamma\tau_M}). \end{aligned}$$

Since ε is arbitrary, the theorem is proved.

Similarly, we can obtain a lower bound on $x_i(t)$.

THEOREM 5.6. *Let $\tau_M < 2\tau_m$. Let $(x_i(t), x_m(t))$ be a solution of system (2.2). Then $\liminf_{t \rightarrow \infty} x_i(t) \geq \alpha^2\beta^{-1}\gamma^{-1}(e^{-\gamma\tau_M} - e^{-2\gamma\tau_m})$.*

Proof. The proof for this theorem is similar to the proof of Theorem 5.5.

In this theorem for the lower bound, we require that $\tau_M < 2\tau_m$ for the lower bound to be positive, otherwise we do not have any new information. That is, if $\tau_M - \tau_m > \tau_m$ (too large a spread), we are unable to obtain an explicit limiting lower bound on $x_i(t)$.

6. Discussion. The main purpose of this paper is to analyze a model of stage-structured population growth where the age to maturity is state dependent. It is found that there always exists a positive equilibrium, but, unlike the constant delay case, this equilibrium may not be unique. Criteria for uniqueness are obtained, as well as criteria for local asymptotic stability.

In §5, we obtained explicit bounds for the eventual behavior of $x_i(t)$ and $x_m(t)$. These bounds were in terms of τ_m and τ_M . In the case that $\tau_M = \tau_m$, i.e., in the case where our system reduces to the constant delay case, then $\lim_{t \rightarrow \infty} (x_i(t), x_m(t))$ exists and tends to (\hat{x}_i, \hat{x}_m) (which is unique), thus incorporating the results of [2]. We should note that Theorem 5.6 allows for the possibility of the number of immatures $x_i(t)$, to become arbitrarily small if $\tau_M < 2\tau_m$. Neither our requirement that $\tau'(z) < 4\beta/\alpha^2$ to avoid retrogression of matures into immatures, nor our requirement for Theorem 3.5 that $\delta_m \int_{t-\tau_m}^t e^{\gamma s} ds > \Delta_m \int_{-\tau_s}^{t-\tau_m} (\alpha^2 \tau'(z)/(4\beta - \alpha^2 \tau'(z))) e^{\gamma s} ds$ for all t precludes τ_M from being less than $2\tau_m$, since for any difference $\tau_M - \tau_m$, $\tau'(z)$ can still be made as small as needed to satisfy our requirements for a valid model. In any case, Theorem 3.6 assures us that we can find admissible initial functions for a wide variety of cases.

There is a connection between the various criteria for uniqueness and stability of equilibria, as well as the criterion for avoidance of retrogression of immatures into matures. Namely, the requirement that $\tau'(z) < 4\alpha^{-2}\beta$ is involved in all three. Biologically, this says that the change in length of time to maturity cannot change too rapidly as the population density changes. This is, of course, biologically reasonable.

We should also note that the requirement that $\tau'(z) < 4\beta/\alpha^2$ to avoid retrogression and the requirement that

$$\delta_m \int_{t-\tau_m}^t e^{\gamma s} ds > \Delta_m \int_{-\tau_s}^{t-\tau_m} (\alpha^2 \tau'(z)/(4\beta - \alpha^2 \tau'(z))) e^{\gamma s} ds$$

in Theorem 3.5 that gives sufficient conditions for the positivity of $x_i(t)$ are linked; as $\tau'(z)$ approaches the value $4\beta/\alpha^2$ where retrogression of mature and immatures occurs, the set of admissible initial functions allowed by that theorem approaches the null set.

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