Canad. Math. Bull.Vol. 36 (2), 1993 pp. 129–138

OSCILLATION AND GLOBAL ATTRACTIVITY IN STAGE-STRUCTURED POPULATION MODELS

YULIN CAO AND H. I. FREEDMAN

ABSTRACT. Stage-structured models of population growth have been considered in the constant delay and state-dependent delay cases, when modeled by retarded functional differential equations. In the first case we settle a conjecture posed by Aiello and Freedman [1] by showing the existence of oscillatory solutions. In the second case, we show that under suitable criteria, all positive solutions tend to a global attractor.

1. **Introduction.** There have recently appeared in the literature several mathematical models of stage-structured population growth, *i.e.* models which take into account the fact that individuals in a population may belong to one of two classes, the immatures and the matures (see [1], [2], [3], [7], [8], [12], [15], [16]). In these models, the age to maturity is represented by a time delay, leading to systems of retarded functional differential equations. For general models of population growth see [13].

A model of single species growth incorporating stage-structure as a reasonable generalization of the logistic model was derived independently in [1] and [16]. This model assumed an average age to maturity which appeared as a constant time delay reflecting a delayed birth of immatures and a reduced survival of immatures to their maturity. Hence the model took the form

$$(1)\qquad \begin{cases} \dot{x}_i(t) = \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t-\tau) \\ \dot{x}_m(t) = \alpha e^{-\gamma\tau} x_m(t-\tau) - \beta x_m^2(t), \end{cases}$$

where $\cdot = d/dt$ and where $x_i(t)$ is the immature population density, $x_m(t)$ is the mature population density. $\alpha > 0$ represents the birth rate, $\gamma > 0$ is the immature death rate, $\beta > 0$ is the mature death and overcrowding rate, and τ is the time to maturity. The term $\alpha e^{-\gamma\tau} x_m(t-\tau)$ represents the immatures who were born at time $t-\tau$ (*i.e.* $\alpha x_m(t-\tau)$) and survive at the time t (with the immature death rate γ), and therefore represent the transformation of immatures to matures.

In [1], system (1) was analyzed, and it was shown that there exists a unique positive equilibrium which is globally asymptotically stable. It was also conjectured there, on the basis of numerical evidence, that all solutions are nonoscillatory. The main focus in

Research carried out while the authors were visiting the Institute of Mathematics and its Applications, University of Minnesota.

The second author was partially supported by the Natural Sciences and Engineering Research Council of Canada, Grant No. NSERC A4823.

Received by the editors March 26, 1991; revised August 24, 1992.

AMS subject classification: Primary: 34K15; secondary: 34K20, 92D40.

[16], in addition to justifying the model (1), was to give reasonable estimates for the parameter γ.

Based on observations over a seventy year time span in the Antarctic Ocean [7], this time delay may upon occasion be taken as state-dependent. The biological idea behind this is as follows [2], [7]. The time to maturity is a function of the amount of food available. In the case of a limited food supply (such as krill in the Antarctic Ocean), the amount of food available per individual (or biomass) is a function of the total population biomass. Hence the time to maturity is a function of that biomass, that is, it is state-dependent.

Hence a reasonable generalization of model (1) to incorporate this state dependency is given by (see [2])

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

where $z = x_i + x_m$, the total population concentration.

Since the time to maturity is a decreasing function of food availability, which is a decreasing function of population, we assume that $\frac{d\tau(z)}{dt} \geq 0$. Further, since there must be a minimum and maximum time to maturity for biological growth reasons, we assume that $\tau(0) = \tau_m > 0$, and $\lim_{z\to\infty} \tau(z) = \tau_M < \infty$.

In order to properly formulate the model, we must specify the initial conditions. Hence we assume that

$$x_i(t) = \varphi_i(t) \geq 0, \quad x_m(t) = \varphi_m(t) \geq 0, \quad -\tau_M \leq t \leq 0, \tag{3}$$

(in the constant delay case, $\tau_M = \tau$). We also will need a further restriction on $\varphi_i(0)$ to guarantee the positivity of solutions, namely

$$\varphi_i(0) = \int_0^{\tau_s} \alpha\varphi_m(s-\tau_s)e^{\gamma(s-\tau_s)}\,ds, \tag{4}$$

where

$$\tau_s = \inf_{\tau_u}\Big\{\tau_u : \tau_u = \tau\Big(\varphi_m(0) + \int_{-\tau_u}^{0} \alpha\varphi_m(s)e^{\gamma s}\,ds\Big)\Big\} \tag{5}$$

(see [2] for details).

The analysis of system (2) yielded results which showed that systems (1) and (2) could have different properties. For instance, system (1) always has a unique positive equilibrium which is globally asymptotically stable, whereas system (2) may have multiple positive equilibria (see [2]) and even in the case where the positive equilibrium exists, it may not be globally asymptotically stable.

From the point of view of ecological managers, it may be desirable to have a unique equilibrium which is globally asymptotically stable, in order to plan harvesting strategies, for example. Such is not always the case as once again demonstrated in the Antarctic Ocean by the overhunting of the Blue Whale. According to Jones and Walters [10], the Blue Whale was not able to recover from a low concentration to its previous level, even though all harvesting of them ceased. The explanation given in [10] as the most likely cause is the existence of multiple stable equilibria.

The outline of this paper is as follows. In the next section we will settle the oscillation-nonoscillation conjecture in [1] by demonstrating that oscillating solutions of system (1) do exist. A similar argument would also show that oscillating solutions exist for system (2), provided regularity conditions are assumed for the system (J. Hale, personal communication).

In Section 3, we consider the question of global stability of the interior equilibrium. In [2], criteria were given for such a positive equilibrium to be unique. Further, a rectangular region was constructed which all positive solutions enter and/or remain. Here we give additional assumptions involving bounds on the derivative of the delay under which this region can be shrunk down to the equilibrium in Section 4.

We end with a discussion of our results in Section 5.

2. **Oscillations.** In the case that $\tau(z) \equiv \tau$, a constant, the model reduces to

$$\begin{aligned} \dot{x}_i(t) &= \alpha x_m(t) - \gamma x_i(t) - \alpha e^{-\gamma\tau} x_m(t-\tau) \\ \dot{x}_m(t) &= \alpha e^{-\gamma\tau} x_m(t-\tau) - \beta x_m^2(t), \\ x_m(t) &= \varphi_m(t) \geq 0, \quad -\tau \leq t \leq 0 \\ x_i(0) &= \int_0^\tau \alpha\varphi_m(s-\tau) e^{\gamma(s-\tau)}\, ds. \end{aligned} \tag{6}$$

It was shown in [1] that all solutions with positive initial conditions converged to the unique positive equilibrium, $\hat{E}(\hat{x}_i, \hat{x}_m)$, where

$$\hat{x}_i = \alpha^2\beta^{-1}\gamma^{-1}e^{-\gamma\tau}(1-e^{-\gamma\tau}), \quad \hat{x}_m = \alpha\beta^{-1}e^{-\gamma\tau}. \tag{7}$$

It was conjectured that based on numerical evidence, all solutions were nonoscillatory. At this time, we show that the conjecture is false.

Using standard techniques and (7) we get the linearized system y_i, y_m about $\hat{E}$ as

$$\begin{aligned} \dot{y}_i(t) &= \alpha y_m(t) - \gamma y_i(t) - \alpha e^{-\gamma\tau} y_m(t-\tau) \\ \dot{y}_m(t) &= \alpha e^{-\gamma\tau} y_m(t-\tau) - 2\alpha e^{-\gamma\tau} y_m(t). \end{aligned} \tag{8}$$

This leads to the characteristic equation obtained by

$$\det \begin{pmatrix} \lambda+\gamma & -\alpha+\alpha e^{-\gamma\tau}e^{-\tau\lambda} \\ 0 & \lambda+2\alpha e^{-\gamma\tau} - \alpha e^{-\gamma\tau}e^{-\tau\lambda} \end{pmatrix} = 0.$$

Therefore $\lambda = -\gamma$ is always an eigenvalue. All other eigenvalues satisfy

$$\lambda = -\alpha e^{-\gamma\tau}(2-e^{-\tau\lambda}) \triangleq f(\lambda). \tag{9}$$

Equation (9) always has a unique real negative solution, since $f(\lambda)$ is a strictly decreasing function of λ such that $f(-\infty) = +\infty, f(0) = -\alpha e^{-\gamma\tau} < 0, f(+\infty) = -2\alpha e^{-\gamma\tau}$. Hence $f(\lambda) = \lambda$ for a unique value, $\lambda = -r < 0$.

In general λ is not necessarily real. Hence if we set $\lambda = \mu + i\nu$, μ and ν satisfy

$$\mu = -2\alpha e^{-\gamma\tau} + \alpha e^{-\gamma\tau} e^{-\tau\mu}\cos\tau\nu \tag{10}$$
$$\nu = -\alpha e^{-\gamma\tau} e^{-\tau\mu}\sin\tau\nu.$$

From the first of equations (10), we see that $\mu \geq 0$ is impossible. Hence all eigenvalues have negative real parts.

To show that there exist complex eigenvalues, by some algebraic manipulations we get μ and ν that satisfy

$$(\mu + 2\alpha e^{-\gamma\tau})^2 + \nu^2 = \alpha^2 e^{-2\gamma\tau} e^{-2\tau\nu}, \tag{11}$$

and for sufficiently large $|\nu|$, ($\mu < 0$) equation (11) can be solved for ν as real functions of μ.

From the above, it follows that system (8) has oscillatory solutions. Finally, we use Theorem 1.1, p. 230 of [9] to conclude that the nonlinear system (which is thought of as a perturbation of the linear system) also has oscillatory solutions.

Finally, noting that the curve

$$\mu = g(\mu,\nu) \triangleq -2\alpha e^{-\gamma\tau} + \alpha e^{-\gamma\tau} e^{-\tau\mu}\cos\tau\nu$$

lies below the curve $\mu = f(\mu)$ which is monotonically decreasing, it follows that either $-\gamma$ or $-r$ is the dominant eigenvalue. Hence the manifolds that the oscillatory solutions lie on are "thin," in the sense that almost all initial functions yield solutions which tend to $\hat{E}$ monotonically, *i.e.* to the manifold corresponding to one of the eigenvalues $-\gamma, -r$. This is why it is difficult to find oscillatory solutions numerically.

As mentioned previously, with suitable regularity conditions, a similar argument is valid in the state-dependent case.

3. **An attracting region.** For the convenience of our analysis, we rewrite the immature and mature population model (2) in terms of the total and the mature populations

$$\begin{cases} \dot{z}(t) = \gamma z(t) + (\alpha+\gamma)x_m(t) - \beta x_m^2(t) \\ \dot{x}_m(t) = \alpha e^{-\gamma\tau(z)} x_m\big(t - \tau(z)\big) - \beta x_m^2(t) \end{cases} t > 0, \tag{12}$$

where $\tau(z) = \tau\big(z(t)\big)$ depends on t. This equation has the equilibria $(0,0)$ and $\tilde{E}(\hat{z},\hat{x}_m)$, where $0 < \hat{x}_m < \hat{z}_m = \hat{x}_m + \hat{x}_i$. These nontrivial equilibria $\tilde{E}(\hat{z},\hat{x}_m)$ of (12) are equivalent to the interior equilibria $\hat{E}(\hat{x}_i,\hat{x}_m)$ of (2).

Note from Theorems 5.4 and 5.5 of [2] that all admissible solutions (*i.e.* $x_i(t) > 0$, $x_m(t) > 0$) are dissipative, and in fact

$$\begin{aligned} \alpha\beta^{-1}e^{-\gamma\tau_M} &\leq \liminf_{t\to\infty} x_m(t) \\ &\leq \limsup_{t\to\infty} x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau_m} \end{aligned} \tag{13}$$

https://doi.org/10.4153/CMB-1993-019-9 Published online by Cambridge University Press

and $\limsup_{t\to\infty} x_i(t) \le \alpha^2\beta^{-1}\gamma^{-1}(e^{-\gamma\tau_m} - e^{-2\gamma\tau_M})$. Note that for a given τ, we can always find admissible solutions according to Theorem 3.6 of [2].

It has been proved in [2] that positive solutions of the system (2) are dissipative. Here we shall give a more precise attracting region for the solutions of (2)–(3). Note that when this attracting region collapses to a unique positive equilibrium $\hat{E}$, then $\hat{E}$ is globally attractive.

THEOREM 1. *Let* $H(z) \triangleq \alpha\beta^{-1}[1+\alpha\gamma^{-1} - \alpha\gamma^{-1}e^{-\gamma\tau(z)}]e^{-\gamma\tau(z)}$. *Let* $[z_1, z^1] \subset (0, +\infty)$ *be the attracting interval of the mapping* $z \longrightarrow H(z)$ $\big(z \in [0,+\infty)\big)$ *and* $\bar{\tau}_M = \tau(z^1)$, $\bar{\tau}_m = \tau(z_1)$. *If* $\big(z(t), x_m(t)\big)$ *is an admissible solution of system (12), then* $\big(z(t), x_m(t)\big)$ *is attracted to the region* $\Omega = [z_1, z^1] \times [\alpha\beta^{-1}e^{-\gamma\bar{\tau}_M}, \alpha\beta^{-1}e^{-\gamma\bar{\tau}_m}]$, *that is,*

$$z_1 \le \liminf_{t\to+\infty} z(t) \le \limsup_{t\to+\infty} z(t) \le z^1 \tag{14}$$

and

$$\alpha\beta^{-1}e^{-\gamma\bar{\tau}_M} \le \liminf_{t\to+\infty} x_m(t) \le \limsup_{t\to+\infty} x_m(t) \le \alpha\beta^{-1}e^{-\gamma\bar{\tau}_m}. \tag{15}$$

To show this theorem, we need several lemmas.

LEMMA 2. *Suppose* $\big(z(t), x_m(t)\big)$ *is an admissible solution of system (12). If there are a priori estimations on the ultimate bounds of* $\big(z(t), x_m(t)\big)$ *such that*

$$z_0 \le \liminf_{t\to+\infty} z(t) \le \limsup_{t\to+\infty} z(t) \le z^0$$

and

$$\bar{x}_m \le \liminf_{t\to+\infty} x_m(t) \le \limsup_{t\to+\infty} x_m(t) \le x_m^0$$

for some positive integers $z_0, z^0, \bar{x}_m$ *and* x_m^0, *then*

$$\tilde{H}_0 \le \liminf_{t\to+\infty} z(t) \le \limsup_{t\to+\infty} z(t) \le \tilde{H}^0,$$

where $\tilde{H}^0$ *and* $\tilde{H}_0$ *are the maximum and minimum values of the function* $g(x_m) = \frac{1}{\gamma}[(\alpha+\gamma)x_m - \beta x_m^2]$ *for* x_m *on* $[\bar{x}_m, x_m^0]$ *respectively.*

PROOF. Since for any $\varphi > 0$, there exists a $t_0 > 0$ such that

$$z_0 - \varepsilon \le z(t) \le z^0 + \varepsilon, \quad \bar{x}_m - \varepsilon \le x_m(t) \le x_m^0 + \varepsilon$$

by the *a priori* estimates for all $t \ge t_0$. Integrating the first equation of (12), we have

$$z(t) = z(t_0)e^{-\gamma(t-t_0)} + \int_{t_0}^{t} [(\alpha+\gamma)x_m(s) - \beta x_m^2(s)]e^{-\gamma(t-s)}\, ds. \tag{16}$$

Therefore, if $\tilde{H}_\varepsilon$ and $\tilde{H}^\varepsilon$ are the minimum and maximum values of $g(x_m) = \frac{1}{\gamma}[(\alpha+\gamma)x_m - \beta x_m^2]$ for x_m on $[\bar{x}_m - \varepsilon, x_m^0 + \varepsilon]$, then

$$\tilde{H}_\varepsilon \le \liminf_{t\to+\infty} z(t) \le \limsup_{t\to+\infty} z(t) \le \tilde{H}^\varepsilon. \tag{17}$$

The proof is completed by letting ε go to zero in (17).

LEMMA 3. *If $\big(z(t), x_m(t)\big)$ is the same as in Lemma 3, then*

$$\alpha\beta^{-1}e^{-\gamma\tau(z^0)} \leq \liminf_{t\longrightarrow+\infty} x_m(t) \leq \limsup_{t\longrightarrow+\infty} x_m(t) \leq \alpha\beta^{-1}e^{-\gamma\tau(z_0)}. \tag{18}$$

PROOF. We divide the proof into two cases.

(a) $x_m(t)$ is eventually monotonic.

Since $x_m(t)$ is bounded, $x_m(t)$ eventually monotone implies that $\lim_{t\longrightarrow+\infty} x_m(t)$ exists. Moreover, from (16), we can see that $\lim_{t\longrightarrow+\infty} x_m(t)$ exists implies that $\lim_{t\longrightarrow+\infty} z(t)$ exists. This means that $\big(z(t), x_m(t)\big)$ approaches an equilibrium of (12), which is the nontrivial equilibrium $\tilde{E}$ by (15). Thus

$$\lim_{t\longrightarrow\infty} x_m(t) = \hat{x}_m = \alpha\beta^{-1}e^{-\gamma\tau(\tilde{z})}. \tag{19}$$

By the a priori estimations on $z(t)$ and the monotonicity of $\tau(z)$, (19) implies (18).

(b) $x_m(t)$ is not eventually monotonic.

In this case we can find $\{t_n\}_{n=1}^{\infty}$ and $\{t_n^0\}_{n=1}^{\infty}$ with t_n, $t_n^0 \longrightarrow +\infty$ as $n \longrightarrow \infty$ such that t_n and t_n^0 are local maxima and minima of $x_m(t)$ respectively, and

$$\liminf_{t\longrightarrow+\infty} x_m(t) = \lim_{n\longrightarrow\infty} x_n(t_n^0), \quad \limsup_{t\longrightarrow+\infty} x_m(t) = \lim_{n\longrightarrow\infty} x_m(t_n). \tag{20}$$

By these choices of t_n and t_n^0 $(n = 1, 2, \ldots)$, the second equation of (12) becomes

$$\alpha e^{-\gamma\tau(z(t_n))} x_m\Big(t_n - \tau\big(z(t_n)\big)\Big) - \beta x_m^2(t_n) = 0 \tag{21}$$

and

$$\alpha e^{-\gamma\tau(z(t_n^0))} x_m\Big(t_n^0 - \tau\big(z(t_n^0)\big)\Big) - \beta x_m^2(t_n^0) = 0. \tag{22}$$

Taking limits in (21) and (22) as $n \longrightarrow +\infty$, we obtain

$$\beta \limsup_{t\longrightarrow+\infty} x_m^2(t) \leq \alpha e^{-\gamma\tau(z_0)} \limsup_{t\longrightarrow+\infty} x_m(t)$$

and

$$\beta \liminf_{t\longrightarrow+\infty} x_m^2(t) \geq \alpha e^{-\gamma\tau(z^0)} \liminf_{t\longrightarrow+\infty} x_m(t)$$

by use of (20) and the a priori estimations on $z(t)$. From (15) we know that $x_m(t)$ is bounded away from infinity and zero when t is large enough and therefore the above inequalities together imply (18), completing the proof.

LEMMA 4. *If $\big(z(t), x_m(t)\big)$ is the same as in Lemma 2, then*

$$\begin{aligned} \min\{H(z) : z \in [z_0, z^0]\} &\leq \liminf_{t\longrightarrow+\infty} z(t) \leq \limsup_{t\longrightarrow+\infty} z(t) \\ &\leq \max\{H(z) : z \in [z_0, z^0]\}. \end{aligned} \tag{23}$$

https://doi.org/10.4153/CMB-1993-019-9 Published online by Cambridge University Press

PROOF. By Lemma 3, we have

$$\alpha\beta^{-1}e^{-\gamma\tau(z^0)} \le \liminf_{t\to+\infty} x_m(t) \le \limsup_{t\to+\infty} x_m(t) \le \alpha\beta^{-1}e^{-\gamma\tau(z_0)}.$$

Replacing the a priori estimates $\bar{x}_m$ and x_m^0 by $\alpha\beta^{-1}e^{-\gamma\tau(z^0)}$ and $\alpha\beta^{-1}e^{-\gamma\tau(z_0)}$ respectively and from Lemma 2, we obtain the inequality (23).

Now we are ready to prove Theorem 1.

PROOF OF THEOREM 1. By (14) and (15) $\big(z(t), x_m(t)\big)$ is eventually bounded away from zero and infinity. If $z_0 = \liminf_{t\to+\infty} z(t)$ and $z^0 = \limsup_{t\to+\infty} z(t)$, then Lemma 4 says that

$$\min\{H(z) : z \in [z_0, z^0]\} \le z_0 \le z^0 \le \max\{H(z) : z \in [z_0, z^0]\},$$

that is, $[z_0, z^0] \subseteq H([z_0, z^0])$. This means that $[z_0, z^0]$ is contained in the attracting interval $[z_1, z^1]$ of the mapping $z \longmapsto H(z)$ $(z \in [0, +\infty)$. Thus the inequality (14) is true. Further, Lemma 3 and the montonicity of $\tau(z)$ show the inequality (15). The proof is completed.

4. **Existence and global attractivity of $\hat{E}$.** In the previous section, we have discussed the relation between the attracting interval of the mapping $z \longmapsto H(z)$ $(z \in [0, +\infty])$ and the attracting region for the solutions of (12). When the attracting interval is just a point, Theorem 1 gives us a global attractivity of the nontrivial equilibrium $\hat{E}$.

In Theorem 5 below, we prove that the positive equilibrium is unique. To show that uniqueness is not automatic for system (2), we indicate a specific system with multiple positive equilibria. The nontrivial equilibria of (12) are determined by solving the sytem of algebraic equations

$$\begin{cases} z = \frac{(\alpha+\gamma)x_m - \beta x_m^2}{\gamma} \\ \alpha e^{-\gamma\tau(z)} - \beta x_m = 0 \end{cases} \tag{24}$$

for $x_m \in (0, \frac{\alpha}{\beta})$. If $g(x_m) = [(\alpha+\gamma)x_m - \beta x_m^2]\gamma^{-1}$ and $G(x_m) = \alpha e^{-\gamma\tau(g(x_m))} - \beta x_m$, then

$$G(0) > 0 \text{ and } G\Big(\frac{\alpha}{\beta}\Big) < 0. \tag{25}$$

Therefore, (12) always has an equilibrium $\hat{E}(\hat{z}, \hat{x}_m)$ (with $\hat{x}_m \in (0, \frac{\alpha}{\beta}), \hat{z} > \hat{x}_m$). One can see that

$$\begin{aligned} G'(\hat{x}_m) &= -\alpha\gamma e^{-\gamma\tau(g(\hat{x}_m))}\tau'\big(g(\hat{x}_m)\big)g'(\hat{x}_m) - \beta \\ &= -\gamma\beta\hat{x}_m\tau'(\hat{z})\frac{(\alpha+\gamma) - 2\beta\hat{x}_m}{2} - \beta \end{aligned} \tag{26}$$

where $\hat{z} = g(\hat{x}_m)$. Suppose that $\tau(z)$ is such that $2e^{-\gamma\tau_M} > 1$ and $\alpha > \gamma/(2e^{-\gamma\tau_M} - 1) > 0$. It follows from the second equation of (24) that

$$\hat{x}_m = \frac{\alpha}{\beta}e^{-\gamma\tau(\hat{z})} > \frac{\alpha}{\beta}e^{-\gamma\tau_M}$$

https://doi.org/10.4153/CMB-1993-019-9 Published online by Cambridge University Press

and, therefore

$$(\alpha+\gamma)-2\beta\hat{x}_m < (\alpha+\gamma)-2\alpha e^{-\gamma\tau_M} < 0. \tag{27}$$

For these fixed $\tau(z)$ and $(\hat{z},\hat{x}_m)$, one can construct any $\tau_1(z)$ such that

$$\tau_1(0)=\tau(0), \quad \tau_1(+\infty)=\tau(+\infty), \quad \tau_1(\hat{z})=\tau(\hat{z})$$

and such that

$$\tau_1'(z)\geq 0, \quad \forall z\geq 0, \quad \tau_1'(\hat{z})\geq \frac{2\beta}{-\gamma\beta\hat{x}_m\big((\alpha+\gamma)-2\beta\hat{x}_m\big)}>0.$$

Replace $\tau(z)$ by $\tau_1(z)$ in $G(x_m)$. It follows that

$$G'(\hat{x}_m)=-\gamma\beta\hat{x}_m\tau_1'(\hat{z})\frac{(\alpha+\gamma)-2\beta\hat{x}_m}{2}-\beta>0.$$

Thus, together with $G(\hat{x}_m)=0$ and (25), it follows that there are at least two other solutions of $G(x_m)=0$ for $x_m\in(0,\frac{\alpha}{\beta})$. Therefore, there are at least three nontrivial equilibria in total when $\tau(z)$ is replaced by $\tau_1(z)$.

THEOREM 5. *If $\hat{z}$ is a globally attractive fixed point of the mapping $z\longmapsto H(z)$, then the equilibrium $\tilde{E}(\hat{z},\hat{x}_m)$ of (12) is unique and attracts all admissible solutions, that is, any admissible solution $\big(z(t),x_m(t)\big)$ of (12) tends to $(\hat{z},\hat{x}_m)$ as t goes to infinity.*

PROOF. Use Theorem 1, with $z_1=z^1=\hat{z}$.

Our next theorem gives us a condition under which the fixed point of the mapping $z\longmapsto H(z)$ is globally attractive, and therefore a condition under which the nontrivial equilibrium $\tilde{E}$ of (12) is globally attractive (and hence for which $\hat{E}$ is globally attractive for admissible solutions of (2)).

THEOREM 6. *If*

$$\tau'(z)<\left|\frac{\alpha}{\gamma\beta}\left[\left(1+\frac{\alpha}{\gamma}\right)-\frac{2\alpha}{\gamma}e^{-\gamma\tau(z)}\right]e^{-\gamma\tau(z)}\right|^{-1} \tag{28}$$

for all $z\in[z_m,z_M]$, where z_M and z_m are the maximum and minimum of the function $h(\tau)=\frac{\alpha}{\beta}[(1+\frac{\alpha}{\gamma})-\frac{\alpha}{\gamma}e^{-\gamma\tau}]e^{-\gamma\tau}$ for τ in $[\tau_m,\tau_M]$ respectively, then the nontrivial equilibrium $\tilde{E}(\hat{z},\hat{x}_m)$ of (12) is unique and is globally attractive for admissible solutions. In particular, when $\gamma>\alpha$, (28) is satisfied if for all $z\geq 0$, and

$$\tau'(z)<8\beta(1+\alpha\gamma^{-1})^{-2} \tag{29}$$

holds.

PROOF. Under assumption (28), we know that $|H'(z)|<1$ for z in $[z_m,z_M]$, since the attracting interval $[z_0,z^0]$ of the mapping $z\longmapsto H(z)$ is contained in $[z_m,z_M]$ (notice that $H\big([0,+\infty)\big)$ is contained in $[z_m,z_M]$). $|H'(z)|<1$ for z in $[z_m,z_M]$ implies that the fixed point $\hat{z}$ of the mapping $z\longmapsto H(z)$ for $z\in[0,+\infty)$ is unique and is globally attractive. Therefore, the nontrivial equilibrium $\tilde{E}(\hat{z},\hat{x}_m)$, is unique and is globally attractive by Theorem 5, completing the proof.

Finally, we note that if admissible solutions of (12) converge to $\tilde{E}$, then positive solutions of (2) converge to $\hat{E}$.

5. **Discussion.** In this paper we have considered a model of single-species population growth where the population is divided into two classes, the immatures and the matures. From ecological considerations as demonstrated by populations feeding on krill in the Antarctic Ocean, the age to maturity (which appears as a time delay in the model) is a function of the population density.

We have shown that it is possible to have oscillatory solutions, even though they may be difficult to find numerically, and have given criteria for the positive equilibrium to be unique and globally attractive. The uniqueness is a nontrivial result, since systems with multiple equilibria may exist both mathematically (as shown in Section 4) and ecologically [10].

In particular, the condition for global attractivity involves a bound on the derivative of the time delay. This may be interpreted as saying that small changes in the population density cannot produce a drastic change in the time to maturity, an observed biological phenomenon.

As in most models that have appeared in the literature to date, there are no terms in our models which describe competition between one segment of the population with another (in our case immatures with matures). However, because each system is described by separate equations for each segment, such terms could be introduced for these populations where they would be appropriate. We leave that to future considerations.

References

1. W. G. Aiello and H. I. Freedman, *A time-delay model of single-species growth with stage structure*, Math. Biosci. **101**(1990), 101–139.

2. W. G. Aiello, H. I. Freedman and J. Wu, *Analysis of a model representing stage-structured population growth with state-dependent time delay*, SIAM J. Appl. Math. **52**(1992), 855–869.

3. H. J. Barclay and P. Van den Driessche, *A model for a single species with two life history stages and added morality*, Ecol. Model, **11**(1980), 157–166.

4. R. Bellman and K. L. Cooke, *Differential-Difference Equations*, Academic Press, New York, 1963.

5. D. L. De Angelis, *Global asymptotic stability criteria for models of density-dependent population growth*, J. Theo. Biol., **50**(1975), 35–43.

6. H. I. Freedman and K. Gopalsamy, *Global stability in time-delayed single species dynamics*, Bull. Math. Biol., **48**(1986), 486–492.

7. R. Gambell, *Birds and mammals—Antarctic whales*. In: "Antarctica", (eds. W. N. Bonner and D. W. H. Walton), Pergamon Press, New York (1985), 223–241.

8. W. S. C. Gurney and R. M. Nisbet, *Fluctuating peridicity, generation separation, and the expression of larval competition*, Theoret. Pop. Biol. **28**(1985), 150–180.

9. J. K. Hale, *Theory of Functional Differential Equations*, Springer-Verlag, Heidelberg, 1977.

10. D. D. Jones and C. J. Walters, *Catastrophe theory and fisheries regulation*, J. Fish. Res. Bd. Can. **33**(1976), 2829–2833.

11. Yu S. Koselsov, *Properties of solutions of a class of equations with lag which describe the dynamics of change in the population of a species with age structure taken into account*, Math. USSR. Sbornick, **45**(1983), 91–100.

12. H. D. Landahl and B. D. Hanson, *A three stage population model with cannibalism*, Bull. Math. Biol., **37**(1975), 11–17.

13. J. D. Murray, *Mathematical Biology*, Biomathematics, **19**, Springer-Verlag, Heidelberg, (1989).

14. R. M. May, G. R. Conway, M. P. Hassell and T. R. E. Southwood, *Time delays, density dependence, and single-species oscillations*, J. Animal Ecol., **43**(1974), 747–770.

15. K. Tognetti, *The two stage stochastic model*, Math. Biosci., **25**(1975), 195–204.

16. S. N. Wood, S. P. Blythe, W. S. C. Gurney and R. M. Nisbet, *Instability in mortality estimation schemes related to stage-structure population models*, IMA J. Math. Appl. in Medicine and Biology, **6**(1989), 47–68.

Department of Mathematics
University of Georgia
Athens, Georgia 30602
U.S.A.

Applied Mathematics Institute
Department of Mathematics
University of Alberta
Edmonton, Alberta
T6G 2G1