ANALYSIS OF A TWO-STAGE POPULATION MODEL WITH SPACE LIMITATIONS AND STATE-DEPENDENT DELAY

SANJAY RAI AND ROBERT L. ROBERTSON

ABSTRACT. Bence and Nisbet introduced a system of nonlinear functional differential equations with constant delay to describe the growth of a population with space limitations. In their work, the population was divided into two groups: the juveniles and the adults. They included a local stability analysis of the system. Kuang and So gave a thorough mathematical analysis of the system, including results on positivity, boundedness, and stability of solutions. In this paper, a more general situation is considered: a system where the delay is a nonconstant function of total population, and the death rate of adults is nonlinear. Results on positivity, boundedness, and stability of solutions are proven.

Introduction. As observed in [8] and [9], most of the traditional mathematical population models are partly founded on the assumption that the population is closed. That is, the adult members of the population are restricted to some region, and new members of the population are produced only from the adults. However, many populations in nature are not modeled effectively if this assumption is used. An example is marine populations with sessile adults and pelagic larvae. These populations feature adults which are restricted to a closed region, while their offspring swim freely. Hence new recruits into the local population may not be produced only by the adults in the local population. As noted in [4] and [5], the size of these open populations can change significantly within the life span of an individual. Physiological structures such as age, size, etc. must be taken into account while attempting to model open populations.

Roughgarden et. al [9] considered the following model for marine invertebrate populations with sessile adults and pelagic larvae:

\[
\frac{\partial n(x, t)}{\partial t} + \frac{\partial n(x, t)}{\partial x} = -u(x)n(x, t),
\]

\[n(0, t) = sF(t);\]

\[n(1, t) = 0;\]

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\[ 1 = F(t) + \int_{0}^{\infty} a(x)n(x,t) \, dx. \]

Here \( n(x,t) \) is the density of individuals of age \( x \) at time \( t \), \( a(x) \) is the area occupied by an individual of age \( x \), \( u(x) \) is the instantaneous death rate of individuals of age \( x \), \( s \) is the settlement rate; \( F(t) \) is the proportion of available free space at time \( t \).

Bence and Nisbet [4] proposed several models for these invertebrate populations. They studied the dynamics of age-structured open populations with space limitation with the following equations:

\begin{align*}
  \dot{A} &= sLF(t-\tau) - m_A A(t); \\
  F(t) &= \left[ 1 - a_A A(t) \right] +.
\end{align*}

Here \( s \) is the settlement rate of juveniles, \( L \) is the through-stage survival probability of juveniles, \( a_A \) is the area occupied by an adult individual, and \( m_A \) is the instantaneous mortality rate of adults. The subscript of “+” that appears in the definition of \( F(t) \) is defined by \([z]_+ = z \) if \( z > 0 \) and \([z]_+ = 0 \) otherwise. The constant \( \tau \) is the amount of time required for a juvenile individual to mature, at which time it enters the adult population. As shown in [5], Bence and Nisbet’s model is a special case of the model of Roughgarden et. al. [8].

Equations (1) and (2) assume that juveniles occupy no space. Bence and Nisbet removed this assumption and proposed the additional model:

\begin{align*}
  \dot{J} &= s\left[ F(t) - e^{-m_J \tau} F(t-\tau) \right] - m_J J(t) \\
  \dot{A} &= s e^{-m_J \tau} F(t-\tau) - m_A A(t) \\
  F(t) &= \left(1 - a_A A(t) - a_J J(t) \right)_+.
\end{align*}

In this model, \( J \) and \( A \) are the densities of the juvenile and adult populations, respectively, and \( F \) is the proportion of space that is available. All parameters which appear in the model are positive constants. The parameters \( m_J \) (\( m_A \)) and \( a_J \) (\( a_A \)) represent, respectively, the mortality rate of juveniles (adults) and the amount of space a member of
the juvenile (adult) population occupies. The remaining parameters $s$ and $\tau$ are the juvenile settlement rate and the time needed for a juvenile to mature, i.e. enter the adult population. In [5], Kuang and So described the complete dynamics of the system (3) through (4). They proved that the solutions are positive and bounded, and gave results on local stability and instability. They also gave results on global stability using Liapunov functionals and Razumikhin-type theorems.

It has been observed (see [2]) that the delay $\tau$ is not necessarily a constant. It may depend, for example, on the available food. In [3] it was noted that the duration of larval development of flies is a nonlinear increasing function of larval density. For this paper, we consider a system which essentially stems out of (3) through (4), but takes into account that the delay $\tau$ may not be constant. Following Aiello et. al. [2], we assume $\tau = \tau(z)$, where $z$ is the total population density. Our model is as follows. Define the function

$$g(u) = \begin{cases} 
0 & \text{if } u < 0 \\
u & \text{if } 0 \leq u \leq 1 \\
1 & \text{if } u > 1 
\end{cases}$$

The system is then

$$\dot{J} = s[F(t) - e^{-m_J\tau(z)}F(t - \tau(z))] - m_JJ(t) \tag{6}$$

$$\dot{A} = se^{-m_J\tau(z)}F(t - \tau(z)) - m_AA^2(t) \tag{7}$$

$$F(t) = g(1 - a_AA(t) - a_JJ(t)). \tag{8}$$

Here, $s$, $m_J$, $m_A$, $a_J$, and $a_A$ are positive constants. The constant $s$ is the settlement rate of juveniles. The juvenile mortality rate and the adult mortality rate are, respectively, $m_J$ and $m_A$. The constants $a_J$ and $a_A$ are, respectively, the size of individual juveniles and the size of individual adults. The variable $z \equiv A + J$ is the total population, and $\tau(z)$ is a smooth function representing the time needed for a juvenile to become an adult. We assume there are constants $\tau_m$ and $\tau_M$ such that $0 < \tau_m \leq \tau(z) \leq \tau_M$. We also assume $\tau'(z) \geq 0$, where the $'$ indicates differentiation with respect to $z$, and $\lim_{z \to \infty} \tau(z) = \tau_M$. Note that we have modified the definition of $F$ somewhat. Our definition prevents the proportion of free space available from growing larger than 1.

In addition to the delay being nonconstant, our adult death rate is assumed to be logistic. For a linear death rate and constant delay, this
model becomes the one considered in [5] and [4]. A state dependent model for a single species population was also considered in [2], but that model did not incorporate space limitations.

For (6) and (7), we specify initial conditions $\phi_A$ and $\phi_J$ on the interval $[-\tau_M, 0]$ as follows. We assume the initial adult population $\phi_A$ satisfies $\phi_A(t) > 0$ and $1 - a_A \phi_A(t) > 0$ for $t \in [-\tau_M, 0]$. That is, we assume the initial adult population is positive, and the adults initially do not occupy all the available free space. We then choose the initial juvenile population $\phi_J$ so that

$$
\phi_J(0) = \int_{-\tau_M}^{0} se^{m_J \tau(\sigma)} F(\sigma) d\sigma.
$$

This condition says $\phi_J(0)$ is the survivors of the juvenile population born during the interval $[-\tau_M, 0]$. Note that it is always possible to choose $\phi_J$ satisfying this condition, for consider the family of functions $J_x : [-\tau_M, 0] \to \mathbb{R}$ depending on the real parameter $x$ given by

$$
J_x(t) = \frac{t + 2\tau_M}{x}.
$$

Notice $\lim_{x \to 0^+} J_x(0) = \infty$ and $\lim_{x \to \infty} J_x(0) = 0$. Let us also define

$$
Q(x) = \int_{-\tau_M}^{0} se^{m_J \tau(\phi_A(\sigma)/J_x(\sigma))} g(1 - a_A \phi_A(\sigma) - a_J J_x(\sigma)) d\sigma.
$$

By the dominated convergence theorem, $Q(x)$ satisfies $\lim_{x \to 0^+} Q(x) = 0$ and $\lim_{x \to \infty} Q(x) = \int_{-\tau_M}^{0} se^{m_J \tau(\phi_A(\sigma))} (1 - a_A \phi_A(\sigma)) d\sigma > 0$. It follows that there exists $x$ such that

$$
J_x(0) = Q(x).
$$

The function $J_x(t)$ would thus be an initial value of $J$ satisfying (9).

The remainder of the paper is concerned with analyzing systems (6) and (7). In particular, we prove results on positivity and boundedness of $J(t)$ and $A(t)$ as well as existence, uniqueness, and local stability of equilibria.
2. Positivity and Boundedness

We first prove positivity of the adult population.

**Theorem 1.** Suppose \( A(0) > 0 \). Then \( A(t) > 0 \) for all \( t > 0 \).

**Proof:** Let \( t_0 = \sup \{ t \mid A(u) > 0 \text{ for all } u \in [0, t) \} \). If \( t_0 \) is finite, then continuity of solutions implies \( A(t_0) = 0 \), and for \( 0 < t < t_0 \), equation (7) and the fact that \( F \geq 0 \) imply
\[
\frac{\dot{A}(t)}{A^2(t)} \geq -m_A.
\]
Integrating both sides of this inequality and solving for \( A(t) \) gives
\[
A(t) \geq \frac{A(0)}{1 + A(0)m_A t}.
\]
This last inequality and the continuity of \( A \) imply
\[
A(t_0) \geq \frac{A(0)}{1 + A(0)m_A t_0} > 0,
\]
which contradicts the fact that \( A(t_0) = 0 \). Thus we conclude that \( t_0 = \infty \). \( \square \)

Our positivity result for the juvenile population depends on there being upper bounds for the two populations. Hence we next give boundedness results.

**Theorem 2.** If \( t > 0 \), then \( A(t) < \max \{ A(0), (se^{-m_J \tau_m}/m_A)^{1/2} \} \).

**Proof:** Let \( t_1 \) be a point in \((0, \infty)\). There are two possibilities.
1. \( \dot{A}(t_1) \geq 0 \).
   In this case, equation (7) and the fact that \( F \leq 1 \) give
   \[
   0 \leq \dot{A}(t_1) = se^{-m_J \tau_m} F(t_1 - \tau(z)) - m_A A^2(t_1) \leq se^{-m_J \tau_m} - m_A A^2(t_1).
   \]
   Solving the above inequality for \( A(t_1) \) gives
   \[
   A(t_1) \leq \left( \frac{se^{-m_J \tau_m}}{m_A} \right)^{1/2}.
   \]
2. $\dot{A}(t_1) < 0$.

In this case, there must be a maximal interval $(t_2, t_1]$ with $t_2 \geq 0$ such that $\dot{A}(t) < 0$ for all $t \in (t_2, t_1]$. Then $A(t_1) < A(t_2)$. Also, either $t_2 > 0$, in which case $A(t_2) = 0$ and we can use case 1 to conclude $A(t_2) \leq (se^{-m_J t_m} / m_A)^{1/2}$, or else $t_2 = 0$. This completes the proof. 

Notice that Theorem 2 says that if the initial number of adults is small, and the mortality rate for either juveniles or adults is large, then the maximum size of the adult population is restricted.

We next give a bound on the juvenile population.

**Theorem 3.** The juvenile population $J(t)$ satisfies

\[ J(t) \leq J(0)e^{-m_J t} + \frac{s}{m_J}(1 - e^{-m_J t}). \]

From the above we easily obtain

\[ J(t) \leq J(0) + \frac{s}{m_J} \]

and

\[ \limsup_{t \to \infty} J(t) \leq \frac{s}{m_J}. \]

**Proof:** Equation (6), the positivity of $F$, and the fact that $F \leq 1$ imply

\[ \dot{J}(t) \leq s - m_J J(t). \]

Solving for $J$ gives the result. 

We observe that the upper bounds for $J(t)$ and $A(t)$ depend on neither $a_J$ nor $a_A$. Thus if $A_M$ and $J_M$ are upper bounds for the adult and juvenile population, respectively, we can make the assumption $a_A A_M + a_J J_M < 1$. This assumption implies $F(t) \geq 1 - a_A A_M - a_J J_M > 0$ if $t > 0$. In other words, if the sizes of individuals are small compared to the maximum number of individuals, then the fraction of free space is bounded below by a positive constant.
The next result is a technical result needed in our proof of the positivity of $J(t)$.

**Lemma 1** Suppose $\tau'(z(t)) < 1/s$ and $J(t) \geq 0$ for $t \in (t_1, t_2)$. Then $\tau'(z)\dot{z}(t) < 1$ and $t - \tau(z(t))$ is an increasing function of $t$ on $(t_1, t_2)$.

**Proof:** By adding equations (6) and (7) we obtain

$$\dot{z}(t) = sF(t) - mJ(t) - m_A A^2(t).$$

Since $F(t) \leq 1$ and $J(t) \geq 0$, we have $\dot{z}(t) \leq s$, from which the result follows. $\Box$

For the remainder of the paper, we assume $\tau'(z) < 1/s$ for all $z$.

**Theorem 4.** Suppose there exists $c > 0$ such that $F(t) \geq c$ for all $t \geq 0$. Also suppose

$$\tau_m > -\frac{1}{m_J} \ln \left( \frac{c}{c+1} \right).$$

Then $J(t) > 0$ for all $t > 0$.

**Proof:** Let $t_1 = \inf\{ t > 0 \mid J(t) = 0 \}$. We observe that

$$\frac{d}{dt} \int_{t - \tau(z)}^{t} e^{m_J \sigma} F(\sigma) d\sigma = e^{m_J t} F(t)$$

$$- e^{m_J (t - \tau(z))} F(t - \tau(z))(1 - \tau'(z)\dot{z}(t))$$

$$= e^{m_J t} (F(t) - e^{-m_J \tau(z)} F(t - \tau(z)))$$

$$+ e^{m_J (t - \tau(z))} F(t - \tau(z))\tau'(z)\dot{z}(t).$$

Thus equation (6) can be written

$$\dot{J}(t) + m_J J(t) = s e^{-m_J t} \frac{d}{dt} \int_{t - \tau(z)}^{t} e^{m_J \sigma} F(\sigma) d\sigma$$

$$- s e^{-m_J \tau(z)} F(t - \tau(z))\tau'(z)\dot{z}(t).$$
Multiplying by the factor $e^{m_j t}$ and integrating yields an expression for $J(t)$:

$$J(t) = se^{-m_j t} \int_{t-\tau(z)}^{t} e^{m_j \sigma} F(\sigma) \, d\sigma$$
$$+ e^{-m_j t} \left( J(0) - s \int_{-\tau(z)}^{0} e^{m_j \tau(\sigma)} F(\sigma) \, d\sigma \right)$$
$$- se^{-m_j t} \int_{0}^{t} e^{m_j (\sigma - \tau(z))} F(\sigma - \tau(z)) \tau'(z) \hat{z}(\sigma) \, d\sigma.$$

The three terms in the above representation will be referred to as $I$, $II$, and $III$. Applying the lower bounds on $F$ and $\tau(z)$ to $I$ gives

$$I > cse^{-m_j t} \int_{t-\tau_m}^{t} e^{m_j \sigma} \, d\sigma$$
$$= \frac{cs}{m_j} (1 - e^{-m_j \tau_m}).$$

To estimate $III$, we recall that $\tau(z) \hat{z}(\sigma) < 1$ for $\sigma \in (0, t_1)$ and $F \leq 1$ by definition. Applying these facts and using the lower bound on $\tau$ gives us

$$III < se^{-m_j t} \int_{0}^{t} e^{m_j (\sigma - \tau_m)} \, d\sigma$$
$$= \frac{se^{-m_j \tau_m}}{m_j} (1 - e^{-m_j t})$$
$$\leq \frac{se^{-m_j \tau_m}}{m_j}.$$

We observe that assumption (11) implies $c(1 - e^{-m_j \tau_m}) - e^{-m_j \tau_m} > 0$. Also, $II \geq 0$ by assumption (9). Thus, for $t \in (0, t_1)$,

$$J(t) = I + II - III > \frac{s}{m_j} (c(1 - e^{-m_j \tau_m}) - e^{-m_j \tau_m}) > 0.$$

However, if $t_1$ is finite, the above inequality and continuity of $J$ imply that $J(t_1) > 0$, which is a contradiction to the definition of $t_1$. We conclude that $t_1 = \infty$. \qed
3. Existence of Steady States. Define $f_1(A, J)$ and $f_2(A, J)$ by
\[
\begin{align*}
    f_1(A, J) &= s[F - e^{-m_J\tau(z)} F] - m_J J; \\
    f_2(A, J) &= s e^{-m_J\tau(z)} F - m_A A^2.
\end{align*}
\]
We prove in this section there exists a solution to the system $f_1(A, J) = 0$, $f_2(A, J) = 0$ satisfying $A > 0$, $J > 0$. Such a solution is called a positive equilibrium for our system.

Let us begin with some definitions. We let $\Omega$ be the open region in the $AJ$-plane bounded by the $J$ and $A$ axes and the line $1 - a_A A - a_J J = 0$.

Any positive equilibria must lie in this region, for suppose $(A, J)$ is in the first quadrant (including the axes) and satisfies $1 - a_A A - a_J J < 0$. Then $F = 0$. Thus $f_1(A, J) = 0$ and $f_2(A, J) = 0$ if and only if $(A, J) = (0, 0)$, which is a contradiction. Also, if $(A, J)$ lies on the portion of the boundary of $\Omega$ that intersects one of the axes, then both $f_1$ and $f_2$ cannot vanish simultaneously.

We now use a homotopy argument (similar to one used in [7]) to prove a positive equilibrium exists.

**Theorem 5.** There exists at least one positive equilibrium in $\Omega$.

**Proof:** We first observe that \(\lim_{(A, J) \to (0, 1/a_J)} f_1(A, J) = -m_J/a_J < 0\). By continuity of $f_1$, there exists $\epsilon > 0$ such that $f_1(A, J) < 0$ for all $(A, J)$ in $B_\epsilon(0, 1/a_J) \cap \Omega$. Here $B_\epsilon(0, 1/a_J)$ means the open disk in the $AJ$-plane centered at $(0, 1/a_J)$ with radius $\epsilon$. 

![FIGURE 1. The region $\Omega$.](image-url)
We choose $0 < J_1 < 1/a_J$ such that $f_1(A, J) < 0$ for all points in $\bar{\Omega}$ of the form $(A, J_1)$, where $\bar{\Omega}$ means the closure of $\Omega$. Then define $\Omega_1$ to be the open region bounded by the $J$ axis, the $A$ axis, the line $1 - a_A A - a_J J = 0$, and the line $J = J_1$.

The boundary of $\Omega_1$ can be divided into four parts: $\Gamma_1$ is the intersection of $\partial \Omega_1$ with the $J$ axis, $\Gamma_2$ is the intersection of $\partial \Omega_1$ with the $A$ axis, $\Gamma_3$ is the intersection of $\partial \Omega_1$ with the line $1 - a_A A - a_J J = 0$, and $\Gamma_4$ is the intersection of $\partial \Omega_1$ with the line $J = J_1$.

We choose a point $(A_0, J_0)$ in the open rectangular subregion of $\Omega_1$ bounded by the $A$ axis, the $J$ axis, the line $J = J_1$, and the line $A = 1 - a_J J_1/a_A$. Note that $J_0 < J_1$ and $A_0 < 1 - a_J J_1/a_A$. We define a homotopy $H_t(A, J)$, $0 \leq t \leq 1$ by

$$H_t(A, J) = ((1 - t)(J_0 - J) + tf_1(A, J), (1 - t)(A_0 - A) + tf_2(A, J)).$$

We now observe that $H_t(A, J) \neq 0$ if $(A, J) \in \partial \Omega_1$, $0 \leq t \leq 1$. There are four cases.

1. $(A, J) \in \Gamma_1$: In this case, since $A = 0$ and $J < 1/a_J$, then $f_2(A, J) = se^{-m_J r(J)}(1 - a_J J) > 0$. Also, $A_0 > A$. Thus $(1 - t)(A_0 - A) + tf_2(A, J) > 0$.

2. $(A, J) \in \Gamma_2$ and $0 < A < 1/a_A$: Here, since $J = 0$ and $A < 1/a_J$, then $f_1(A, J) = s(1 - e^{-m_J r(J)})(1 - a_A A) > 0$. Also, $J_0 > J$. Thus $(1 - t)(J_0 - J) + tf_1(A, J) > 0$.

3. $(A, J) \in \Gamma_3$. In this case, $F = 0$, and so $f_2(A, J) = -m_A A^2 < 0$. Since $A_0 > A$, it follows that $(1 - t)(A_0 - A) + tf_2(A, J) < 0$. 

FIGURE 2. The region $\Omega_1$ and its boundary.
4. \((A, J) \in \Gamma_4\). In this case, the choice of \(J_1\) gives \(f_1(A, J) < 0\) and \(J_0 - J < 0\). Thus \((1 - t)(J_0 - J) + tf_1(A, J) < 0\).

We finish the argument by supposing there are no positive equilibria in \(\Omega\). This means \(H_1\) never vanishes in \(\Omega_1\). Let \(B^2\) be the unit disk in \(\mathbb{R}^2\) and \(S^1\) be the unit circle. Choose \(\phi : \overline{\Omega_1} \to \overline{B^2}\) to be a homeomorphism which takes \(\partial\Omega_1\) to \(S^1\). Then \(H_1 \circ \phi^{-1}\) is a continuous mapping from \(B^2\) to \(\mathbb{R}^2 / \{(0,0)\}\). However, since a mapping \(G : S^1 \to \mathbb{R}^2 / \{(0,0)\}\) can be extended to a mapping from \(B^2\) to \(\mathbb{R}^2 / \{(0,0)\}\) if and only if it is homotopic to a constant map (see [6], Lemma 8.1), we have that \(H_1 \circ \phi^{-1}\) is homotopic to a constant map. Thus \(H_0\) has a root in \(\Omega_1\).

The linearized stability theory used in the next section is only valid if the steady states are isolated. The next result gives conditions under which this is true.

**Theorem 6.** Suppose \(e^{m_J \tau M} < sa_A^2/m_A\). Then the number of equilibria in \(\Omega\) is finite.

**Proof:** Let \((A_*, J_*)\) be an equilibrium in \(\Omega\). Then \(f_1(A_*, J_*) = 0\) and \(f_2(A_*, J_*) = 0\). Adding \(f_1(A_*, J_*)\) and \(f_2(A_*, J_*)\) gives the equation \((sa_J + m_J)J_* = -m_AA_*^2 - sa_AA_* + s\). Multiplying \(f_1(A_*, J_*)\) by \(m_A A_*^2\) and \(f_2(A_*, J_*)\) by \(m_J J_*\), subtracting the results, and then factoring out \(F\) gives \(0 = m_A A_*^2 (1 - e^{-m_J \tau(z_*)}) - m_J J_* e^{-m_J \tau(z_*)}\) (here, \(z_* = A_* + J_*\)). Thus any positive equilibrium must lie at a point of intersection of the two curves

\[
(12) \quad (sa_J + m_J)J = -m_A A^2 - sa_A A + s
\]

and

\[
(13) \quad 0 = m_A A^2 (e^{m_J \tau(z)} - 1) - m_J J.
\]

Curve (12) defines \(J\) as a decreasing function of \(A\) for \((A, J)\) in \(\Omega\). Also, if we define \(h(A, J) = m_A A^2 (e^{m_J \tau(z)} - 1) - m_J J\), the condition
stated in the theorem implies that $\partial h/\partial J < 0$ in $\Omega$. So the implicit function theorem gives that curve (13) defines $J$ as a function of $A$ in a neighborhood of $(A_*, J_*)$. Since $\partial h/\partial A > 0$ in $\Omega$, the function defined by (13) is increasing. Thus any equilibrium is contained in an open set wherein it is the only equilibrium. Since the set of equilibria is compact, there is only a finite number of equilibria.

4. Stability of Steady States. From the results of the previous section, we know there exists at least one positive steady state to our system in the region $\Omega$. We also know that conditions exist under which steady states are isolated. Assuming that some such conditions are satisfied, let $(A_*, J_*)$ be an isolated steady state of the system. We make the definitions $z_* = A_* + J_*$, $F_* = 1 - aJ_* - a_A A_*$, and $\alpha = sm_j e^{-m_J (z_*)} \tau(z_*) F_*$. Linearizing the system at the point $(A_*, J_*)$ gives the variational matrix

$$V(A_*, J_*) = \begin{pmatrix}
-sa_J + \alpha - m_J + sa_A e^{-\tau(z_*) (m_J + \lambda)} & -sA_A + \alpha - m_J + sa_A e^{-\tau(z_*) (m_J + \lambda)} \\
-\alpha - sa_J e^{-\tau(z_*) (m_J + \lambda)} & -\alpha - 2m_A A_* - sa_A e^{-\tau(z_*) (m_J + \lambda)}
\end{pmatrix}.$$ 

From which we obtain the characteristic equation

$$\lambda^2 + (sa_J - sa_A e^{-\tau(z_*) (m_J + \lambda)}) \lambda + m_J + 2m_A A_* + sa_A e^{-\tau(z_*) (m_J + \lambda)} + sa_A e^{-\tau(z_*) (m_J + \lambda)} \lambda + sa_A \alpha + 2sa_J m_A A_* - 2\alpha m_A A_* + m_J \alpha + 2m_J m_A A_* + m_J sa_A e^{-\tau(z_*) (m_J + \lambda)} - 2sa_J m_A e^{-\tau(z_*) (m_J + \lambda)} A_* - \alpha sA_A = 0.$$ 

Note that equation (14) can be written

$$\lambda^2 + \beta \lambda + \gamma \lambda e^{-\tau(z_*) (m_J + \lambda)} + \delta + \epsilon e^{-\tau(z_*) (m_J + \lambda)} = 0,$$

where

$$\beta = sa_J + m_J + 2m_A A_*,$$
$$\gamma = -sa_J + sa_A,$$
$$\delta = 2sa_J m_A A_* + 2m_J m_A A_* + sa_A \alpha - 2\alpha m_A A_* + m_J \alpha - \alpha sA_A;$$
$$\epsilon = m_J sA_A - 2sa_J m_A A_*.$$

We wish to analyze the solutions to equation (14). We begin with a general result about equation (15).
Theorem 7. Suppose

\[ \tau_m > \max\{-\frac{1}{2mJ} \log((\beta^2 - 2\delta)/\gamma^2), -\frac{1}{2mJ} \log(\delta^2/\epsilon^2)\}, \ \beta^2 - 2\delta > 0, \]

and the roots of the equation \( \lambda^2 + \beta\lambda + \delta = 0 \) are real and negative. Then there are no roots of equation (15) either in the right half plane or on the imaginary axis. (Note: If \( \gamma^2 = 0 \) or \( \epsilon^2 = 0 \), then \(-1/(2mJ)\log((\beta^2 - 2\delta)/\gamma^2) \) or \(-1/(2mJ)\log(\delta^2/\epsilon^2) \) is interpreted as \(-\infty\).)

Proof: For \( R > 0 \), define a contour \( \Gamma_R \) in the complex plane consisting of two pieces:

\[ \Gamma^1_R = \{z | \text{Re} z > 0, |z| = R\}; \]
\[ \Gamma^2_R = \{z | \text{Re} z = 0, -R \leq \text{Im} z \leq R\}. \]

We also define two functions:

\[ f(\lambda) = \lambda^2 + \beta\lambda + \delta; \]
\[ h(\lambda, \tau(z)) = \gamma\lambda e^{-\tau(z)} + \epsilon e^{-\tau(z)}. \]

Equation (15) can then be written

\[ f(\lambda) + h(\lambda, \tau(z)) = 0. \]

We now suppose \( \lambda \in \Gamma^1_R \). Then

\[ |f(\lambda)| \geq |R^2 - R|\beta + \delta/\lambda| \geq R^2 - R|\beta + \delta/\lambda| \geq R^2 - |\beta|R - |\delta|. \]

Also, if \( R > (|\beta| + |\gamma| + \sqrt{(|\beta| + |\gamma|^2 + 4(|\delta| + |\epsilon|)^2}/2, \) then using the fact that \( \text{Re} \lambda > 0 \) yields

\[ |h(\lambda, \tau(z))| \leq e^{-\tau(z)}|\gamma\lambda + \epsilon| \leq |\gamma|R + |\epsilon| < R^2 - |\beta|R - |\delta|. \]

In short, we have shown

\[ |h(\lambda, \tau(z))| < |f(\lambda)| \]
as long as $\lambda \in \Gamma^1_R$ and $R > (|\beta| + |\gamma| + \sqrt{(|\beta| + |\gamma|)^2 + 4(|\delta| + |\epsilon|)/2}$.

If $\lambda \in \Gamma^2_R$, then $\lambda = i\nu$, where $-R \leq \nu \leq R$. Hence

$$|f(\lambda)|^2 = \nu^4 + (\beta^2 - 2\delta)\nu^2 + \delta^2 \geq (\beta^2 - 2\delta)\nu^2 + \delta^2$$

and

$$|h(\lambda, \tau(z_\star))|^2 = e^{-2\tau(z_\star)mJ(\nu^2\gamma^2 + \epsilon^2)}.$$ 

By the assumption on the size of $\tau_m$ made in the statement of the theorem, we obtain the inequalities

$$e^{-2\tau(z_\star)mJ} < \beta^2 - 2\delta$$

and

$$e^{-2\tau(z_\star)mJ}\epsilon^2 < \delta^2.$$ 

Thus $|h(\lambda, \tau(z_\star))| < |f(\lambda)|$ for $\lambda \in \Gamma^2_R$. By Rouche’s Theorem, $f(\lambda)$ and $f(\lambda) + h(\lambda, \tau(z_\star))$ have the same number of roots inside the contour $\Gamma_R$. Since all roots of $f(\lambda)$ are in the left half plane, (15) has no roots in the right half plane. Also, the inequality $|h(\lambda, \tau(z_\star))| < |f(\lambda)|$ implies (15) has no roots on the imaginary axis.

To ensure local stability of the steady state, we need to know that the roots of the characteristic equation do not approach the imaginary axis. We have the following result.

**Theorem 8.** Suppose

$$\tau_m > \max \left\{ -\frac{1}{2mJ} \log \left( \frac{\beta^2 - 2\delta}{\gamma^2} \right), -\frac{1}{2mJ} \log \left( \frac{\delta^2}{\epsilon^2} \right) \right\}, \quad \beta^2 - 2\delta > 0,$$

and the roots of the equation $\lambda^2 + \beta\lambda + \delta = 0$ are real and negative. Then the roots of equation (15) have negative real parts and are bounded uniformly away from the imaginary axis.

**Proof:** By the previous theorem, all the roots have negative real parts. Suppose the roots are not bounded uniformly away from the imaginary axis. Then there must exist a sequence $\lambda_n = -\mu_n + i\nu_n$ of roots with $\mu_n > 0$ and $\mu_n \to 0$. Substituting $\lambda_n$ into equation (15) gives

$$\lambda_n^2 + \beta\lambda_n + \delta = -e^{-\tau(z_\star)(mJ+\lambda_n)}(\epsilon + \gamma\lambda_n).$$
If $\epsilon + \gamma \lambda_n = 0$, then $\lambda_n$ is one of the negative real roots of $\lambda^2 + \beta \lambda + \delta = 0$. In the case that $\epsilon + \gamma \lambda_n \neq 0$, we can divide both sides of (15) by $\epsilon + \gamma \lambda_n = 0$ and factor out $\nu_n$ to get

$$\lambda_n^2 + \beta \lambda_n + \delta = 0.$$  

We wish to show that $\{\nu_n\}$ is a bounded sequence. Suppose not. Then there must exist a subsequence $\{\nu_n_k\}$ such that $\nu_{n_k} \to \infty$ (or $-\infty$). But then the left hand side of equation (17) becomes infinite while the right side is bounded, a contradiction.

The above showed that $\{\nu_n\}$ is a bounded sequence of real numbers. By the Bolzano-Weierstrass theorem, there exists a subsequence $\{\nu_{n_k}\}$ which converges to some number $\nu$. Then $\{\lambda_{n_k}\}$ is a subsequence of roots which converges to $i\nu$. But since $f(\lambda)$ and $h(\lambda, \tau)$ are continuous functions of $\lambda$, we get

$$f(i\nu) + h(i\nu, \tau(z_\ast)) = 0.$$  

However, we know that there are no roots of (15) on the imaginary axis for $\tau$ satisfying the conditions of the theorem - a contradiction which finishes the proof.

We now apply these results to equation (14). Notice that if $\tau'(z_\ast) = 0$, then $\alpha = 0$ and the coefficients of (14) become $\beta = sa_J + m_J + 2m_A A_s$, $\gamma = -sa_J + sa_A$, $\delta = 2sa_J m_A A_s + 2m_J m_A A_s$, and $\epsilon = m_J sa_A - 2sa_J m_A A_s$. It is not hard to check that with these definitions the roots of the equation $\lambda^2 + \beta \lambda + \delta = 0$ are $-2m_A A_s$ and $-(sa_J + m_J)$, both of which are real and negative. Also, $\beta^2 - 2\delta > 0$. We have the following corollary of Theorems 7 and 8.

**Theorem 9.** Suppose $\tau'(z_\ast) = 0$ and

$$\tau_m > \max \left\{ -\frac{1}{2m_J} \log \left( \frac{\beta^2 - 2\delta}{\gamma^2} \right), -\frac{1}{2m_J} \log \left( \frac{\delta^2}{\epsilon^2} \right) \right\}.$$  

Then the roots of (14) have negative real parts and are bounded uniformly away from the imaginary axis.
Corollary 9. Suppose $\tau(z)$ is constant and

$$\tau(z) > \max\left\{-\frac{1}{2m_J} \log \left(\frac{\beta^2 - 2\delta}{\gamma^2}\right), -\frac{1}{2m_J} \log \left(\frac{\delta^2}{\epsilon^2}\right)\right\}. $$

Then the equilibrium $(A_*, J_*)$ is locally asymptotically stable.

The linear stability theory for nonconstant delays is not yet fully developed. However, we conclude with the following theorem concerning (14).

Theorem 10. Suppose $2m_J + sa_J > 4mA_*, \ 2A_* > 1, mA_*, > m_J, a_A > a_J$, and $\tau_m > \max\left\{-\frac{1}{2m_J} \log \left(\frac{\beta^2 - 2\delta}{\gamma^2}\right), -\frac{1}{2m_J} \log \left(\frac{\delta^2}{\epsilon^2}\right)\right\}$. Then the roots of (14) have negative real parts and are bounded uniformly away from the imaginary axis.

Proof: The result will follow from Theorem 8 if we can show $\beta^2 - 4\delta \geq 0$. An elementary calculation gives

$$\beta^2 - 4\delta = 4\alpha s(a_A - a_J) + 4\alpha m_J(2A_* - 1) + 4mA_* (m_A A_* - m_J) + m_J^2 + sa_J(2m_J + sa_J - 4mA_*)$$

which is nonnegative by the conditions given in the statement of the theorem.

5. Summary. As noted in the Introduction, equations (6) and (7) are a direct descendant of a system considered in [4] and [5], and this latter system had its origins with a model proposed in [9]. These models were all used to study marine populations with sessile adults and pelagic larvae, e.g, barnacles. Our changes to the equations from [4] and [5] consisted of changing the delay from a constant to a function dependent on the total population density, and changing the adult death rate from a linear term to a logistic term.

Our changes made the system highly nonlinear, and thus the analysis became very difficult. In section 2, we were able to prove that both the
adult and juvenile populations are positive and bounded. In section 3, we proved that system (6) and (7) always has at least one positive equilibrium solution \((A_*, J_*)\). We also showed that conditions exist under which equilibrium solutions are isolated. Finally, in section 4 we gave results concerning the roots of the characteristic equation for the linearized system. We also gave local stability results. At present, we do not have results on the global stability of \((A_*, J_*)\). We would like to find conditions on the parameters \(s, \tau(z), m_J, m_A, a_J,\) and \(a_A\) such that \(\lim_{t \to \infty} (A(t), J(t)) = (A_*, J_*)\). This will be the subject of a future publication.

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Jacksonville University, Jacksonville, FL, USA
E-mail address: srai@ju.edu

Drury University, Springfield, MO, 65802 USA
E-mail address: rroberts@drury.edu