

# Intra-specific competition and insect larval development: a model with time-dependent delay

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We derive a stage-structured model for an insect population in which a larva matures on reaching a certain size, and in which there is intra-specific competition among larvae that hinders their development, thereby prolonging the larval phase. The model, a system of delay differential equations for the total numbers of adults and larvae, assumes two forms. One of these is a system with a variable state-dependent time delay determined by a threshold condition, the other has constant and distributed delays, a size-like independent variable replacing time  $t$ , and no threshold condition. We prove theorems on boundedness and on the linear stability of equilibria.

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## 1. Introduction

In insects, and other species that undergo metamorphosis, individuals often undergo a larval stage of development before becoming sexually mature adults. Mathematical models of such populations often take the form of delay differential equations for the total numbers of larval and adult individuals, in which the delay is the developmental time from egg to adult, which is often assumed to be constant. These are stage-structured models, derived from well-known modelling frameworks for age structured populations such as the McKendrick–von Foerster equation [3]. It is a well-known and straightforward way to model a population if the maturation delay is constant. However, in reality, larval developmental times for mosquitoes depend on a number of factors such as the weather (particularly temperature), diet and

intra- or inter-specific competition [5, 6, 8, 11, 14]. Intra-specific larval competition is known to occur in some mosquito populations [12]. In insects generally, the metamorphic molt is actually triggered by the size of the larva and not by chronological age [2, 4, 13]. In *Drosophila*, pupariation seems to be triggered by a large pulse of a steroid hormone known as 20-hydroxyecdysone (ecdysone), and this happens when enough larval growth has been achieved to produce an adult of the correct size [10, 13].

Adopting the view that maturation is triggered by size, not age, this paper considers the role of intra-specific competition in determining the developmental time of insect larvae. The immediate effect of competition among larvae is to slow down their growth, with the consequence that maturation is delayed. In this paper maturation is triggered when a larva reaches a prescribed length  $l$ , and the maturation time for the cohort that matures at time  $t$  is  $\tau(t)$ , which is determined from the threshold condition (2.12) and involves the number of larvae  $I$  present at all times during the maturation, since those other larvae were exerting competitive pressure. Larval development rate decreases as larval density increases, and we model this using (2.2) with  $P$  decreasing in its second variable. These assumptions lead to a system of delay differential equations for the numbers of adults  $A(t)$  and larvae  $I(t)$ . These equations have a variable (state-dependent) delay determined from the threshold condition and, unlike in many similar models with a constant delay, are fully coupled. The model can be transformed into one that has terms with constant delay, and other terms with distributed delay. In the second model a size-like variable  $x$  is used as the independent variable, and for larvae it corresponds to actual physical length.

We prove theorems that provide conditions sufficient for the population to be bounded or to go extinct. Delay equation models for stage-structured populations commonly involve a function  $B(\cdot)$  that is the birth rate (egg-laying rate) and it seems to be common practice to assume that this function is bounded, because such an assumption usually makes it possible to prove that solution variables remain bounded. The birth function is usually a function  $B(A)$  of the number of adults  $A$ . It is usually argued that the assumption of boundedness of the birth function is reasonable on the basis that the per-capita egg-laying rate  $B(A)/A$  tends to decrease at higher densities due to competition among adults. While this does not, by itself, imply that  $B(A)$  is bounded, one often has in mind the choice  $B(A) = rA \exp(-qA)$ , the Nicholson's blowflies birthrate [7], which is a bounded function. However, in this paper we prefer to establish boundedness results without the requirement of boundedness of our birth function  $B(A)$ . This is because of the expectation that intra-specific competition among insect larvae should prolong maturation, thereby exposing larvae to mortality risks for longer, lowering the maturation rate and stabilizing the population that way. We have therefore aimed to prove boundedness results that admit unbounded birth functions (within certain restrictions) and results that elucidate the role of a decreasing function  $P_0$  that specifies how the growth rate of an individual larva depends, due to the intra-specific competition, on the total number of larvae.

We also establish a result on the linear stability of any equilibrium. The characteristic equation is of a format that does not lend itself well to commonly used tricks, but in some situations (particularly if the competition is sufficiently weak, in

a sense that can be quantified) a technique involving the use of Rouché’s theorem can be applied to yield verifiable conditions sufficient for the local stability of an equilibrium.

**2. Model derivation**

We have in mind an insect population with larval and adult life stages. Maturation is triggered by size or weight, but the growth of an individual larva is at each instant affected by the total number of larvae present, since all larvae compete for resources, thereby slowing the growth of each individual. For larvae, we work with a variable  $x$  that could denote the size or weight (we choose size, to be definite) of a larva. Rather than specifying that a larva matures on reaching a certain age, we specify that it matures when its size  $x$  reaches a fixed threshold  $l$ . We derive a delay differential equation for the total number of adults, following an approach similar to that used by Smith in [15]. (Smith [15] non-dimensionalizes and takes  $l = 1$ , but we do not do that here.)

Let  $A(t)$  denote the number of mature adult insects at time  $t$  and let  $i(x, t)$  denote the larvae population density at time  $t$  of length  $x$ . The total number  $I(t)$  of larvae is given by

$$I(t) = \int_0^l i(x, t) dx. \tag{2.1}$$

Differently from Smith [15], we suppose that the rate of change of the length of a larva at time  $t$  is given by

$$\frac{dx}{dt} = P(t, I(t)), \tag{2.2}$$

i.e. the rate of change depends explicitly on  $t$  and also on the total number of larvae  $I(t)$  (in reality it may also depend on other factors). If  $P(t, I)$  is decreasing in  $I$ , then (2.2) models competition among the larvae because an increase in their numbers will slow down the rate at which larvae grow. Smith [15] took  $dx/dt$  to be a function of his variable for the total number of adults, not larvae. This would be realistic in some situations. However, for many species that undergo metamorphosis the larvae and adults live in different habitats and are in competition for different things (larvae for food, adults for mates, is typical). In such cases competition that hinders the growth of an individual larva is likely to come mainly from other larvae, and therefore we believe that (2.2) is the appropriate assumption. It is, however, a complication in the sense that it prevents us from deriving a single delay differential equation for the number of adults  $A(t)$ , as was done in [15]. Instead, we obtain a fully coupled system of equations for the numbers of larvae  $I(t)$  and adults  $A(t)$ , as we shall see.

After a small time  $\delta t$  a larva will have grown an amount  $\delta x$  and therefore

$$i(x + \delta x, t + \delta t) = i(x, t) - \mu_i i(x, t) \delta t,$$

where  $\mu_i$  is the per-capita mortality rate for larvae. From a Taylor expansion, and using (2.2),

$$\frac{\partial i(x, t)}{\partial t} + P(t, I(t)) \frac{\partial i(x, t)}{\partial x} = -\mu_i i(x, t). \tag{2.3}$$

Note that since larvae metamorphose into adults, it makes no sense to write down an equation for  $i(x, t)$  for lengths  $x$  exceeding  $l$ . Equation (2.3) is strictly for  $x \in (0, l)$  only. We may still derive an equation for the number of adults  $A(t)$ .

Differentiating (2.1) and using (2.3),

$$I'(t) = -\mu_i I(t) + P(t, I(t))(i(0, t) - i(l, t)).$$

The term  $P(t, I(t))i(0, t)$  is the only inflow term and is therefore the birth rate, while  $P(t, I(t))i(l, t)$  is the only outflow term other than the mortality term, and is therefore the maturation rate. For the birth rate, we assume that

$$P(t, I(t))i(0, t) = B(A(t)), \quad (2.4)$$

where  $B(\cdot)$  is a non-negative function such that  $B(0) = 0$ . The maturation rate  $P(t, I(t))i(l, t)$  needs to be calculated in terms of the birth rate at a previous time  $t - \tau(t)$ . The time-varying delay  $\tau(t)$  turns out to be the solution of the integral condition (2.12) that appears later. We proceed by solving (2.3) by the method of integration along characteristics.

The  $(x, t)$  plane can be partitioned into two subsets, with some characteristics lying above the characteristic  $x = X(t)$  and others below it, where

$$X(t) = \int_0^t P(\xi, I(\xi)) d\xi.$$

The curve  $x = X(t)$  is a special characteristic that passes through the origin (like the line  $t = a$  in age-structured models). The expression for  $i(x, t)$  depends on whether  $(x, t)$  is above or below this special characteristic  $x = X(t)$ .

In general, characteristics satisfy (2.2). Let  $s$  be a parameter describing position along a particular characteristic such that  $s = 0$  corresponds to a boundary (which could be either the  $x$ - or the  $t$ -axis), and such that  $dt/ds = 1$ . Then  $dx/ds = P(t, I(t))$ .

Recall that we are only concerned with  $x \in (0, l)$ . First let us consider the situation when  $x \geq X(t)$ . This will only in practice be the case for small  $t$ , since  $x \in (0, l)$  and  $X(t)$  is increasing. A characteristic  $(x(s), t(s))$  in the region  $x \geq X(t)$  of the  $(x, t)$  plane meets the  $x$ -axis and has  $t = 0$  when  $s = 0$ . Since  $t(0) = 0$  these characteristics are given by  $t = s$  and  $x - x(0) = X(t)$ . Now, from (2.3),

$$\frac{d}{ds} i(x(s), t(s)) = -\mu_i i(x(s), t(s)) \quad (2.5)$$

so that

$$i(x(s), t(s)) = i(x(0), t(0))e^{-\mu_i s}. \quad (2.6)$$

At a particular given point  $(x, t)$ , with  $x \geq X(t)$ , we have  $s = t$  and thus

$$i(x, t) = i(x - X(t), 0)e^{-\mu_i t}, \quad x \geq X(t). \quad (2.7)$$

Expression (2.7) is the solution of (2.3) during an initial transient of times  $t$  such that  $x \geq X(t)$ , and involves the initial size distribution  $i(x, 0)$ .

Next we consider the region  $x \leq X(t)$  in the  $(x, t)$  plane (equivalent to  $t \geq T(x, t)$ , where  $T(x, t)$  is defined in (2.8)), typically holding for larger  $t$  and ultimately giving

rise to a delay equation that describes the adult population dynamics after the initial transient. A characteristic  $(x(s), t(s))$  in this region meets the  $t$ -axis and has  $x(0) = 0$  and  $t = s + t(0)$ .

We need to find the  $s$ -value for a particular point  $(x, t)$ . From (2.2), using that  $x = 0$  when  $t = t(0)$ ,

$$x = \int_{t(0)}^t P(\xi, I(\xi)) \, d\xi = \int_{t-s}^t P(\xi, I(\xi)) \, d\xi,$$

which determines the required  $s$ . The root  $s$  of the above equation is denoted  $T(x, t)$ , so that the function  $T(x, t)$  is defined by

$$\int_{t-T(x,t)}^t P(\xi, I(\xi)) \, d\xi = x. \tag{2.8}$$

Equation (2.6) still holds but now  $x(0) = 0$ ,  $t(0) = t - s$  and  $s$  is the quantity  $T(x, t)$  defined in (2.8). Therefore,

$$i(x, t) = i(0, t - T(x, t))e^{-\mu_i T(x,t)}, \quad x \leq X(t). \tag{2.9}$$

The birth law is (2.4) and is used to compute  $i(0, t - T(x, t))$ , giving

$$i(0, t - T(x, t)) = \frac{B(A(t - T(x, t)))}{P(t - T(x, t), I(t - T(x, t)))}. \tag{2.10}$$

We require the maturation rate  $P(t, I(t))i(l, t)$  and we can now find  $i(l, t)$  from (2.9) and (2.10), giving

$$i(l, t) = i(0, t - T(l, t))e^{-\mu_i T(l,t)} = \frac{B(A(t - T(l, t)))}{P(t - T(l, t), I(t - T(l, t)))} e^{-\mu_i T(l,t)}.$$

Since the size variable  $x$  only applies to larvae, for the adults  $A(t)$  we simply write

$$\frac{dA(t)}{dt} = -\mu_a A(t) + \text{maturation rate} \tag{2.11}$$

on the assumption that there is no competition between adults, with  $\mu_a$  the per-capita natural death rate for adults. We also write  $\tau(t) = T(l, t)$ . From (2.8), the delay  $\tau(t)$  in (2.13) satisfies the threshold condition

$$\int_{t-\tau(t)}^t P(\xi, I(\xi)) \, d\xi = l. \tag{2.12}$$

Differentiating (2.12) yields that  $\tau'(t) < 1$ , and this has an important interpretation, namely, that if the maturation time  $\tau(t)$  is increasing, there is a limit to how fast it may do so. Otherwise, it is possible for a matured individual to become immature again. Barbarossa *et al.* [1] explain the same point in relation to a government that suddenly raises the age at which individuals may vote. It is easy to see that it creates a situation where some individuals who could vote suddenly become ineligible to do so. The problem arises because if voting age at time  $t$  is  $\tau(t)$ , a sudden instantaneous increase of the voting age cannot satisfy  $\tau'(t) < 1$ . The problem would disappear if the voting age were continuously raised in a manner satisfying such a constraint.

The constraint  $\tau'(t) < 1$  is equivalent to the assertion that if  $t_1 < t_2$ , then  $t_1 - \tau(t_1) < t_2 - \tau(t_2)$ . Indeed, if this were false, then  $t_1 - \tau(t_1) \geq t_2 - \tau(t_2)$  and

$$l = \int_{t_1 - \tau(t_1)}^{t_1} P(\xi, I(\xi)) \, d\xi < \int_{t_2 - \tau(t_2)}^{t_2} P(\xi, I(\xi)) \, d\xi = l,$$

a contradiction. Thus, if two individuals are born at different times, the individual born first matures first.

From (2.11), the equation for the number of adults  $A(t)$  is

$$\frac{dA(t)}{dt} = -\mu_a A(t) + P(t, I(t)) \frac{B(A(t - \tau(t)))}{P(t - \tau(t), I(t - \tau(t)))} e^{-\mu_i \tau(t)} \tag{2.13}$$

and the equation for the number of larvae  $I(t)$  is

$$\frac{dI(t)}{dt} = -\mu_i I(t) + B(A(t)) - P(t, I(t)) \frac{B(A(t - \tau(t)))}{P(t - \tau(t), I(t - \tau(t)))} e^{-\mu_i \tau(t)}. \tag{2.14}$$

Here,  $\tau(t)$ , which depends on the function  $I$ , is determined by the threshold condition (2.12). Equations (2.13) and (2.14) have to be treated as a fully coupled system. This is different from the situation in [15], in which the number of adults is determined from a *single* differential equation with a threshold condition. The simpler situation in [15] is consequent upon Smith’s assumption that  $dx/dt$  is a function of the number of adults, rather than the number of larvae as in (2.2). In general, model (2.13)–(2.14) has a state-dependent delay because the growth of an individual larva, as described by (2.2), depends directly on  $t$  due to factors such as seasonality, and also more indirectly on  $t$  via the total number  $I(t)$  of larvae, since an increase in the latter is likely to slow down growth due to competition. As expected,  $\tau(t)$ , which is found from (2.12), depends on the state variable  $I(\cdot)$  over the development time  $[t - \tau(t), t]$  for the cohort that matures at time  $t$ . State-dependent delays are automatically time dependent but the converse would not be true if, in (2.2), we took  $P$  to depend only on its first variable  $t$  and not on  $I$ . The maturation time  $\tau(t)$  would then be time dependent but not state dependent. However, we actually focus mainly on the opposite situation when  $P$  depends only on  $I$ , which does give rise to state-dependent delay equations.

Equation (2.14) can be replaced by the integral equation

$$I(t) = \int_{t - \tau(t)}^t B(A(\xi)) e^{-\mu_i(t - \xi)} \, d\xi \tag{2.15}$$

with  $\tau(t)$  again given by (2.12). Equation (2.15) can be directly derived from the fact that

$$\begin{aligned} I(t) &= \int_0^l i(x, t) \, dx = \int_0^l i(0, t - T(x, t)) e^{-\mu_i T(x, t)} \, dx \\ &= \int_0^l \frac{B(A(t - T(x, t)))}{P(t - T(x, t), I(t - T(x, t)))} e^{-\mu_i T(x, t)} \, dx, \end{aligned}$$

which becomes (2.15) on changing variables from  $x$  to  $\xi$ , where  $t - T(x, t) = \xi$  with  $T(x, t)$  defined by (2.8), noting that  $T(0, t) = 0$ ,  $T(l, t) = \tau(t)$  and, using (2.8),  $\partial \xi / \partial x = -\partial T / \partial x = -1 / P(\xi, I(\xi))$ .

**3. Model analysis**

We focus on the autonomous case when  $P(t, I) = P_0(I)$ . In this case it is possible to convert the model (2.13)–(2.14) into one without a threshold condition of the form (2.12). To do so, we introduce the new size-like independent variable

$$x = \int_0^t P_0(I(\xi)) \, d\xi.$$

This amounts to adopting the physiological time-scale of larvae. Indeed, for larvae the variable  $x$  corresponds to physical size, with a fixed threshold value  $l$  for maturation. We write

$$A(t) = \mathcal{A}\left(\int_0^t P_0(I(\xi)) \, d\xi\right) = \mathcal{A}(x), \quad I(t) = \mathcal{I}\left(\int_0^t P_0(I(\xi)) \, d\xi\right) = \mathcal{I}(x).$$

Note that

$$x = \int_0^{t-\tau(t)} P_0(I(\xi)) \, d\xi + \int_{t-\tau(t)}^t P_0(I(\xi)) \, d\xi = \int_0^{t-\tau(t)} P_0(I(\xi)) \, d\xi + l$$

by (2.12). Thus, if  $x$  corresponds to  $t$ , then  $x - l$  corresponds to  $t - \tau(t)$ . Also,

$$A(t - \tau(t)) = \mathcal{A}\left(\int_0^{t-\tau(t)} P_0(I(\xi)) \, d\xi\right) = \mathcal{A}(x - l) \quad \text{and} \quad I(t - \tau(t)) = \mathcal{I}(x - l)$$

so the effect of the transformation is to transform (2.13)–(2.14) into a model with a constant delay  $l$ , and without a threshold condition. We calculate  $\tau(t)$  in terms of  $x$  as

$$\begin{aligned} \tau(t) = t - (t - \tau(t)) &= \int_{x-l}^x \frac{dt}{d\bar{x}} \, d\bar{x} = \int_{x-l}^x \frac{1}{P_0(\mathcal{I}(\bar{x}))} \, d\bar{x} \\ &= \int_{-l}^0 \frac{1}{P_0(\mathcal{I}(x + \bar{x}))} \, d\bar{x} \\ &= \int_{-l}^0 \frac{1}{P_0(\mathcal{I}_x(\bar{x}))} \, d\bar{x} \\ &= \tau_0(\mathcal{I}_x), \end{aligned}$$

where the subscript notation has its standard meaning in delay differential equations, i.e.  $\mathcal{I}_x(\bar{x}) = \mathcal{I}(x + \bar{x})$  for  $\bar{x} \in [-l, 0]$  and the functional  $\tau_0(\cdot)$  is defined by

$$\tau_0(\phi) = \int_{-l}^0 \frac{1}{P_0(\phi(\bar{x}))} \, d\bar{x}. \tag{3.1}$$

The model equations (2.13)–(2.14) become

$$\frac{d\mathcal{A}(x)}{dx} = -\mu_a \frac{\mathcal{A}(x)}{P_0(\mathcal{I}(x))} + e^{-\mu_i \tau_0(\mathcal{I}_x)} \frac{B(\mathcal{A}(x - l))}{P_0(\mathcal{I}(x - l))} \tag{3.2}$$

and

$$\frac{d\mathcal{I}(x)}{dx} = -\mu_i \frac{\mathcal{I}(x)}{P_0(\mathcal{I}(x))} + \frac{B(\mathcal{A}(x))}{P_0(\mathcal{I}(x))} - e^{-\mu_i \tau_0(\mathcal{I}_x)} \frac{B(\mathcal{A}(x - l))}{P_0(\mathcal{I}(x - l))}. \tag{3.3}$$

In the autonomous case  $P(t, I) = P_0(I)$  that is now under consideration, either of the systems (2.13)–(2.14) or (3.2)–(3.3) can be used to study the linear stability of an equilibrium. In §3.2 we present an approach that uses (2.13)–(2.14) for this purpose. Next, we establish bounds for  $A(t)$  and  $I(t)$  from a study that uses both systems. The second equation, (3.3), can be replaced by the integral equation

$$\mathcal{I}(x) = \int_{x-l}^x \frac{B(\mathcal{A}(z))}{P_0(\mathcal{I}(z))} \exp\left(-\mu_i \int_z^x \frac{d\bar{x}}{P_0(\mathcal{I}(\bar{x}))}\right) dz. \tag{3.4}$$

**3.1. Boundedness**

Good bounds on the variables  $A(t)$  and  $I(t)$  can be obtained from a study that uses both system (2.13)–(2.14) and the reformulated system (3.2)–(3.3), in which  $x$  is the independent variable. Theorem 3.1 admits some unbounded birth functions  $B(\cdot)$  and establishes bounds that depend on the function  $P_0(\cdot)$ , which describes the intra-specific competitive effect among larvae and its tendency to prolong the larval stage by slowing down the rate at which a larva grows.

**THEOREM 3.1.** *Suppose the function  $B(\cdot)$  is non-negative and satisfies  $B(A) \leq \bar{B}(A)$  for all  $A \geq 0$ , where  $\bar{B}(A)$  is some non-decreasing function with the property that there exists  $K > 0$  such that  $\bar{B}(A) < \min(\mu_a, \mu_i)A$  whenever  $A > K$ . Then solutions  $(A(t), I(t))$  of (2.13)–(2.14) subject to non-negative initial data satisfy*

$$\limsup_{t \rightarrow \infty} (A(t) + I(t)) \leq K. \tag{3.5}$$

Suppose further that  $P(t, I) = P_0(I)$  in (2.2), with  $P_0(\cdot)$  being a strictly positive decreasing function. Then, if  $(\mathcal{A}(x), \mathcal{I}(x))$  satisfies system (3.2)–(3.3):

(i) if the inequality

$$\frac{e^{-\mu_i l / P_0(0)}}{P_0(K)} \bar{B}(\mathcal{A}) < \frac{\mu_a}{P_0(0)} \mathcal{A} \tag{3.6}$$

holds for all  $\mathcal{A} > 0$ , then  $(\mathcal{A}(x), \mathcal{I}(x)) \rightarrow (0, 0)$  as  $x \rightarrow \infty$ ;

(ii) if (3.6) does not hold for all  $\mathcal{A} > 0$  but there exists  $K_1 > 0$  such that (3.6) holds for all  $\mathcal{A} > K_1$ , then

$$\limsup_{x \rightarrow \infty} \mathcal{A}(x) \leq K_1 \tag{3.7}$$

and

$$\limsup_{x \rightarrow \infty} \mathcal{I}(x) \leq \frac{\bar{B}(K_1) P_0(0)}{P_0(K) \mu_i} (1 - e^{-\mu_i l / P_0(0)}). \tag{3.8}$$

*Proof.* It is straightforward to see that  $A(t) \geq 0$  and  $I(t) \geq 0$  for all  $t \geq 0$ . For  $A(t)$  this follows immediately from the structure of (2.13) and an argument similar to that described in the proof of theorem 5.2.1 in [16]. For  $I(t)$ , non-negativity follows from the integral equation (2.15). Adding (2.13) and (2.14) gives

$$\begin{aligned} \frac{d}{dt} (A(t) + I(t)) &= B(A(t)) - \mu_a A(t) - \mu_i I(t) \\ &\leq \bar{B}(A(t)) - \min(\mu_a, \mu_i) (A(t) + I(t)) \\ &\leq \bar{B}(A(t) + I(t)) - \min(\mu_a, \mu_i) (A(t) + I(t)). \end{aligned}$$



From a standard comparison argument, and basic properties of one-dimensional ordinary differential equations, we immediately deduce (3.5).

Obviously,  $\limsup_{t \rightarrow \infty} A(t)$  and  $\limsup_{t \rightarrow \infty} I(t)$  are independently bounded by  $K$ , and the same asymptotic bound also applies to the functions  $\mathcal{A}(x)$  and  $\mathcal{I}(x)$  satisfying (3.2)–(3.3). In what follows, we treat the bound  $K$  as if it applies to  $A(t)$  and  $I(t)$  for all  $t$ , and  $\mathcal{A}(x)$  and  $\mathcal{I}(x)$  for all  $x$ . This can be justified by standard arguments involving the addition of a small quantity  $\varepsilon$  to  $K$ . For example,  $A(t) \leq K + \varepsilon$  for  $t$  sufficiently large, so  $K + \varepsilon$  can be used as a true bound on  $A(t)$  if all analysis is understood to be for large enough  $t$ . But, eventually,  $\varepsilon$  is shrunk to zero. For brevity we omit these routine details of justification and use the asymptotic bound  $K$  on each variable as if it were valid for all times.

Since  $P_0(\cdot)$  is decreasing,  $P_0(\mathcal{I}(x)) \leq P_0(0)$  and therefore, from (3.2) and the definition of  $\tau_0(\mathcal{I}_x)$ ,

$$\frac{d\mathcal{A}(x)}{dx} \leq -\frac{\mu_a}{P_0(0)}\mathcal{A}(x) + \bar{B}(\mathcal{A}(x-l)) \left[ \frac{1}{P_0(\mathcal{I}(x-l))} \exp\left(-\mu_i \int_{x-l}^x \frac{1}{P_0(\mathcal{I}(\bar{x}))} d\bar{x}\right) \right]. \tag{3.9}$$

Since  $0 \leq \mathcal{I}(x) \leq K$ ,

$$\frac{d\mathcal{A}(x)}{dx} \leq -\frac{\mu_a}{P_0(0)}\mathcal{A}(x) + \frac{e^{-\mu_i l/P_0(0)}}{P_0(K)}\bar{B}(\mathcal{A}(x-l)). \tag{3.10}$$

The proof of statement (i), that  $\mathcal{A}(x) \rightarrow 0$  as  $x \rightarrow \infty$  under the assumption that (3.6) holds for all  $\mathcal{A} > 0$ , follows from a comparison argument using that  $\bar{B}(\cdot)$  is non-decreasing. Smith [16, theorem 5.1.1] assures us that  $\mathcal{A}(x)$  is bounded above by the solution of the differential equation corresponding to (3.10), i.e. the differential equation obtained if ‘ $\leq$ ’ in (3.10) is replaced by ‘ $=$ ’. Zero is the only equilibrium of that equation under the assumptions of statement (i). By the results on generic convergence to equilibria in [16, ch. 5],  $\mathcal{A}(x) \rightarrow 0$  as  $x \rightarrow \infty$ . It then follows from the integral equation (3.4) that  $\mathcal{I}(x) \rightarrow 0$ . Note that  $P_0(\mathcal{I}(z))$ , in the denominator of the integrand of (3.4), is bounded away from zero because of the boundedness of  $\mathcal{I}$ .

Next we prove statement (ii) of the theorem. Let  $\mathcal{A}^\infty = \limsup_{x \rightarrow \infty} \mathcal{A}(x)$ , and let  $\varepsilon > 0$  be an arbitrary small number. There exists  $X > 0$  such that  $\mathcal{A}(x) \leq \mathcal{A}^\infty + \varepsilon$  whenever  $x \geq X$ . Also, by the fluctuation lemma (see [17, proposition A.22]), there is a sequence  $x_j \rightarrow \infty$  such that  $\mathcal{A}(x_j) \rightarrow \mathcal{A}^\infty$  and  $\mathcal{A}'(x_j) \rightarrow 0$  as  $j \rightarrow \infty$ . From (3.10), for  $j$  sufficiently large,

$$\begin{aligned} \mathcal{A}'(x_j) &\leq -\frac{\mu_a}{P_0(0)}\mathcal{A}(x_j) + \frac{e^{-\mu_i l/P_0(0)}}{P_0(K)}\bar{B}(\mathcal{A}(x_j-l)) \\ &\leq -\frac{\mu_a}{P_0(0)}\mathcal{A}(x_j) + \frac{e^{-\mu_i l/P_0(0)}}{P_0(K)}\bar{B}(\mathcal{A}^\infty + \varepsilon) \end{aligned}$$

since  $\bar{B}$  is non-decreasing. Letting  $j \rightarrow \infty$  and then  $\varepsilon \rightarrow 0$ ,

$$\frac{\mu_a}{P_0(0)}\mathcal{A}^\infty \leq \frac{e^{-\mu_i l/P_0(0)}}{P_0(K)}\bar{B}(\mathcal{A}^\infty).$$

But we are now assuming that (3.6) holds when  $\mathcal{A} > K_1$ , so it follows that  $\mathcal{A}^\infty \leq K_1$ . Finally, to deduce (3.8) we use (3.4) and the bounds  $\mathcal{A}^\infty \leq K_1, \mathcal{I}^\infty \leq K$ . Let

$\varepsilon$  be an arbitrary small positive number; then  $\mathcal{A}(z) \leq K_1 + \varepsilon$  and  $\mathcal{I}(z) \leq K + \varepsilon$  for all  $z$  sufficiently large. Therefore, for  $x$  sufficiently large, and using that  $B \leq \bar{B}$  with  $\bar{B}$  increasing,

$$\begin{aligned} \mathcal{I}(x) &= \int_{x-l}^x \frac{B(\mathcal{A}(z))}{P_0(\mathcal{I}(z))} \exp\left(-\mu_i \int_z^x \frac{d\bar{x}}{P_0(\mathcal{I}(\bar{x}))}\right) dz \\ &\leq \frac{\bar{B}(K_1 + \varepsilon)}{P_0(K + \varepsilon)} \int_{x-l}^x \exp\left(-\frac{\mu_i}{P_0(0)}(x - z)\right) dz \\ &= \frac{\bar{B}(K_1 + \varepsilon)}{P_0(K + \varepsilon)} \frac{P_0(0)}{\mu_i} (1 - e^{-\mu_i l / P_0(0)}). \end{aligned}$$

Taking the limsup as  $x \rightarrow \infty$  and then letting  $\varepsilon \rightarrow 0$ , we obtain (3.8). □

Our next boundedness result has the advantage of holding under much weaker assumptions on the birth function  $B(\cdot)$ . Theorem 3.2 holds for any increasing birth function that grows no faster than linearly. There is no restriction on the linear growth rate  $\kappa$  in theorem 3.2, and in this respect the theorem admits a wider class of birth functions than theorem 3.1. However, theorem 3.2 is restrictive to the extent that it only ensures the nonexistence of *monotone* solutions that increase without bound.

**THEOREM 3.2.** *Suppose that  $B(\cdot)$  is continuous, non-negative, monotone non-decreasing, and satisfies  $B(A) \leq \kappa A$  for some  $\kappa > 0$ . Suppose further that  $P(t, I) = P_0(I)$  in (2.2), with  $P_0(\cdot)$  a strictly positive decreasing function such that  $P_0(\infty) = 0$ . Then, it is impossible for a monotone solution  $(\mathcal{A}, \mathcal{I})$  of system (3.2)–(3.3) to increase without bound.*

*Proof.* From (3.4), for a solution of (3.2)–(3.3) with  $\mathcal{A}$  and  $\mathcal{I}$  increasing, we have

$$\begin{aligned} \mathcal{I}(x) &\geq \int_{x-l}^x \frac{B(\mathcal{A}(z))}{P_0(\mathcal{I}(z))} \exp\left(-\mu_i \int_{x-l}^x \frac{d\bar{x}}{P_0(\mathcal{I}(\bar{x}))}\right) dz \\ &= e^{-\mu_i \tau_0(\mathcal{I}_x)} \int_{x-l}^x \frac{B(\mathcal{A}(z))}{P_0(\mathcal{I}(z))} dz \geq l e^{-\mu_i \tau_0(\mathcal{I}_x)} \frac{B(\mathcal{A}(x-l))}{P_0(\mathcal{I}(x-l))}. \end{aligned} \tag{3.11}$$

From (3.4) again,

$$\begin{aligned} \mathcal{I}(x) &\leq \max_{z \in [x-l, x]} B(\mathcal{A}(z)) \int_{x-l}^x \frac{1}{P_0(\mathcal{I}(z))} \exp\left(-\mu_i \int_z^x \frac{d\bar{x}}{P_0(\mathcal{I}(\bar{x}))}\right) dz \\ &= \frac{1}{\mu_i} \max_{z \in [x-l, x]} B(\mathcal{A}(z)) \int_{x-l}^x \frac{d}{dz} \exp\left(-\mu_i \int_z^x \frac{d\bar{x}}{P_0(\mathcal{I}(\bar{x}))}\right) dz \\ &= \frac{1}{\mu_i} \max_{z \in [x-l, x]} B(\mathcal{A}(z)) \left[1 - \exp\left(-\mu_i \int_{x-l}^x \frac{d\bar{x}}{P_0(\mathcal{I}(\bar{x}))}\right)\right] \end{aligned}$$

so that

$$\mathcal{I}(x) \leq \frac{1}{\mu_i} \max_{z \in [x-l, x]} B(\mathcal{A}(z)). \tag{3.12}$$

It follows from (3.2), and the bound for  $\mathcal{I}(x)$  in (3.11), that

$$\frac{d\mathcal{A}(x)}{dx} \leq -\mu_a \frac{\mathcal{A}(x)}{P_0(\mathcal{I}(x))} + \frac{\mathcal{I}(x)}{l}.$$

By (3.12), for increasing functions  $\mathcal{A}(x)$  we have  $\mathcal{I}(x) \leq B(\mathcal{A}(x))/\mu_i$  and therefore

$$\frac{d\mathcal{A}(x)}{dx} \leq -\mu_a \frac{\mathcal{A}(x)}{P_0(\mathcal{I}(x))} + \frac{B(\mathcal{A}(x))}{\mu_i l} \leq -\mu_a \frac{\mathcal{A}(x)}{P_0(\mathcal{I}(x))} + \frac{\kappa \mathcal{A}(x)}{\mu_i l}.$$

Now, suppose  $\mathcal{I}(x)$  increases monotonically without bound. Then, since  $P_0(\infty) = 0$ , it follows that, for  $x$  sufficiently large,  $d\mathcal{A}(x)/dx < 0$  and therefore  $\mathcal{A}(x)$  is bounded. From (3.12),  $\mathcal{I}(x)$  is also bounded, a contradiction.  $\square$

### 3.2. Linear stability of equilibria

When  $P(t, I) = P_0(I)$ , any equilibrium  $(A^*, I^*)$  of system (2.13)–(2.14) must satisfy

$$\mu_a A^* = e^{-\mu_i \tau_0(I^*)} B(A^*), \quad \mu_i I^* = B(A^*) (1 - e^{-\mu_i \tau_0(I^*)}) \tag{3.13}$$

with

$$\tau_0(I^*) = \frac{l}{P_0(I^*)}.$$

To investigate the linear stability of an equilibrium we set  $A(t) = A^* + \tilde{A}(t)$  and  $I(t) = I^* + \tilde{I}(t)$  with  $\tilde{A}$  and  $\tilde{I}$  small. System (2.13)–(2.14) is a system with state-dependent delay, since  $\tau(t)$  is given by (2.12) (with  $P(t, I) = P_0(I)$  now) and involves the variable  $I$  and its history. In the linearization of an autonomous system with state-dependent delay about an equilibrium solution, it is usually understood that the state-dependent delays end up evaluated at the equilibrium under consideration. This turns out to be the case for (2.13)–(2.14) for the delays that appear in the arguments, but not for the delays in the  $e^{-\mu_i \tau(t)}$  terms. For those terms,  $\tau(t)$ , which is really a functional of  $I$ , needs to be expanded for small  $\tilde{I}$  keeping linear terms, and not simply replaced by its value at the equilibrium  $I^*$ . Such an expansion can be calculated as follows. From (2.12),

$$1 - \tau'(t) = \frac{P_0(I^* + \tilde{I}(t))}{P_0(I^* + \tilde{I}(t - \tau(t)))}.$$

If we expand the right-hand side for small  $\tilde{I}$  and replace  $\tau(t)$ , where it appears in the right-hand side, by its equilibrium value  $\tau_0(I^*) = l/P_0(I^*)$ , we obtain

$$-\tau'(t) = \frac{P'_0(I^*)}{P_0(I^*)} \left\{ \tilde{I}(t) - \tilde{I}\left(t - \frac{l}{P_0(I^*)}\right) \right\}$$

and therefore, since we need  $\tau(t)$  to equal  $l/P_0(I^*)$  when  $\tilde{I} = 0$ , the linearization of  $\tau(t)$  at the equilibrium  $(A^*, I^*)$  is

$$\tau(t) \approx \frac{l}{P_0(I^*)} - \frac{P'_0(I^*)}{P_0(I^*)} \int_{t-l/P_0(I^*)}^t \tilde{I}(\xi) d\xi. \tag{3.14}$$

With this information, tedious calculations yield that the linearization of (2.13)–(2.14) at the equilibrium  $(A^*, I^*)$  is

$$\begin{aligned} \frac{d\tilde{A}(t)}{dt} = & -\mu_a \tilde{A}(t) \\ & + e^{-\mu_i l/P_0(I^*)} \left[ \frac{\mu_i B(A^*) P_0'(I^*)}{P_0(I^*)} \int_{t-l/P_0(I^*)}^t \tilde{I}(\xi) d\xi \right. \\ & + B'(A^*) \tilde{A}(t - l/P_0(I^*)) \\ & \left. + \frac{B(A^*) P_0'(I^*)}{P_0(I^*)} \left\{ \tilde{I}(t) - \tilde{I}\left(t - \frac{l}{P_0(I^*)}\right) \right\} \right], \end{aligned} \tag{3.15}$$

$$\begin{aligned} \frac{d\tilde{I}(t)}{dt} = & -\mu_i \tilde{I}(t) + B'(A^*) \tilde{A}(t) \\ & - e^{-\mu_i l/P_0(I^*)} \left[ \frac{\mu_i B(A^*) P_0'(I^*)}{P_0(I^*)} \int_{t-l/P_0(I^*)}^t \tilde{I}(\xi) d\xi \right. \\ & + B'(A^*) \tilde{A}(t - l/P_0(I^*)) \\ & \left. + \frac{B(A^*) P_0'(I^*)}{P_0(I^*)} \left\{ \tilde{I}(t) - \tilde{I}\left(t - \frac{l}{P_0(I^*)}\right) \right\} \right]. \end{aligned} \tag{3.16}$$

Equation (3.16) can be replaced by the integral equation

$$\begin{aligned} \tilde{I}(t) = & -\frac{B(A^*) P_0'(I^*)}{P_0(I^*)} e^{-\mu_i l/P_0(I^*)} \int_{t-l/P_0(I^*)}^t \tilde{I}(\xi) d\xi \\ & + B'(A^*) \int_{t-l/P_0(I^*)}^t \tilde{A}(\xi) e^{-\mu_i(t-\xi)} d\xi, \end{aligned} \tag{3.17}$$

which can also be derived by linearizing (2.15) and using that the linearization of  $\tau(t)$  is given by (3.14). The most tractable form of the characteristic equation of the linearization seems to arise from the combination of (3.15) with the linearized integral equation (3.17). With

$$\hat{\mu}_i = \frac{\mu_i l}{P_0(I^*)}, \quad \hat{\mu}_a = \frac{\mu_a l}{P_0(I^*)}, \quad \varepsilon = \frac{l B(A^*) P_0'(I^*) e^{-\hat{\mu}_i}}{P_0^2(I^*)}, \tag{3.18}$$

non-trivial solutions of that system of the form  $(\tilde{A}(t), \tilde{I}(t)) = (c_1, c_2) \exp(\lambda t)$  exist whenever  $\Lambda := \lambda l/P_0(I^*)$  satisfies the characteristic equation

$$\frac{P_0(I^*)}{l} (\Lambda + \hat{\mu}_a) - B'(A^*) e^{-(\Lambda + \hat{\mu}_i)} = \frac{\varepsilon B'(A^*) (\Lambda + \hat{\mu}_i) k(\Lambda) k(\Lambda + \hat{\mu}_i)}{1 + \varepsilon k(\Lambda)}, \tag{3.19}$$

where

$$k(x) = \frac{1 - e^{-x}}{x}. \tag{3.20}$$

If developing larvae grow in size at a constant rate (i.e. the function  $P$  in (2.2) is constant and so is  $P_0$ ), then  $P_0'(I^*) = 0$  and the linearized equations decouple with (3.15) involving  $\tilde{A}$  only. In this situation  $\varepsilon = 0$  and the characteristic equation (3.19) simplifies considerably. Indeed, if  $P_0(I) \equiv P_0^*$  is a constant function,

then the time taken for a larva to reach length  $l$  and mature is always  $l/P_0^*$ . In this case  $\tau(t) = l/P_0^*$ , the  $P$  terms in (2.13) cancel, and that equation then assumes a well-studied form, for which general results can be found in [9]. The effect of competition among larvae is that  $P$  in (2.2) is not a constant, the development time  $\tau(t)$  for the cohort that matures at time  $t$  is dependent on the number of larvae and how this has been changing over the time when the cohort was developing. The linearized equations become fully coupled with a characteristic equation (3.19) that is not easy to treat. We may, however, prove theorem 3.3 concerning any equilibrium  $(A^*, I^*)$  of system (2.13)–(2.14). The theorem establishes that if an equilibrium is locally asymptotically stable in the absence of competition among the larvae (which is the case if (3.21) holds), then it remains stable in the presence of competition if the competitive effect as measured by  $\varepsilon$  is sufficiently small (more precisely, small enough such that (3.22) and (3.23) both hold). Complete absence of larval competition arises as a particular case of the model, namely, the case in which the function  $P$  in (2.2), and hence also the function  $P_0$ , is constant. In this case  $\varepsilon = 0$  and larvae grow at a rate independent of how many larvae are present.

**THEOREM 3.3.** *Let  $(A^*, I^*)$  be any equilibrium of system (2.13)–(2.14). With  $\hat{\mu}_i$ ,  $\hat{\mu}_a$  and  $\varepsilon$  defined in (3.18), and the function  $k(\cdot)$  in (3.20), suppose that*

$$\frac{P_0(I^*)}{l} \hat{\mu}_a > |B'(A^*)| e^{-\hat{\mu}_i} \tag{3.21}$$

and that  $\varepsilon \in (-1, 1)$  is sufficiently small that

$$\frac{P_0(I^*)}{l} \min\left(1, \frac{\hat{\mu}_i}{\hat{\mu}_a}\right) > \frac{|\varepsilon|}{1 - |\varepsilon|} |B'(A^*)| k(\hat{\mu}_i) \tag{3.22}$$

and

$$\frac{P_0(I^*)}{l} \hat{\mu}_a - \frac{|\varepsilon|}{1 - |\varepsilon|} |B'(A^*)| k(\hat{\mu}_i) \hat{\mu}_i > |B'(A^*)| e^{-\hat{\mu}_i}. \tag{3.23}$$

Then the equilibrium  $(A^*, I^*)$  of (2.13)–(2.14) is locally asymptotically stable.

*Proof.* We prove the theorem using Rouché’s theorem, which states that if two functions  $f(z)$  and  $g(z)$ ,  $z \in \mathbb{C}$ , are holomorphic inside and on a contour  $\Gamma$  in the complex plane, and if  $|f(z)| > |g(z)|$  on  $\Gamma$ , then  $f$  and  $f + g$  have the same number of zeros inside  $\Gamma$ . We take

$$f(z) = \frac{P_0(I^*)}{l} (z + \hat{\mu}_a) - B'(A^*) e^{-(z + \hat{\mu}_i)}$$

and

$$g(z) = -\frac{\varepsilon B'(A^*) (z + \hat{\mu}_i) k(z) k(z + \hat{\mu}_i)}{1 + \varepsilon k(z)}$$

and the contour  $\Gamma = \Gamma_R$  to be the semicircle of radius  $R$  in  $\text{Re } z \geq 0$  with curved part  $z = Re^{i\theta}$ ,  $\theta \in [-\pi/2, \pi/2]$ , and straight part  $z = iy$ ,  $y \in [-R, R]$ . We claim that, under the hypotheses,  $|f(z)| > |g(z)|$  on  $\Gamma_R$  for all  $R$  sufficiently large. This establishes that the full characteristic equation (3.19), corresponding to  $f + g = 0$ , has the same number of roots in  $\text{Re } z > 0$  as does the equation  $f = 0$ ; in other

words, none at all under assumption (3.21), as we shall show. The absence of roots on the imaginary axis will follow from a particular step in our argument. These facts establish the local asymptotic stability of the equilibrium  $(A^*, I^*)$  under inequalities (3.21)–(3.23).

Clearly,  $f(z)$  is holomorphic. Since  $k(z)$  is holomorphic,  $g(z)$  can only fail to be holomorphic in the region of interest if there exists  $z_0$ , with  $\text{Re } z_0 \geq 0$ , such that  $1 + \varepsilon k(z_0) = 0$ . But then, using the integral representation of  $k$  (expression (3.24)),

$$1 = |\varepsilon| |k(z_0)| \leq |\varepsilon| \int_0^1 |e^{-\xi z_0}| d\xi = |\varepsilon| \int_0^1 e^{-\xi \text{Re } z_0} d\xi \leq |\varepsilon|,$$

which contradicts  $\varepsilon \in (-1, 1)$ . Thus,  $g(z)$  is holomorphic in  $\text{Re } z \geq 0$ .

The equation  $f = 0$  is

$$\frac{P_0(I^*)}{l}(z + \hat{\mu}_a) = B'(A^*)e^{-(z + \hat{\mu}_i)}.$$

Suppose for a contradiction that it has a root  $z$  with  $\text{Re } z \geq 0$ . Then, taking the modulus,

$$\frac{P_0(I^*)}{l}|z + \hat{\mu}_a| = |B'(A^*)|e^{-(\text{Re } z + \hat{\mu}_i)} \leq |B'(A^*)|e^{-\hat{\mu}_i}$$

so that  $z$  lies in the circle in  $\mathbb{C}$  of radius  $|B'(A^*)|e^{-\hat{\mu}_i}(l/P_0(I^*))$  centred at the point  $-\hat{\mu}_a$  in  $\mathbb{C}$ . But (3.21) implies that this circle is contained entirely in the open left half-plane  $\text{Re } z < 0$ , giving a contradiction. Thus,  $f = 0$  has no roots with  $\text{Re } z \geq 0$ , as claimed.

With the bar denoting complex conjugation,  $\overline{f(z)} = f(\bar{z})$  and  $\overline{g(z)} = g(\bar{z})$ , and therefore it is enough to check that  $|f(z)| > |g(z)|$  on the upper half  $\text{Im } z \geq 0$  of the contour  $\Gamma_R$ . Thus, for the curved part,  $z = Re^{i\theta}$  with  $\theta \in [0, \pi/2]$ . The function  $k$  defined in (3.20) can be expressed in the form

$$k(x) = \int_0^1 e^{-\xi x} d\xi, \tag{3.24}$$

and therefore

$$|k(Re^{i\theta})| \leq \int_0^1 |\exp(-\xi Re^{i\theta})| d\xi = \int_0^1 \exp(-\xi R \cos \theta) d\xi \leq 1$$

and, similarly,

$$|k(Re^{i\theta} + \hat{\mu}_i)| \leq \int_0^1 \exp(-\xi(R \cos \theta + \hat{\mu}_i)) d\xi \leq \int_0^1 e^{-\xi \hat{\mu}_i} d\xi = k(\hat{\mu}_i).$$

These estimates, and standard triangle inequalities for sums and differences of complex numbers, yield

$$|g(Re^{i\theta})| \leq \frac{|\varepsilon| |B'(A^*)|(R + \hat{\mu}_i)k(\hat{\mu}_i)}{1 - |\varepsilon|}.$$

Similarly,

$$\begin{aligned} |f(Re^{i\theta})| &\geq \left| \frac{P_0(I^*)}{l}(Re^{i\theta} + \hat{\mu}_a) \right| - |B'(A^*)| \exp(-(Re^{i\theta} + \hat{\mu}_i)) \\ &\geq \frac{P_0(I^*)}{l}(R - \hat{\mu}_a) - |B'(A^*)| \exp(-(R \cos \theta + \hat{\mu}_i)) \\ &\geq \frac{P_0(I^*)}{l}(R - \hat{\mu}_a) - |B'(A^*)| \exp(-\hat{\mu}_i). \end{aligned}$$

Therefore, on the curved part of the contour  $\Gamma_R$ , we have  $|f(z)| > |g(z)|$  if

$$\frac{P_0(I^*)}{l}(R - \hat{\mu}_a) - |B'(A^*)| \exp(-\hat{\mu}_i) > \frac{|\varepsilon| |B'(A^*)| (R + \hat{\mu}_i) k(\hat{\mu}_i)}{1 - |\varepsilon|}. \tag{3.25}$$

But assumption (3.22) implies that

$$\frac{P_0(I^*)}{l} > \frac{|\varepsilon|}{1 - |\varepsilon|} |B'(A^*)| k(\hat{\mu}_i) \tag{3.26}$$

holds, and therefore it follows that (3.25) is true for all  $R$  sufficiently large.

On the upper half of the straight part of the contour  $\Gamma_R$ ,  $z = iy$  with  $y \in [0, R]$ . It is easy to show that  $|k(iy)| \leq 1$ ,  $|k(iy + \hat{\mu}_i)| \leq k(\hat{\mu}_i)$  and  $|1 + \varepsilon k(iy)| \geq 1 - |\varepsilon| |k(iy)| \geq 1 - |\varepsilon|$ , and therefore

$$|g(iy)| = \frac{|\varepsilon| |B'(A^*)| |iy + \hat{\mu}_i| |k(iy)| |k(iy + \hat{\mu}_i)|}{|1 + \varepsilon k(iy)|} \leq \frac{|\varepsilon| |B'(A^*)| \sqrt{y^2 + \hat{\mu}_i^2} k(\hat{\mu}_i)}{1 - |\varepsilon|}.$$

Similarly,

$$|f(iy)| \geq \frac{P_0(I^*)}{l} |iy + \hat{\mu}_a| - |B'(A^*)| |e^{-(iy + \hat{\mu}_i)}| = \frac{P_0(I^*)}{l} \sqrt{y^2 + \hat{\mu}_a^2} - |B'(A^*)| e^{-\hat{\mu}_i}.$$

We claim that  $|f(iy)| > |g(iy)|$  for all  $y \in [0, \infty)$ , and this is the case if

$$\frac{P_0(I^*)}{l} \sqrt{y^2 + \hat{\mu}_a^2} - \frac{|\varepsilon| |B'(A^*)| \sqrt{y^2 + \hat{\mu}_i^2} k(\hat{\mu}_i)}{1 - |\varepsilon|} > |B'(A^*)| e^{-\hat{\mu}_i} \quad \forall y \in [0, \infty). \tag{3.27}$$

We now prove (3.27). The left-hand side has the structure

$$A_1 \sqrt{y^2 + \alpha^2} - A_2 \sqrt{y^2 + \beta^2},$$

and routine differentiation shows that it is a monotonic increasing function of  $y \in [0, \infty)$  if

$$\sqrt{\frac{y^2 + \beta^2}{y^2 + \alpha^2}} > \frac{A_2}{A_1} \quad \forall y \in [0, \infty),$$

i.e. if

$$\min \left( 1, \frac{\beta}{\alpha} \right) > \frac{A_2}{A_1},$$

which is the origin of assumption (3.22). With its left-hand side being monotonically increasing in  $y$ , (3.27) holds for all  $y \in [0, \infty)$  if and only if it holds when  $y = 0$ ,

and the latter is guaranteed by assumption (3.23). Thus,  $|f| > |g|$  on the straight part of the contour  $\Gamma_R$ .

We have now shown that  $|f(z)| > |g(z)|$  on all parts of  $\Gamma_R$ . By Rouché's theorem, the full characteristic equation (3.19) has the same number of roots in  $\operatorname{Re} z > 0$  as does  $f = 0$ , i.e. none at all. The absence of roots of (3.19) on the imaginary axis follows from what has just been shown, since such a root would imply the existence of a real  $y$  such that  $f(iy) = -g(iy)$ , contradicting  $|f(iy)| > |g(iy)|$  for all  $y \in [0, \infty)$ . Thus, all roots of (3.19) satisfy  $\operatorname{Re} \lambda < 0$ , completing the proof.  $\square$

#### 4. Conclusion

In this paper, a system of state-dependent delay differential equations is formulated to describe the population growth of a species in which maturation of larvae is triggered by size rather than chronological age, and in which individual larvae grow at a rate that decreases as the total number of larvae increases, thereby modelling intra-specific competition among larvae. By introducing a new size-like independent variable, which amounts to adopting the physiological time-scale for larvae, the system is transformed into a system with constant and distributed delays, which is a simplification in some respects. In a previous study, Smith [15] took the growth rate of individual larvae to be a function of the total number of adults, not larvae. Both his study and ours yield differential equations with state-dependent delays determined from threshold conditions, and similar mathematical challenges. An important difference between our work in this paper and that of Smith [15] is that in this paper  $A(t)$  and  $I(t)$  are determined from a fully coupled system. Smith [15], based on his different assumption for larval growth rate, was able to decouple his equations and derive a single delay differential equation for the number of adults.

For our model we established some boundedness results that, very importantly, hold even for unbounded birth functions within certain restrictions. This is important because it is not always reasonable to treat birth functions as bounded. Boundedness of the birth function  $B(A)$  implies that the per-capita egg-laying rate  $B(A)/A$  decreases to arbitrarily low levels as the adult population increases. This is perfectly reasonable in many scenarios since one expects the adults to be in strong competition with each other for food. However, it is not always a reasonable assumption, particularly in the case of a species in which larvae are confined to small spaces but adults can easily move to new territory. Our argument is that, for such species, intra-specific competition might affect mainly the larvae, with relatively little competition among adults so that unbounded birth functions become realistic. In our model, with unbounded birth functions the populations themselves may still be bounded because large numbers of larvae restrict the development of individual larvae, prolonging their maturation, reducing the probability of maturing into adults and thereby limiting the adult population which, in turn, limits the egg-laying rate.

We also proved a theorem on the local stability of any equilibrium, showing in particular that if an equilibrium is locally stable in the absence of competition among larvae, then it remains stable in the presence of competition if the competitive effect is sufficiently weak in a quantifiable sense. The proof illustrates one possible approach to tackling the characteristic equation, which is difficult and of a form that does not yield to standard and frequently applied techniques.



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