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Age-dependent intra-specific competition in pre-adult life stages and its effects on adult population dynamics

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Intra-specific competition in insect and amphibian species is often experienced in completely different ways in their distinct life stages. Competition among larvae is important because it can impact on adult traits that affect disease transmission, yet mathematical models often ignore larval competition. We present two models of larval competition in the form of delay differential equations for the adult population derived from age-structured models that include larval competition. We present a simple prototype equation that models larval competition in a simplistic way. Recognising that individual larvae experience competition from other larvae at various stages of development, we then derive a more complex equation containing an integral with a kernel that quantifies the competitive effect of larvae of age \bar{a} on larvae of age a . In some parameter regimes, this model and the famous spruce budworm model have similar dynamics, with the possibility of multiple co-existing equilibria. Results on boundedness and persistence are also proved.

Key words: Competition, larva, juvenile, stage-structure, delay, stability

1 Introduction

Mathematical models of populations often divide the population into immature and mature individuals. In insect and amphibian species, immature individuals are those passing through larval and other pre-adult life stages and, if maturation is triggered by age, can be defined as those of age less than some fixed threshold age τ , the age at which sexual activity begins. Mature individuals are those of age exceeding τ . With a denoting age and a variable $u(t, a)$ defined as the age density of the species at time t , it is common practice to start with a McKendrick–von Foerster equation. In the case of a single species, and in the absence of larval competition, a simple reasonable starting point is

$$\left(\frac{\partial}{\partial t} + \frac{\partial}{\partial a}\right) u(t, a) = \begin{cases} -\mu_l u(t, a), & 0 < a < \tau, \\ -\mu_m u(t, a), & a > \tau, \end{cases} \quad (1.1)$$

subject to the boundary condition $u(t, 0) = b(A(t))$, where $A(t) = \int_{\tau}^{\infty} u(t, a) da$ is the total number of sexually mature adults and the function $b(\cdot)$ is the egg-laying rate. In (1.1), μ_l and μ_m are the per-capita death rates for immature (larval) and mature individuals (the subscripts l and m meaning larval and mature, respectively). Model (1.1) is a particular case of the model we present in Section 2.1, and one can reformulate it as the following delay differential equation for $A(t)$:

$$\frac{dA(t)}{dt} = e^{-\mu_l \tau} b(A(t - \tau)) - \mu_m A(t), \quad (1.2)$$

which is equation (2.8) of this paper, in the case $k_l = 0$. A significant problem with this approach is that it presumes that competitive effects occur only among the adults. In fact the competition effect is modelled solely by the choice of $b(\cdot)$. This function might level off or even decrease at large densities due to competition among the adults for space or resources, and in this way we reason that their egg-laying rate is affected by this competition. Competition enters model (1.2) in no other way. Model (1.2) assumes that there is no competition among immature individuals – they simply experience a density-independent per-capita death rate μ_l throughout their development.

In this paper, we are interested in larval competition and how it might affect adult population dynamics. The modelling of competition among larvae raises interesting issues, some of which were considered in a series of papers from the early 1980s by Gurney, Nisbet and their co-workers. The idea that maturation would be triggered by age, with individuals maturing on reaching a fixed threshold age τ , as in (1.2), is only one possibility. Nisbet and Gurney [11] remark that if maturation were actually triggered by size or weight, then the immediate effect of larval competition is to slow down the growth of larvae, with the possible consequence of delaying maturation and reducing egg to adult survival. The time required to reach maturity would then become dependent on larval density and become a function of time t . Such scenarios often give rise to threshold type delay equations (Gurney and Nisbet [6]). Moeller *et al.* [9] discuss the mechanisms by which maturation is triggered in *Drosophila*, and they seem to include a series of assessments by the endocrine system to ensure that enough growth has been completed to produce an adult of the correct size. In these circumstances, maturation time again becomes a function of time t . Even if maturation were triggered by age, slower growth would likely imply smaller size on maturation, possibly lowering fecundity in adults (especially if adults do not feed), and increasing risks of mortality in pupation. Nisbet and Gurney [10] model competition among larvae for food by coupling their equations for the numbers of larvae and adults to another differential equation describing food dynamics. The idea of cohort competition (competition only among individuals of the same age or size) is raised in Gurney *et al.* [7]. In the present paper, larvae compete with larvae and adults with adults but individual larvae do not necessarily compete only with others at the same stage of development.

In this paper, we retain the idea that maturation is triggered by age and occurs at a fixed age τ . This simplification allows us to deal to some extent with the significant mathematical complications resulting from the possibility that a larva may face competition not only from other larvae of its own age but potentially from all larvae (though not from adults). In fact, we aim for a model that is general enough to allow for a wide range of possibilities including the two particular cases of equal competition from all larvae, and competitive

pressure only from older larvae in the form of intimidatory tactics or cannibalism, which is common in amphibians in early life stages (see, for example, Crump [2], Rosen [13] and Wells [16]), and can be complicated by various factors (for example, cannibalistic tadpoles may try to avoid eating kin (Pfennig [12])). Our modelling assumptions should be realistic for some insect and amphibian species that undergo metamorphosis, especially if larvae and adults have a different diet and are adapted to different environments. In amphibians, larvae often live in an aquatic environment and the adults in a terrestrial one, as is usually the case for the urodeles, a carnivorous order that includes salamanders (Wells [16]). On the other hand, in beetles of the genus *helichus* the larvae are terrestrial and the adults are aquatic, living mostly in running water (Clifford [1]). Some beetles are aquatic as both larvae and adults, for example the *elmidae* (riffle beetles). The modelling in this paper may not be so realistic for such species due to an increased likelihood of competition between larvae and adults.

In Section 2.1, we briefly present a simple way to model intra-specific competition among the larvae of a species, by simply introducing an additional, quadratic, death term so that (2.3) becomes the starting point. This leads to a delay equation, equation (2.8), that is a little more complicated than (1.2) but still belongs to the same (well studied) class of equations. Equation (2.8) has similarities to the well-known Nicholson's blowflies equation [5], but with a more complicated maturation rate incorporating a parameter k_l that quantifies immature competition. A problem with this approach is that it assumes individual larvae only compete with others at their own stage of development. Nevertheless, we propose (2.8) as a simple prototype model for larval competition that could perhaps be suitable as a starting point for modelling populations that experience immature life stage competition. Model (2.8) incorporates competition among adults, via the birth function $b(\cdot)$. Thus, both immature and mature competition are catered for in (2.8), in simple but completely different ways. Solutions of the prototype model (2.8) are bounded for any birth function.

The heart of this paper is the model we derive in Section 2.2. Here, we aim to recognise that in reality a larva does not compete only with other larvae at its own stage of development. It is more realistic to assume that an individual larva competes with all other larvae, since they all compete for space and resources. Sometimes this competitive pressure might come equally from all larvae irrespective of age, while in other situations it might be age-specific. For example, individuals might be subject to competition only from older larvae who seek preferential access to food, as is often the case with tadpoles. We aim for a model formulation that is sufficiently general to cover these possibilities, with (2.9) as the starting point and (2.19) as one version of the model it leads to, in the case when the larval competition effect is not too strong. This model is again a delay equation for the total number of adults $A(t)$, but it no longer belongs to the same class as (1.2).

It seems to be common practice to assume that the egg-laying rate $b(\cdot)$ should level off or even drop at high densities, due to intra-specific competition among adults, and therefore to treat $b(\cdot)$ as bounded. We feel that in some situations intra-specific competition might be experienced mainly at the larval stage, with adults able to avoid it by simply invading new territory, especially in the case of an invasive species. We therefore question the validity of the common assumption that $b(\cdot)$ should be bounded, and we have aimed

for an understanding of the properties of model (2.19) even for unbounded choices for $b(\cdot)$ including consideration of the case when $b(\cdot)$ is linear (the model (2.19) itself is still non-linear). A central result of this paper is that, if competition among adults is important and modelled through an appropriate (non-linear and non-monotone) $b(\cdot)$, then the model may have multiple positive equilibria and have similar properties to the famous spruce budworm model, including the possibility of co-existing refuge and outbreak equilibria. Numerical simulations confirm the predictions.

2 Model derivation

2.1 A simple prototype model

Gourley and Liu [3] recently derived a scalar delay differential equation for the total number $A(t)$ of adult individuals in a population the immature members of which experience intra-specific competition. They derived a general equation corresponding to the use of a general function to describe the larval competition. In the particular case when the competition is modelled by a quadratic term, their equation is equation (2.8) below, and for convenience we present here a self-contained derivation of that equation.

Immature individuals are defined as individuals of age less than some threshold age τ , while adults are individuals of age exceeding τ . Letting $u(t, a)$ be the density of individuals at time t of age a , using a standard age-structured modelling approach, we may write

$$\frac{\partial u(t, a)}{\partial t} + \frac{\partial u(t, a)}{\partial a} = -\mu_l u(t, a) - k_l (u(t, a))^2, \quad 0 < a < \tau \quad (2.3)$$

as a model for the evolution of the larval population, where we include the usual linear death term $\mu_l u(t, a)$ plus an additional quadratic term with coefficient k_l which models the effect of intra-specific competition among larvae for space or resources, and the subscript l stands for larvae. The adult insects are assumed to be governed by

$$\frac{\partial u(t, a)}{\partial t} + \frac{\partial u(t, a)}{\partial a} = -\mu_m u(t, a), \quad a > \tau \quad (2.4)$$

where μ_m is the per-capita death rate for mature (adult) insects. Now, $u(t, 0)$ is the birth rate (egg-laying rate) and if we assume that this is some function $b(\cdot)$ of the total number of adults $A(t)$, then we may write

$$u(t, 0) = b(A(t)), \quad \text{where } A(t) = \int_{\tau}^{\infty} u(t, a) da. \quad (2.5)$$

Differentiating the expression for $A(t)$ in (2.5) and using (2.4) and assuming that $\lim_{a \rightarrow \infty} u(t, a) = 0$, we obtain

$$\frac{dA(t)}{dt} = u(t, \tau) - \mu_m A(t). \quad (2.6)$$

Next, we calculate $u(t, \tau)$ in terms of $u(t - \tau, 0)$, and hence in terms of $A(t - \tau)$, by integrating (2.3) along characteristics. This is most easily achieved by introducing the

function $u^\xi(a) = u(a + \xi, a)$. Using (2.3),

$$\frac{du^\xi(a)}{da} = \left[\frac{\partial u(t, a)}{\partial t} + \frac{\partial u(t, a)}{\partial a} \right]_{t=a+\xi} = [-\mu_l u(t, a) - k_l(u(t, a))^2]_{t=a+\xi}$$

so that

$$\frac{du^\xi(a)}{da} = -\mu_l u^\xi(a) - k_l(u^\xi(a))^2.$$

Therefore

$$u^\xi(a) = \frac{\mu_l u^\xi(0) e^{-\mu_l a}}{\mu_l + k_l u^\xi(0) (1 - e^{-\mu_l a})} \tag{2.7}$$

and, since $u^\xi(0) = u(\xi, 0) = b(A(\xi))$,

$$u(a + \xi, a) = \frac{\mu_l b(A(\xi)) e^{-\mu_l a}}{\mu_l + k_l b(A(\xi)) (1 - e^{-\mu_l a})}.$$

Choosing $a = \tau$ and $\xi = t - \tau$ gives an expression for $u(t, \tau)$, and when this is inserted into (2.6), we obtain a delay differential equation for the variable $A(t)$:

$$\frac{dA(t)}{dt} = \frac{\mu_l e^{-\mu_l \tau} b(A(t - \tau))}{\mu_l + k_l (1 - e^{-\mu_l \tau}) b(A(t - \tau))} - \mu_m A(t). \tag{2.8}$$

Equation (2.8) is suggested in Gourley and Liu [3] as a prototype model for a single population the larval members of which experience intra-specific competition as modelled by a quadratic death term. It could be considered as an alternative to the logistic equation, or equation (1.2), as a simple model for limited population growth in situations where immature (e.g. larval) individuals experience competition. Competition among adults is described solely by the egg-laying rate $b(\cdot)$, which could be any function. If in fact there is little competition between adults then one could choose $b(\cdot)$ as linear. These points could be important, for example, in modelling invasive populations. The larvae of such species may have no or limited ability to move and therefore compete for space or resources. But the adults can move to find new territory and, in the case of an invasive species, adults may experience little or no competition and effectively unlimited space and food resources.

Equation (2.8) belongs to the class of well-studied population models of the form $A'(t) = F(A(t - \tau)) - \mu_m A(t)$ that include the Nicholson's blowflies equation and the Mackey–Glass equation; see for example Kuang [8] or Smith [15]. It generates a monotone dynamical system if $b(\cdot)$ is monotone increasing. Periodic solutions will exist in some situations. It was shown in [3] that the solution $A(t)$ of (2.8) is bounded for *any* egg-laying rate $b(\cdot)$.

2.2 Age-dependent larval competition

A difficulty with equation (2.3) is the assumption that a larva at a particular stage in its development only competes with other larvae of its own age. In practice, an individual larva is likely to also compete with larvae of other ages, quite possibly with other larvae at all stages of development since they all compete for space and resources. In some

situations, a larva may only experience competition from older larvae since the latter may cannibalise or exhibit intimidatory tactics towards younger larvae to obtain preferential access to food (Crump [2], Rosen [13], Wells [16]). These issues can be accommodated by using, rather than (2.3), the following equation as a starting point:

$$\frac{\partial u(t, a)}{\partial t} + \frac{\partial u(t, a)}{\partial a} = -\mu_l u(t, a) - \epsilon u(t, a) \int_0^\tau p(a, \bar{a}) u(t, \bar{a}) d\bar{a}, \quad 0 < a < \tau \quad (2.9)$$

in which the variables have the same meaning as in Section 2.1. The parameter ϵ measures the intensity of the competition among the larvae. If a larva experiences the same competition pressure from all other larvae, irrespective of age, then we could take $p(a, \bar{a})$ to be constant. Or, we could choose $p(a, \bar{a})$ such that $p(a, \bar{a}) = 0$ when $\bar{a} < a$, implying that an individual only experiences competition from older individuals. In the case when $p(a, \bar{a}) = \delta(a - \bar{a})$, where $\delta(\cdot)$ is the Dirac delta function, and $\epsilon = k_l$, equation (2.9) reduces to (2.3).

In the case when ϵ is small, it is possible to derive a delay differential equation comparable to (2.8) for the total number of adults $A(t)$. Concerning those adults, we still assume (2.4) and (2.5), and therefore (2.6) still holds. It is necessary to calculate $u(t, \tau)$, and to do so we now need to use (2.9). We proceed on the assumption that ϵ is small and use perturbation theory. There are two reasonable ways to do so, and the first is to seek a solution of (2.9) of the form

$$u(t, a) = u_0(t, a) + \epsilon u_1(t, a) + O(\epsilon^2) \quad (2.10)$$

with the birth rate $u(t, 0)$ given by $u(t, 0) = b(A(t))$ so that

$$u_0(t, 0) = b(A(t)), \quad u_n(t, 0) = 0, \quad n = 1, 2, \dots \quad (2.11)$$

Substituting into (2.9) and comparing coefficients of ϵ^0 gives

$$\frac{\partial u_0(t, a)}{\partial t} + \frac{\partial u_0(t, a)}{\partial a} = -\mu_l u_0(t, a), \quad 0 < a < \tau; \quad u_0(t, 0) = b(A(t)) \quad (2.12)$$

and for $t > a$ the solution of this is

$$u_0(t, a) = b(A(t - a))e^{-\mu_l a}. \quad (2.13)$$

Comparing coefficients of ϵ , and using (2.13) gives

$$\begin{aligned} \frac{\partial u_1(t, a)}{\partial t} + \frac{\partial u_1(t, a)}{\partial a} &= -\mu_l u_1(t, a) \\ &\quad - b(A(t - a))e^{-\mu_l a} \int_0^\tau p(a, \bar{a}) b(A(t - \bar{a}))e^{-\mu_l \bar{a}} d\bar{a}. \end{aligned} \quad (2.14)$$

This is easily converted into an ordinary differential equation for the function $u_1^\xi(a) = u_1(a + \xi, a)$, and when it is solved using the condition $u_1^\xi(0) = u_1(\xi, 0) = 0$, we obtain

$$u_1(a + \xi, a) = -e^{-\mu_l a} \int_0^a b(A(\xi)) \int_0^\tau p(s, \bar{a}) b(A(s + \xi - \bar{a}))e^{-\mu_l \bar{a}} d\bar{a} ds.$$

Setting $\xi = t - a$,

$$u_1(t, a) = -e^{-\mu_1 a} \int_0^a b(A(t-a)) \int_0^\tau p(s, \bar{a}) b(A(s+t-a-\bar{a})) e^{-\mu_1 \bar{a}} d\bar{a} ds. \quad (2.15)$$

We calculate $u(t, \tau)$ from (2.10), (2.13) and (2.15), and insert the result into (2.6) to obtain the following delay differential equation for the number of adults $A(t)$:

$$\begin{aligned} \frac{dA(t)}{dt} = & -\mu_m A(t) \\ & + b(A(t-\tau)) e^{-\mu_1 \tau} \left[1 - \epsilon \int_0^\tau \int_0^\tau p(s, \bar{a}) b(A(s+t-\tau-\bar{a})) e^{-\mu_1 \bar{a}} d\bar{a} ds \right]. \end{aligned} \quad (2.16)$$

The second perturbation approach to solving (2.9) is to attempt a solution of the form

$$u(t, a) = u_0(t, a) \exp(-\epsilon u_1(t, a) + O(\epsilon^2)). \quad (2.17)$$

With this ansatz, u_0 again satisfies (2.12) and is given by (2.13). However, this time the powers of ϵ yield that u_1 satisfies

$$\frac{\partial u_1(t, a)}{\partial t} + \frac{\partial u_1(t, a)}{\partial a} = \int_0^\tau p(a, \bar{a}) b(A(t-\bar{a})) e^{-\mu_1 \bar{a}} d\bar{a} \quad (2.18)$$

subject to $u_1(t, 0) = 0$. Again with the aid of the function $u_1^\xi(a) = u_1(a + \xi, a)$, we solve this for $u_1(t, a)$, and find that

$$u_1(t, \tau) = \int_0^\tau \int_0^\tau p(s, \bar{a}) b(A(s+t-\tau-\bar{a})) e^{-\mu_1 \bar{a}} d\bar{a} ds.$$

Then, $u(t, \tau) = u_0(t, \tau) \exp(-\epsilon u_1(t, \tau))$ and, from (2.6), the outcome of this perturbation approach is that $A(t)$ satisfies

$$\begin{aligned} \frac{dA(t)}{dt} = & -\mu_m A(t) \\ & + b(A(t-\tau)) e^{-\mu_1 \tau} \exp\left(-\epsilon \int_0^\tau \int_0^\tau p(s, \bar{a}) b(A(s+t-\tau-\bar{a})) e^{-\mu_1 \bar{a}} d\bar{a} ds\right). \end{aligned} \quad (2.19)$$

Equations (2.16) and (2.19) provide two alternative models for the adult population $A(t)$ where the larvae experience competition as described by (2.9) for small ϵ . Equation (2.19) is arguably better because it is in a form that guarantees that the solution $A(t)$ will remain positive for all time (Smith [14], page 81). If in (2.19) the exponential containing the double integral in its argument is expanded for small ϵ , (2.19) reduces to (2.16). If $p(a, \bar{a}) = \delta(a - \bar{a})$ and $\epsilon = k_l$ is small, (2.16) becomes

$$\frac{dA(t)}{dt} = -\mu_m A(t) + b(A(t-\tau)) e^{-\mu_1 \tau} \left(1 - \frac{k_l}{\mu_l} (1 - e^{-\mu_l \tau}) b(A(t-\tau)) \right)$$

which coincides with the equation obtained by expanding the right-hand side of (2.8) for small k_l .

We focus mainly on (2.19), but some comments may be made that apply to both (2.16) and (2.19). These equations retain the function $p(a, \bar{a})$ in (2.9) in its full generality. The delay in the right-hand side of either differential equation involves values of $A(\cdot)$ extending back to time $t - 2\tau$, but no further back. This can be understood as follows. In the double integral, the dummy variable s is the age of an individual at a particular stage in its development, and \bar{a} is the age of another individual that was exerting competition pressure on the individual at that stage. Both ages have to be summed over, hence the double integral. If the individual experiencing competition matures at time t , then it was born at time $t - \tau$ and was of age s at time $s + t - \tau$. At that instant, some of the competing individuals were of age \bar{a} , those individuals were born at time $s + t - \tau - \bar{a}$, the birth rate at that time was $b(A(s + t - \tau - \bar{a}))$ and they survived to age \bar{a} . If one ignores the fact that those individuals themselves experienced competition during their development, then the probability of surviving to age \bar{a} is $\exp(-\mu\bar{a})$ and the term $b(A(s + t - \tau - \bar{a}))e^{-\mu\bar{a}}$ in the integrand is the rate at which the competing individuals pass through age \bar{a} . The latter expression also equals $u_0(s + t - \tau, \bar{a})$ which is the solution of the unperturbed problem with $\epsilon = 0$. These remarks help us to understand how the perturbation solution procedure works both mathematically and ecologically. It recognises that a maturing larva experiences competition from all other larvae including older larvae but it fails, at the order to which we have carried out the computations, to recognise that those older competing larvae also experienced competition in their own development. In theory, carrying out the perturbation procedure to higher orders could correct for this, but the calculations rapidly become intractable.

For the rest of this paper, we focus on (2.19) as it has a positivity preserving property under minimal assumptions. Although ϵ was treated as a small parameter for purposes of the model derivation, we will henceforth assume that equation (2.19) remains reasonable as a model for the adult population even in the presence of stronger larval competition. Thus, in the subsequent analysis, ϵ is just an arbitrary positive number.

3 Model analysis

In this section, we study the properties of model (2.19), beginning with the positivity and boundedness of its solutions and later proceeding to a study of the equilibria and their stability. If $b(\cdot)$ is locally Lipschitz then local existence of a solution follows from standard results for delay equations since it is straightforward to show that the non-linear functional $H(\phi)$ defined in (3.34) is also locally Lipschitz.

3.1 Positivity and boundedness

In the literature, it is common for the birth function $b(\cdot)$ to be taken as bounded, and the justification is usually that intra-specific competition among adults limits egg production at high densities. However, as the emphasis of this paper is on competitive effects at the immature (larval) life stages, we have formulated a boundedness result (Proposition 3.3) that does not require the birth function $b(\cdot)$ to be bounded. Proposition 3.3 admits unbounded birth functions that satisfy (3.23). We feel this could be particularly important in modelling insects that readily disperse, and invasive insects in particular. Insect larvae

are sometimes confined to small habitats (aquatic, in the case of mosquitoes) in which they may experience strong intra-specific competition from other larvae, but the adults of insect species are in general more mobile and this raises the possibility that they might avoid competition for space or resources simply by moving into previously uninhabited territory. Therefore, we have aimed for results that do not require strong restrictions on the birth function $b(\cdot)$.

Proposition 3.1 *Suppose the birth function $b(\cdot)$ is non-negative, continuous and locally Lipschitz, and suppose that $A(s) = A_0(s) \geq 0$ for $s \in [-2\tau, 0]$, where $A_0(s)$ is a prescribed continuous initial function. Then, the solution $A(t)$ of (2.19), for as long as it exists, satisfies $A(t) \geq 0$.*

We omit the proof as it is a standard application of Theorem 5.2.1 on page 81 of Smith [14].

Lemma 3.2 *Suppose that $b(\cdot)$ is non-negative and continuous, and that there exists $A^0 > 0$ such that*

$$e^{-\mu_1 \tau} b(A) < \mu_m A \quad \text{for all } A > A^0. \tag{3.20}$$

Define the increasing upper hull \bar{b} of b as

$$\bar{b}(A) = \sup_{a \in [0, A]} b(a)$$

and define

$$\check{A} = \frac{e^{-\mu_1 \tau} \bar{b}(A^0)}{\mu_m}. \tag{3.21}$$

Then, \bar{b} is monotone increasing and continuous and $b(A) \leq \bar{b}(A)$ for all $A \geq 0$. Moreover, $\check{A} \geq A^0$ and

$$e^{-\mu_1 \tau} \bar{b}(A) < \mu_m A \quad \text{for all } A > \check{A}. \tag{3.22}$$

Finally, if $b(\cdot)$ is monotone increasing on $[0, A^0]$ then these results hold with \check{A} replaced by A^0 .

We omit the proof since a very similar result, with proof, appears in Gourley *et al.* [4]. Our main boundedness result is the following.

Proposition 3.3 *Suppose the birth function $b(\cdot)$ is non-negative, continuous and locally Lipschitz, and suppose there exists $A^0 > 0$ such that*

$$e^{-\mu_1 \tau} b(A) < \mu_m A \quad \text{for all } A > A^0. \tag{3.23}$$

Then, if the initial data $\{A_0(\theta), \theta \in [-2\tau, 0]\}$ is continuous and non-negative, the solution $A(t)$ of (2.19) remains bounded for all $t \geq 0$, more precisely

$$A(t) \leq \max \left\{ \check{A}, \max_{\theta \in [-2\tau, 0]} A_0(\theta) \right\} \tag{3.24}$$

and

$$\limsup_{t \rightarrow \infty} A(t) \leq \check{A}, \quad (3.25)$$

where \check{A} is defined in (3.21).

Moreover, if $b(A)$ is increasing for $0 \leq A \leq A^0$ then these results hold with $\check{A} = A^0$.

Proof Let $\sigma \in (0, \infty]$ be such that the solution $A(t)$ of (2.19) exists for $t \in [-2\tau, \sigma]$, with $A(t)$ differentiable on $(0, \sigma)$. For $t \in (0, \sigma)$,

$$\frac{dA(t)}{dt} \leq b(A(t - \tau))e^{-\mu_1\tau} - \mu_m A(t)$$

by (2.19). Now, let $r \in (0, \sigma)$. Since $A(t)$ is continuous it is bounded on $[-2\tau, r]$ and therefore it assumes its maximum on that interval at some value $t^* \in [-2\tau, r]$. If $t^* \in [-2\tau, 0]$ then $A(t) \leq \max_{\theta \in [-2\tau, 0]} A_0(\theta)$. Suppose that $t^* \in (0, r]$. Then, $A'(t^*) \geq 0$ and $A(t^*) \geq A(t^* - \tau)$. Suppose, for contradiction, that $A(t^*) > \check{A}$. Then, using the definition and properties of \bar{b} in Lemma 3.2,

$$\begin{aligned} 0 &\leq A'(t^*) \leq b(A(t^* - \tau))e^{-\mu_1\tau} - \mu_m A(t^*) \\ &\leq \bar{b}(A(t^* - \tau))e^{-\mu_1\tau} - \mu_m A(t^*) \\ &\leq \bar{b}(A(t^*))e^{-\mu_1\tau} - \mu_m A(t^*) \\ &< 0, \end{aligned}$$

since $A(t^*) > \check{A}$ and therefore (3.22) applies. This contradiction shows that $A(t^*) \leq \check{A}$ and so (3.24) follows for $t \in [-2\tau, r]$, and therefore also for $t \in [-2\tau, \sigma]$ since $r \in (0, \sigma)$ was arbitrary. Inequality (3.24) constitutes an a priori bound for $A(t)$, from which we may conclude that in fact $\sigma = \infty$.

By the fluctuation method (Thieme [17]), there exists a sequence $t_j \rightarrow \infty$ such that $A(t_j) \rightarrow A^\infty = \limsup_{t \rightarrow \infty} A(t)$ and $A'(t_j) \rightarrow 0$ as $j \rightarrow \infty$. But

$$\begin{aligned} A'(t_j) &\leq b(A(t_j - \tau))e^{-\mu_1\tau} - \mu_m A(t_j) \\ &\leq \bar{b}(A(t_j - \tau))e^{-\mu_1\tau} - \mu_m A(t_j). \end{aligned}$$

Let $\delta > 0$ be arbitrary. Then, for j sufficiently large, $A(t_j - \tau) \leq A^\infty + \delta$ and

$$A'(t_j) \leq \bar{b}(A^\infty + \delta)e^{-\mu_1\tau} - \mu_m A(t_j),$$

since \bar{b} is increasing. Letting $j \rightarrow \infty$, and then $\delta \rightarrow 0$, we find that

$$\bar{b}(A^\infty)e^{-\mu_1\tau} \geq \mu_m A^\infty$$

and it follows from Lemma 3.2 that $A^\infty \leq \check{A}$, so that (3.25) holds. \square

3.2 Equilibria

In this section, we study the equilibria of model (2.19) and their stability, always assuming that b is differentiable and that $b(0) = 0$ so that zero is an equilibrium. The analysis

is tractable up to a point but is numerically assisted. It turns out that for some birth functions, and some parameter domains, the model may have multiple positive equilibria while in other situations it may have only one positive equilibrium, or none. These different outcomes show a strong dependence on the choice of birth function $b(\cdot)$ and on parameters such as ϵ that measure the strength of larval competition. The possibilities are reminiscent of those associated with the much simpler spruce budworm model, which is often written down in non-dimensional form as

$$\frac{du}{dt} = ru \left(1 - \frac{u}{q} \right) - \frac{u^2}{1 + u^2} \tag{3.26}$$

in which the last term is a simple representation of predation by birds on a spruce budworm population $u(t)$ which otherwise grows logistically. In (3.26), suppose that q is given a sufficiently large fixed value and that r is viewed as a bifurcation parameter which is slowly increased from a very small value. Then, in addition to the zero equilibrium, (3.26) has one small (refuge) equilibrium if r is very small, three co-existing equilibria if r is intermediate and one large (outbreak) equilibrium if r is sufficiently large. The quadratic behaviour of the predation term for small u models the tendency of the birds to look elsewhere for food if there are very few budworm, since they are too hard to find. This allows the budworm to survive in low numbers at a stable equilibrium called a refuge equilibrium. For some values of r and q , stable refuge and outbreak equilibria may co-exist with an unstable equilibrium of intermediate size. In this situation, slowly raising or lowering a parameter and then restoring it to its original value can have the effect of permanently switching the population from the refuge to the outbreak equilibrium or vice versa, because of the tendency of the population not to leave a stable equilibrium.

It appears that our more complex model (2.19) can have similar properties to the spruce budworm model although this does depend on how the birth function $b(\cdot)$ is chosen. As explained earlier, to first order the larval competition effect is taken care of solely through the exponential term with the double integral in its argument, and ϵ can be considered as a measure of the strength of this competition.

The linear stability of the zero solution of (2.19) does not depend on ϵ . Even if larval competition as measured by ϵ is strong, the competitive effect weakens if the population gets low and extinction is only the outcome if the population would be doomed to extinction in the absence of competition. We therefore focus on the situation when the zero equilibrium is unstable. The condition for this emerges as a particular case of the linearised analysis for a general equilibrium and is

$$e^{-\mu\tau} b'(0) > \mu_m \tag{3.27}$$

which, of course, requires $b'(0) > 0$. Any non-zero equilibrium A_ϵ^* of (2.19) must satisfy

$$f(A_\epsilon^*) := b(A_\epsilon^*) e^{-\mu\tau} \exp \left(-\epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \right) = \mu_m A_\epsilon^* \tag{3.28}$$

Even in the case of a linear $b(A)$, the left-hand side of (3.28) is non-monotone as a function of A_ϵ^* although for a linear choice, the left-hand side behaves qualitatively like $A_\epsilon^* \exp(-A_\epsilon^*)$ and so at most one positive equilibrium can exist. However, if $b(A)$ is itself

non-monotone, for example if $b(A)$ has the form of the well-known Nicholson’s blowflies birthrate [5], then the left-hand side of (3.28) is highly non-monotone as a function of A_ϵ^* . It is in this kind of situation that there is the possibility of multiple positive equilibria for some parameter ranges, including the possibility of refuge and outbreak equilibria with the characteristics as summarised above for the spruce budworm model. Figures 1–3 show plots of the left- and right-hand sides of (3.28) in the case when $b(A) = rA \exp(-A/K)$ revealing, in Figure 2, the possibility of multiple positive equilibria for a window of values of ϵ .

Assume (3.27) holds and that $b(\cdot)$ is such that, when $\epsilon = 0$, (2.19) has a unique positive stable equilibrium A_0^* (conditions sufficient for this are embodied within the hypotheses of Theorem 3.4). As ϵ is increased from 0, A_0^* perturbs to a new equilibrium A_ϵ^* of (2.19) which is just below A_0^* , at least for small ϵ , as shown in Figure 1. Increasing ϵ further may cause new equilibria to appear, as shown in Figure 2, but for now we assume ϵ is small enough such that there is just one positive equilibrium A_ϵ^* . We show that A_ϵ^* is linearly stable for sufficiently small ϵ . Setting $A(t) = A_\epsilon^* + \bar{A}(t)$, substituting into (2.19) and linearising, we find that $\bar{A}(t)$ satisfies

$$\begin{aligned} \bar{A}'(t) = & -\mu_m \bar{A}(t) + e^{-\mu t} \exp \left(-\epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu \bar{a}} d\bar{a} ds \right) \\ & \times b'(A_\epsilon^*) \left(\bar{A}(t - \tau) - \epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu \bar{a}} \bar{A}(s + t - \tau - \bar{a}) d\bar{a} ds \right) \end{aligned} \quad (3.29)$$

and solutions of the form $\bar{A}(t) = \exp(\lambda t)$ exist whenever λ satisfies the characteristic equation

$$\begin{aligned} \lambda + \mu_m = & e^{-\mu t} \exp \left(-\epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu \bar{a}} d\bar{a} ds \right) \\ & \times b'(A_\epsilon^*) \left(e^{-\lambda \tau} - \epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu \bar{a}} e^{\lambda(s-\tau-\bar{a})} d\bar{a} ds \right) =: F(\lambda; A_\epsilon^*). \end{aligned} \quad (3.30)$$

This characteristic equation is not easy to analyse. Only at the zero equilibrium of (2.19), for which the characteristic equation is (3.30) with A_ϵ^* replaced by zero, is there an assurance that we can restrict attention to its real roots; this is because $b(0) = 0$ and $b'(0) > 0$ so that, in the case of the zero equilibrium, the only surviving delay term in the linearised equation (3.29) has a positive coefficient which allows the application of Theorem 5.5.1 in Smith [14]. At a positive equilibrium A_ϵ^* , the presence of the other delay term in (3.29), the term involving the double integral, makes those results inapplicable since the two delay terms have opposite sign. However, analytic progress is possible if ϵ is small. In Theorem 3.4, the hypotheses up to and including (3.31) imply the stability of the equilibrium A_0^* as a solution of the unperturbed problem (equation (2.19) with $\epsilon = 0$) – this follows from known results (Kuang [8]). Addition of the smallness hypothesis on ϵ guarantees that the perturbed equilibrium A_ϵ^* remains linearly stable as a solution of (2.19).

Theorem 3.4 *Suppose that $b(\cdot)$ is differentiable, that $b(0) = 0$ and that (3.27) holds. Suppose also that there exists $A_0^* > 0$ such that $e^{-\mu t} b(A) > \mu_m A$ when $0 < A < A_0^*$ and*

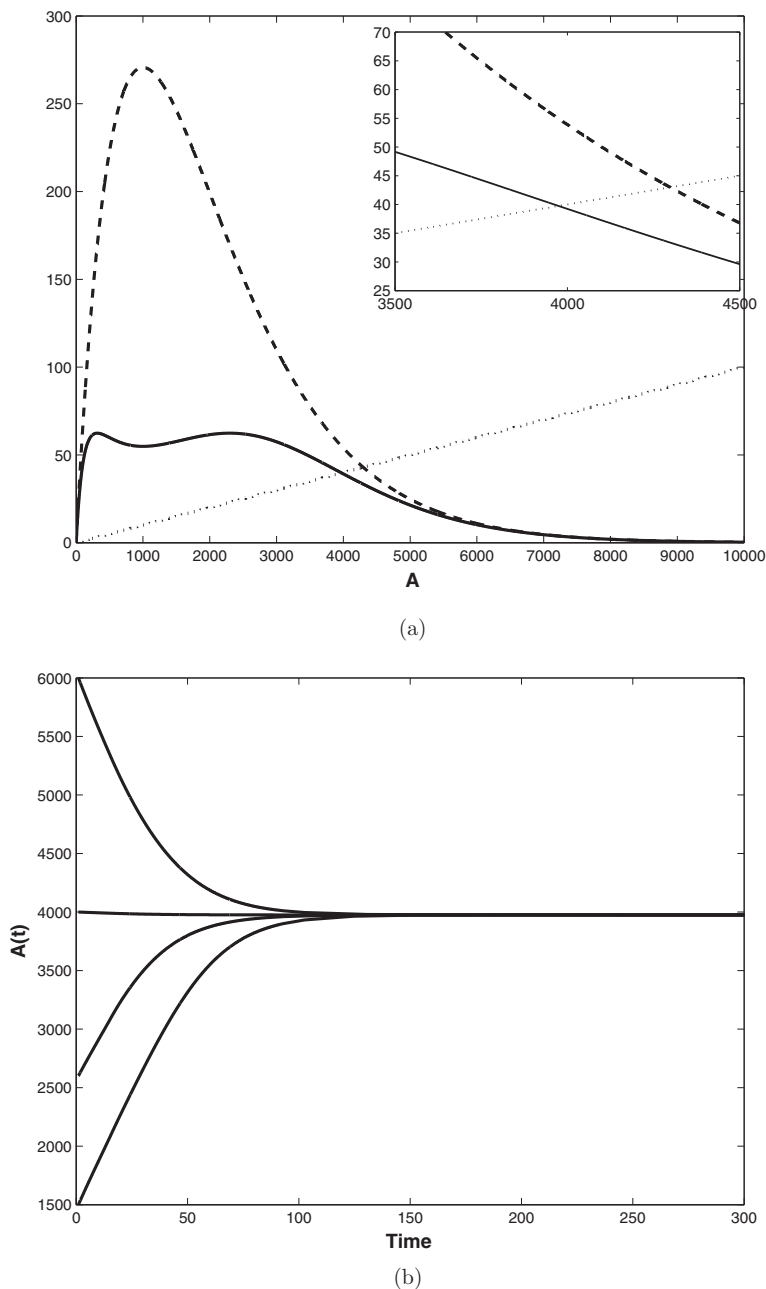


FIGURE 1. Simulation of (2.19) when $b(A) = rA \exp(-A/K)$, $r = 2$, $K = 1000$, $\mu_m = 1/100$, $\mu_L = 1/15$, $\tau = 15$, $\epsilon = 0.00005$ and $p(s, \bar{a}) \equiv p_0 = 0.305$. In this case, (2.19) has just one positive (outbreak) equilibrium. In panel (a), plots of the left- and right-hand sides of (3.28) against A_c^* reveal this equilibrium as the value of A at which the dotted line intersects the solid curve. The dashed curve is the left-hand side of (3.28) when $\epsilon = 0$. Evolution of $A(t)$ to the outbreak equilibrium is shown in panel (b). (a) The large outbreak equilibrium. (b) Evolution of $A(t)$ to the outbreak equilibrium.

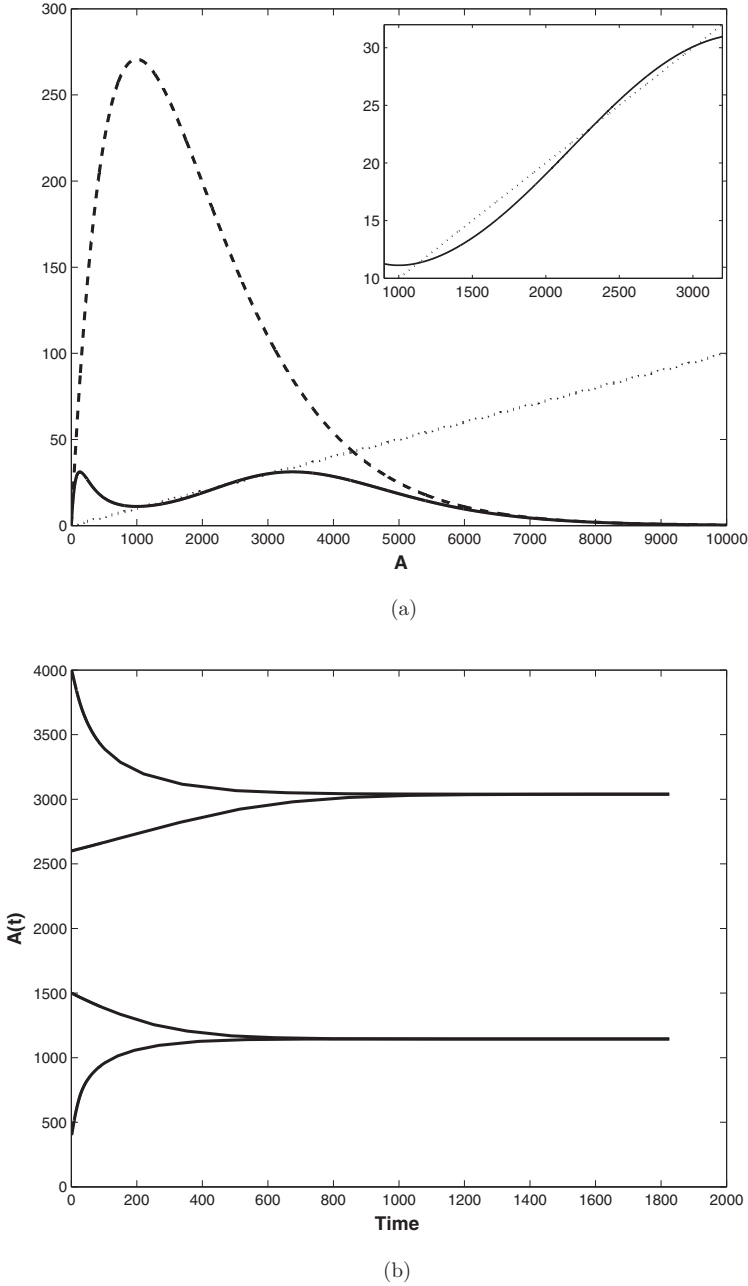
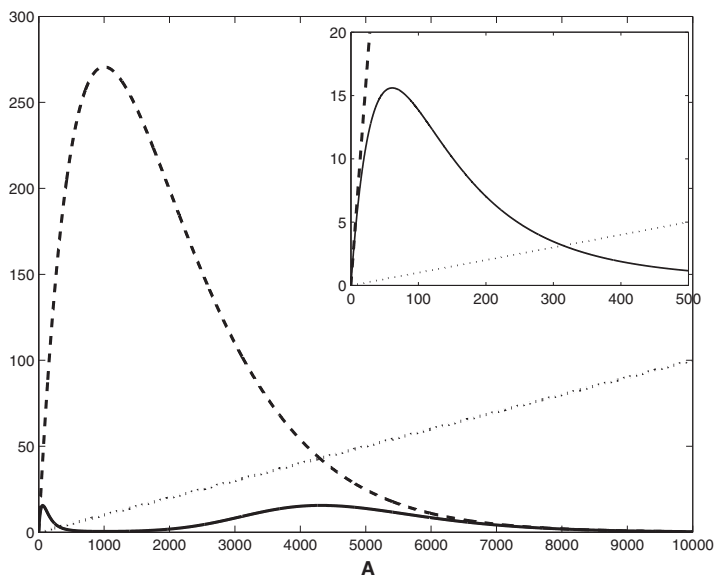
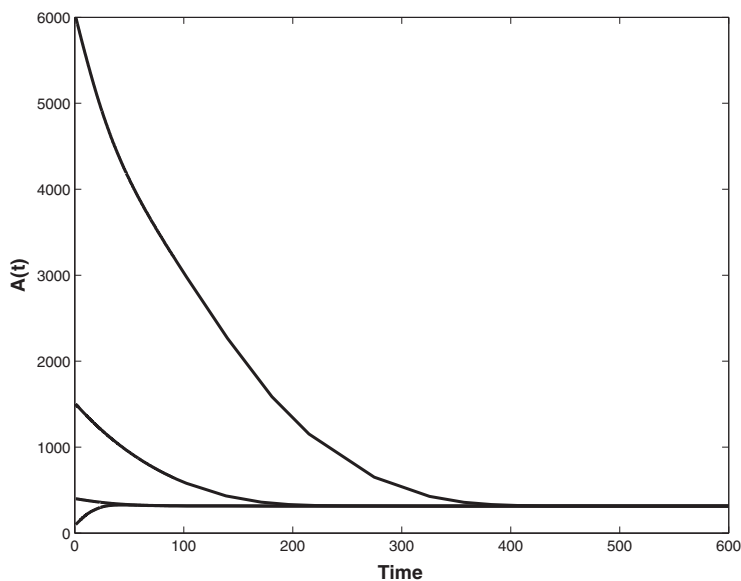


FIGURE 2. Simulation of (2.19) using parameter values and $b(A)$ from Figure 1, but with ϵ increased to $\epsilon = 0.0001$. Model (2.19) now has three positive equilibria and, in panel (a), plots of the left- and right-hand sides of (3.28) against A_c^* reveal these three equilibria as the values of A at which the dotted line intersects the solid curve. The dashed curve is the left-hand side of (3.28) when $\epsilon = 0$, in which case there is just one positive equilibrium. The evolution shown in panel (b) suggests that the smallest (refuge) and largest (outbreak) equilibria are both stable. (a) Multiple equilibria. (b) Evolution of $A(t)$ for various initial values.



(a)



(b)

FIGURE 3. Simulation of (2.19) using parameter values and $b(A)$ from Figure 1, except that ϵ has been increased to $\epsilon = 0.0002$ thereby increasing larval competition further. The effect of this increase is that model (2.19) now has just one small positive (refuge) equilibrium which is shown in panel (a) as the value of A at which the dotted line intersects the solid curve. The dashed curve shows the situation when $\epsilon = 0$. Panel (b) shows the evolution of $A(t)$ to the refuge equilibrium. (a) The small refuge equilibrium. (b) Evolution of $A(t)$ to the refuge equilibrium.

$e^{-\mu\tau}b(A) < \mu_m A$ when $A > A_0^*$, and suppose that

$$0 < e^{-\mu\tau}b'(A_0^*) < \mu_m. \tag{3.31}$$

Then, for sufficiently small ϵ , (2.19) has a unique positive equilibrium A_ϵ^* that is linearly asymptotically stable.

Proof Existence and uniqueness of the positive equilibrium A_ϵ^* for sufficiently small ϵ has already been discussed. The equilibrium A_ϵ^* has to satisfy $f(A_\epsilon^*) = \mu_m A_\epsilon^*$ with f defined in (3.28). Note that $f(0) = 0$ and $f'(0) > \mu_m$, by (3.27). A graph of the left- and right-hand sides of (3.28) plotted against A_ϵ^* makes it clear that the unique (for small ϵ) positive root A_ϵ^* of (3.28) must satisfy $f'(A_\epsilon^*) < \mu_m$, and the latter can be rewritten as

$$\begin{aligned} \mu_m > e^{-\mu\tau} \exp \left(-\epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \right) \\ \times b'(A_\epsilon^*) \left(1 - \epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \right) = F(0; A_\epsilon^*) \end{aligned} \tag{3.32}$$

with F defined in (3.30). In general, $f'(A_\epsilon^*)$ could be of either sign (it is negative in the situation illustrated in Figure 1). However, we assume here that $b'(A_0^*) > 0$ and so, by continuity, $b'(A_\epsilon^*) > 0$ and $F(0; A_\epsilon^*) > 0$ if ϵ is sufficiently small.

To show that A_ϵ^* is linearly stable, we start by showing that the *real* roots of (3.30) are negative when ϵ is sufficiently small, and then we show that any complex roots have negative real parts. Let $\delta > 0$ be sufficiently small that $F(0; A_\epsilon^*) + \delta < \mu_m$, which is possible by (3.32). For $\lambda \geq 0$,

$$\begin{aligned} & F(\lambda; A_\epsilon^*) - F(0; A_\epsilon^*) \\ &= b'(A_\epsilon^*) e^{-\mu\tau} \exp \left(-\epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \right) \\ & \times \left(e^{-\lambda\tau} - \epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} e^{\lambda(s-\tau-\bar{a})} d\bar{a} ds \right. \\ & \left. - 1 + \epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \right) \\ &\leq b'(A_\epsilon^*) e^{-\mu\tau} \exp \left(-\epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \right) \\ & \times \epsilon b(A_\epsilon^*) \left(-\int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} e^{\lambda(s-\tau-\bar{a})} d\bar{a} ds + \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \right) \\ &\leq b'(A_\epsilon^*) e^{-\mu\tau} \exp \left(-\epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \right) \\ & \times \epsilon b(A_\epsilon^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu\bar{a}} d\bar{a} ds \\ &< \delta \end{aligned}$$

for ϵ sufficiently small (note that A_ϵ^* remains bounded as a function of ϵ). Therefore, if ϵ

is sufficiently small then

$$F(\lambda; A_\epsilon^*) < F(0; A_\epsilon^*) + \delta < \mu_m \leq \lambda + \mu_m,$$

for all $\lambda \geq 0$, and it follows that (3.30) has no real positive roots λ .

As previously mentioned the two delay terms in (3.29) have opposite sign and there are no general results that would assure us that the dominant root of the characteristic equation (3.30) is real. However, we know that all real roots of (3.30) are negative, and this fact helps us to show that the real parts of any complex roots must also be negative. To see this, let $\lambda^*(\epsilon) < 0$ be the dominant real root (i.e. the real root closest to 0) for a particular ϵ . We claim that, for sufficiently small ϵ , any complex roots of (3.30) must have negative real parts. Suppose this is false. Then, there exists a sequence $\epsilon_j \rightarrow 0$, $j \in \mathbb{N}$, of values of ϵ such that for each j the dominant *complex* roots (the complex conjugate pair of roots that have greatest real part) $\lambda = x_j \pm iy_j$ of (3.30) have non-negative real part $x_j \geq 0$. Setting $\lambda = x_j \pm iy_j$ in (3.30) with $\epsilon = \epsilon_j$, taking the real part and using that

$$\text{Re} \left[e^{(x_j \pm iy_j)(s - \tau - \bar{a})} \right] \geq -e^{x_j(s - \tau - \bar{a})}$$

gives

$$\begin{aligned} x_j + \mu_m &\leq e^{-\mu_j \tau} \exp \left(-\epsilon_j b(A_{\epsilon_j}^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu_j \bar{a}} d\bar{a} ds \right) \\ &\times b'(A_{\epsilon_j}^*) \left(e^{-x_j \tau} + \epsilon_j b(A_{\epsilon_j}^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu_j \bar{a}} e^{x_j(s - \tau - \bar{a})} d\bar{a} ds \right). \end{aligned} \tag{3.33}$$

Subtracting (3.30), with $\epsilon = \epsilon_j$ and $\lambda = \lambda^*(\epsilon_j)$, from (3.33) gives

$$\begin{aligned} -\lambda^*(\epsilon_j) &\leq x_j - \lambda^*(\epsilon_j) \leq b'(A_{\epsilon_j}^*) e^{-\mu_j \tau} \exp \left(-\epsilon_j b(A_{\epsilon_j}^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu_j \bar{a}} d\bar{a} ds \right) \\ &\times \left(e^{-x_j \tau} - e^{-\lambda^*(\epsilon_j) \tau} + \epsilon_j b(A_{\epsilon_j}^*) \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu_j \bar{a}} \left[e^{x_j(s - \tau - \bar{a})} + e^{\lambda^*(\epsilon_j)(s - \tau - \bar{a})} \right] d\bar{a} ds \right). \end{aligned}$$

Now, consider what happens if we let $j \rightarrow \infty$. Then, $\epsilon_j \rightarrow 0$, $\lambda^*(\epsilon_j) \rightarrow \lambda^*(0) < 0$ and $A_{\epsilon_j}^* \rightarrow A_0^*$. We do not know so much about x_j , but the double integral in the second line is bounded in j because $x_j(s - \tau - \bar{a}) \leq 0$ and $\lambda^*(\epsilon_j)$ approaches $\lambda^*(0)$. Therefore, we may take the limit as $j \rightarrow \infty$ and conclude that

$$-\lambda^*(0) \leq b'(A_0^*) e^{-\mu_j \tau} \left(\liminf_{j \rightarrow \infty} e^{-x_j \tau} - e^{-\lambda^*(0) \tau} \right).$$

Since $\lambda^*(0) < 0$ it follows that

$$\liminf_{j \rightarrow \infty} e^{-x_j \tau} > e^{-\lambda^*(0) \tau}$$

and therefore, since the above inequality is strict, we have, for j sufficiently large, $x_j < \lambda^*(0) < 0$ which contradicts $x_j \geq 0$.

In summary, we have shown that all roots of (3.30) have negative real parts for sufficiently small ϵ . Hence, A_ϵ^* is linearly stable for such ϵ . □

3.3 Persistence

Next, we show that if zero is an unstable equilibrium of (2.19), then the population strongly uniformly persists. Denote by C , the Banach space of continuous real-valued functions on $[-2\tau, 0]$, equipped with the usual supremum norm $\|\cdot\|$. Let C_+ be the subset of C containing all positive functions. To denote a particular solution with initial function $\phi \in C_+$, we use the notation $A^\phi(t)$. Recall that if $A(0) > 0$ then the solution $A(t) > 0$ for all $t \geq 0$. The segment of a solution is denoted by $A_t = A_t^\phi \in C$ and defined by the relation $A_t(s) = A(t + s)$ for $s \in [-2\tau, 0]$. For any $\phi \in C_+$, we define $m^\phi := \liminf_{t \rightarrow \infty} A^\phi(t)$. We introduce the notation

$$H(\phi) := \exp \left(-\epsilon \int_0^\tau \int_0^\tau p(s, \bar{a}) b(\phi(s - \tau - \bar{a})) e^{-\mu \bar{a}} d\bar{a} ds \right) \tag{3.34}$$

for any $\phi \in C$. Then, (2.19) can be written as

$$A'(t) = -\mu_m A(t) + b(A(t - \tau)) e^{-\mu \tau} H(A_t).$$

Theorem 3.5 *Suppose that b is continuously differentiable, $b(0) = 0$, $b(A) > 0$ for $A > 0$, (3.20) holds and*

$$e^{-\mu \tau} b'(0) > \mu_m. \tag{3.35}$$

Then, there exists $\delta > 0$ such that

$$\liminf_{t \rightarrow \infty} A(t) \geq \delta \tag{3.36}$$

for any solution of (2.19) satisfying $A(\theta) \geq 0$ for $\theta \in [-2\tau, 0)$ and $A(0) > 0$.

Proof Choose a positive $q < 1$ such that $q^5 e^{-\mu \tau} b'(0) > \mu_m$ holds, which is possible by (3.35). We shall take advantage of the variation of constants formula

$$A(\omega) = e^{-\mu_m(\omega - \theta)} \left(A(\theta) + \int_\theta^\omega e^{\mu_m(s - \theta)} b(A(s - \tau)) e^{-\mu \tau} H(A_s) ds \right), \tag{3.37}$$

which holds for all $\omega \geq \theta$. Assume for contradiction that the statement of the theorem is false. Then, there exists a sequence $\phi_n \in C_+$ such that $\lim_{n \rightarrow \infty} m^{\phi_n} = 0$. There is a sequence T_n such that $T_n \rightarrow \infty$ as $n \rightarrow \infty$ and $A^{\phi_n}(t) \in [qm^{\phi_n}, \check{A}/q]$, for all $t \geq T_n - 2\tau$. Also, we can find $t_n > T_n + n$ such that $A^{\phi_n}(t_n) < m^{\phi_n}/q$. For the particular case $A = A^{\phi_n}$, $\omega = t_n$ and $\theta = T_n$, the variation of constants formula gives

$$A^{\phi_n}(t_n) = e^{-\mu_m(t_n - T_n)} \left(A^{\phi_n}(T_n) + \int_{T_n}^{t_n} e^{\mu_m(s - T_n)} b(A^{\phi_n}(s - \tau)) e^{-\mu \tau} H(A_s^{\phi_n}) ds \right),$$

and, by the integral mean value theorem, there exists $\sigma_n \in [T_n, t_n]$ such that

$$A^{\phi_n}(t_n) = e^{-\mu_m(t_n-T_n)} \left[A^{\phi_n}(T_n) + b(A^{\phi_n}(\sigma_n - \tau))e^{-\mu_l\tau} H(A^{\phi_n}_{\sigma_n})e^{-\mu_m T_n} \int_{T_n}^{t_n} e^{\mu_m s} ds \right]$$

so that

$$A^{\phi_n}(t_n) = e^{-\mu_m(t_n-T_n)} A^{\phi_n}(T_n) + b(A^{\phi_n}(\sigma_n - \tau))e^{-\mu_l\tau} H(A^{\phi_n}_{\sigma_n}) \frac{1 - e^{-\mu_m(t_n-T_n)}}{\mu_m}. \tag{3.38}$$

Now, $A^{\phi_n}(t_n) < m^{\phi_n}/q \rightarrow 0$, $e^{-\mu_m(t_n-T_n)} A^{\phi_n}(T_n) < e^{-\mu_m n} \check{A}/q \rightarrow 0$ and $\frac{1 - e^{-\mu_m(t_n-T_n)}}{\mu_m} \rightarrow \mu_m^{-1} > 0$ as $n \rightarrow \infty$. Therefore, $b(A^{\phi_n}(\sigma_n - \tau))e^{-\mu_l\tau} H(A^{\phi_n}_{\sigma_n}) \rightarrow 0$ must hold as well, as $n \rightarrow \infty$. Let $K := \max\{b(A) : A \in [0, \check{A}/q]\}$, then $H(A^{\phi_n}_{\sigma_n}) \geq e^{-\varepsilon K P} > 0$, where $P = \int_0^\tau \int_0^\tau p(s, \bar{a}) d\bar{a} ds$. Hence, $b(A^{\phi_n}(\sigma_n - \tau)) \rightarrow 0$ as $n \rightarrow \infty$. Given that 0 is the only zero of $b(A)$ on $[0, \check{A}/q]$, this implies $A^{\phi_n}(\sigma_n - \tau) \rightarrow 0$ as $n \rightarrow \infty$.

Next, we claim that $A^{\phi_n}(\sigma_n - \tau) \rightarrow 0$ implies $H(A^{\phi_n}_{\sigma_n}) \rightarrow 1$ as $n \rightarrow \infty$. Since $H(\phi)$ defined by (3.34) is continuous in ϕ and $H(0) = 1$, it is sufficient to show that $\|A^{\phi_n}_{\sigma_n}\| \rightarrow 0$ as $n \rightarrow \infty$. From the inequality $A'(t) \geq -\mu_m A(t)$, we find that

$$A^{\phi_n}(w) \leq e^{\mu_m \tau} A^{\phi_n}(\sigma_n - \tau) \text{ for } w \in [\sigma_n - 2\tau, \sigma_n - \tau]. \tag{3.39}$$

For the other part of the domain of A^{ϕ_n} , if $w \in [\sigma_n - \tau, \sigma_n]$ we use the variation of constants formula

$$A^{\phi_n}(w) = e^{-\mu_m(w-\sigma_n+\tau)} \left(A^{\phi_n}(\sigma_n - \tau) + \int_{\sigma_n-\tau}^w e^{\mu_m(s-\sigma_n+\tau)} b(A^{\phi_n}(s - \tau))e^{-\mu_l\tau} H(A^{\phi_n}_s) ds \right). \tag{3.40}$$

Let $\Delta := \max\{b'(A) : A \in [0, \check{A}/q]\}$. Then, $b(A) \leq \Delta A$ on $[0, \check{A}/q]$ and hence, using (3.39), (3.40) and $H(\cdot) \leq 1$,

$$A^{\phi_n}(w) \leq A^{\phi_n}(\sigma_n - \tau) + \int_{\sigma_n-\tau}^w e^{\mu_m \tau} \Delta A^{\phi_n}(s - \tau) ds \leq (1 + \tau \Delta e^{2\mu_m \tau}) A^{\phi_n}(\sigma_n - \tau). \tag{3.41}$$

Thus, $\|A^{\phi_n}_{\sigma_n}\| \leq (1 + \tau \Delta e^{2\mu_m \tau}) A^{\phi_n}(\sigma_n - \tau)$ and so $H(A^{\phi_n}_{\sigma_n}) \rightarrow 1$ as $n \rightarrow \infty$.

There exists $\xi > 0$ such that, on the interval $(0, \xi]$, $b(A) > qb'(0)A$ holds. There is an n_0 such that $A^{\phi_n}(\sigma_n - \tau) < \xi$ for all $n > n_0$. For sufficiently large n , we have the following estimates:

$$\begin{aligned} \frac{1 - e^{-\mu_m(t_n-T_n)}}{\mu_m} &> \frac{q}{\mu_m}, \\ b(A^{\phi_n}(\sigma_n - \tau)) &> qb'(0)A^{\phi_n}(\sigma_n - \tau) > qb'(0)qm^{\phi_n}, \\ H(A^{\phi_n}_{\sigma_n}) &> q. \end{aligned}$$

Therefore, from the variation of constants formula and (3.38), we obtain

$$m^{\phi_n}/q > A^{\phi_n}(t_n) \geq qm^{\phi_n}qb'(0)e^{-\mu_l\tau} q \frac{q}{\mu_m}.$$

Dividing by m^{ϕ_n} and rearranging,

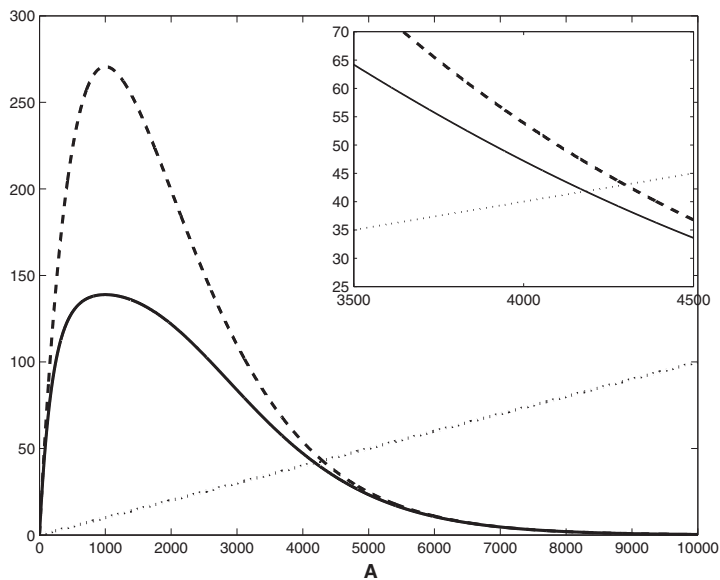
$$\mu_m \geq q^5 b'(0) e^{-\mu\tau},$$

which is a contradiction. Thus, we can conclude the uniform persistence. \square

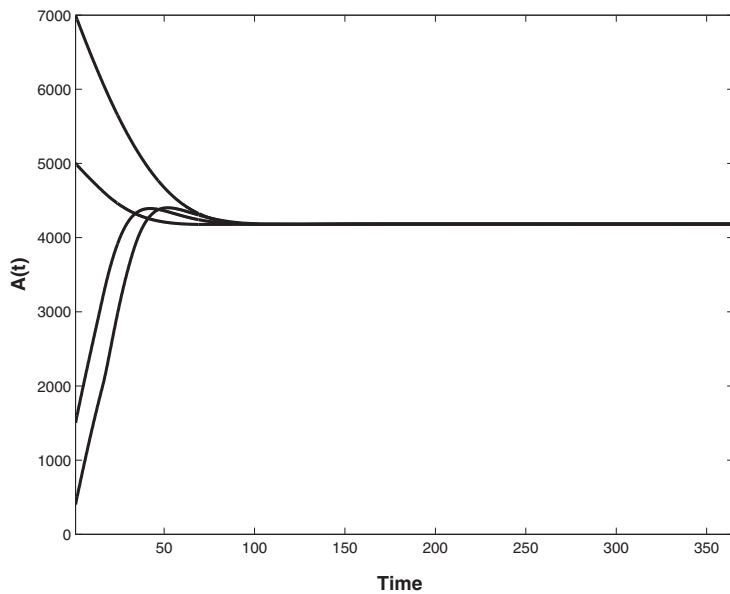
Remark The hypotheses on the initial data in Theorem 3.5 can be relaxed to include any initial function that is non-negative and not identically zero on $[-2\tau, 0]$. Such hypotheses imply that $A(t)$ becomes strictly positive at some future time, and remains so thereafter. The arguments in the above proof then apply after a translate in time.

4 Numerical simulations

We present the results of some simulations of (2.19) and (2.8), and a numerical study of the equation that determines the equilibria of (2.19), equation (3.28). Figures 1–3 show the results for a case when the competition function $p(s, \bar{a})$ in (2.19) is a constant and the birth function $b(A) = rA \exp(-A/K)$, the Nicholson's blowflies birthrate [5]. As explained in the paragraph after (3.28), this choice makes the left-hand side of (3.28) highly non-monotone and brings about the possibility of (2.19) having multiple equilibria, though this only happens for intermediate values of the parameter ϵ that measures the strength of the larval competition. If $\epsilon = 0$, (2.19) has at most one positive equilibrium, which in Figures 1–3 appears as the horizontal coordinate of the intersection of the dashed curve with the dotted line as explained in the captions. Even when $\epsilon = 0$, for some other parameter combinations (results not shown), (2.19) has no positive equilibrium at all, the outcome being extinction. With the parameter values given in the caption to Figure 1, if ϵ is increased from zero the initial effect is that the single large equilibrium of (2.19), called the outbreak equilibrium, begins to decrease. If ϵ is further increased then at some point the resulting distortion of the graph of the left-hand side of (3.28) is such as to bring about two further equilibria, the smaller of which is known as the refuge equilibrium. Equation (2.19) then has three positive equilibria and simulations suggest that the outbreak and refuge equilibria are both stable for the parameter combinations under consideration while the equilibrium of intermediate size is unstable. If ϵ is further increased, which implies a strengthening of the larval competition, then the two larger equilibria disappear leaving only the small refuge equilibrium which appears to be stable on the basis of the simulations and the analysis presented in Section 3.2. Thus, if the population is subject to intense competitive pressure (as measured by ϵ) at the immature life stage, then it may survive at low numbers by exploiting the fact that the competitive pressure drops with density. Recall that the linear stability of the zero equilibrium of (2.19) does not depend on ϵ . We have taken parameter values which make it unstable (see inequality (3.27)). In this situation, increasing ϵ further will not make the refuge equilibrium disappear, though it will get smaller. So the species can always survive at low numbers. However, for some other parameter combinations, model (2.19) has only the zero equilibrium and the competitive effect simply aids the population toward extinction.



(a)



(b)

FIGURE 4. Simulation of (2.19) when $\epsilon = 0.00005$, $p(s, \bar{a})$ is given by (4.42), and other parameters and the birth function are the same as in Figure 1. In this case, (2.19) has just one positive (outbreak) equilibrium. In panel (a), plots of the left- and right-hand sides of (3.28) against A_c^* reveal this equilibrium as the value of A at which the dotted line intersects the solid curve. The dashed curve is the left-hand side of (3.28) when $\epsilon = 0$. Evolution of $A(t)$ to the outbreak equilibrium is shown in panel (b). (a) The large outbreak equilibrium. (b) Evolution of $A(t)$ to the outbreak equilibrium.

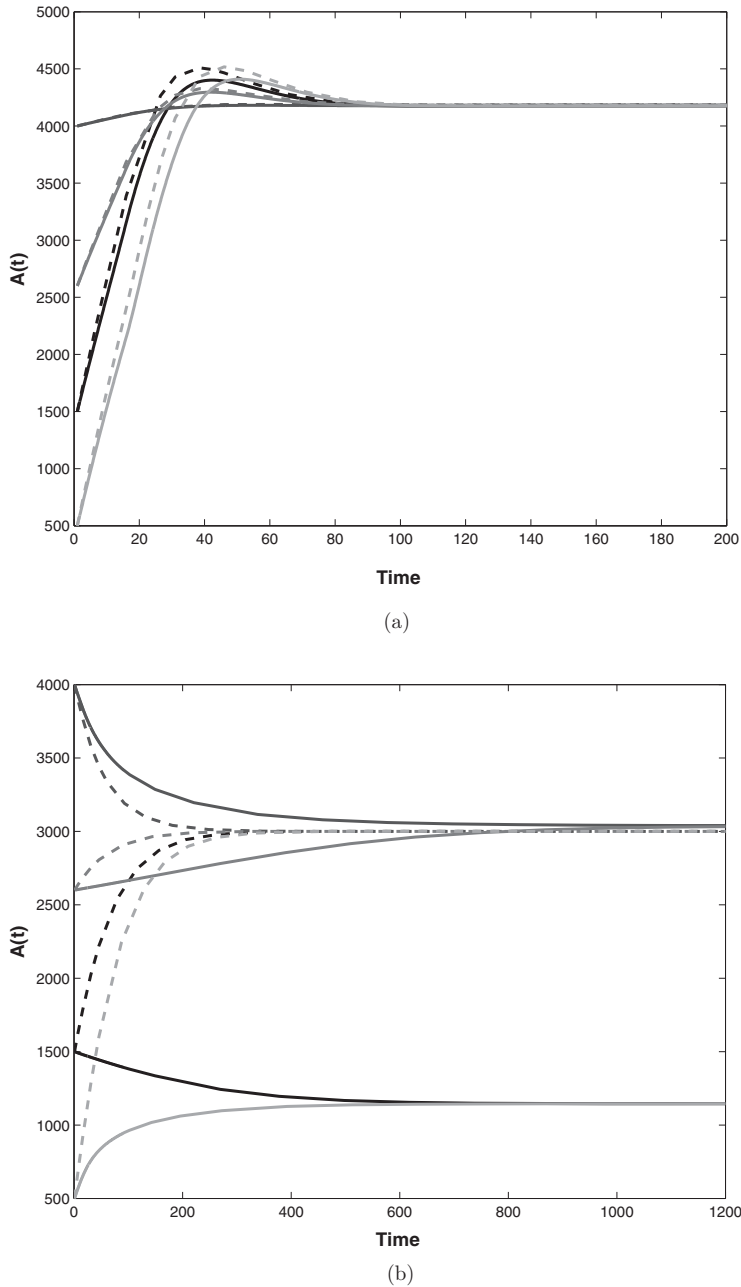


FIGURE 5. Comparison of solutions of (2.19) (solid curves) and (2.8) (dashed curves) for various initial data. Parameter values for panel (a): $b(A) = rA \exp(-A/K)$, $r = 2$, $K = 1000$, $\mu_m = 1/100$, $\mu_L = 1/15$, $\tau = 15$, $\epsilon = 0.0001$, $k_l = 0.0001$ and $p(s, \bar{a}) \equiv p_0 = 1/\tau = 1/15$. For these values, (2.19) has just one positive equilibrium. Parameter values for panel (b): as for panel (a) except that $k_l = 0.00094$ and $p(s, \bar{a}) \equiv p_0 = 0.305$, giving rise to a situation in which (2.19) has both an outbreak and a refuge equilibrium. (a) Solutions of (2.19) (solid) and (2.8) (dashed). (b) Solutions of (2.19) (solid) and (2.8) (dashed).

We also explored a case when the competition function $p(s, \bar{a})$ in (2.19) is non-constant, namely

$$p(s, \bar{a}) = \begin{cases} 0, & \bar{a} < s, \\ 0.305, & \bar{a} \geq s. \end{cases} \quad (4.42)$$

With this choice, a larva experiences competition only from older larvae. Expression (4.42) is therefore relevant to species in which there is cannibalism of larvae, or intimidatory tactics by older larvae toward younger ones. The choice of the value 0.305 for $\bar{a} \geq s$ is to facilitate comparison with the case in Figures 1–3, in which $p(s, \bar{a}) \equiv 0.305$.

Various simulations suggest that the solutions of (2.19) exhibit similar dynamics in the two cases of a constant $p(s, \bar{a})$ (see Figures 1–3), and the particular non-constant case (4.42), with similar properties to the famous spruce budworm model in both cases. In fact, we may summarise our findings with the statement that, when $p(s, \bar{a})$ is given by (4.42), the solution set of (2.19) has the same properties as for a constant $p(s, \bar{a})$, if the value of ϵ is adjusted appropriately. Figures 1 and 4 actually use the same (very small) ϵ value, and Figure 4 indicates the existence of a single outbreak equilibrium which is larger than the corresponding one in Figure 1, with a hint in Figure 4 that the convergence to equilibrium has become oscillatory. For the case (4.42), we generated other simulation results so similar to those for constant $p(s, \bar{a})$ shown in Figures 1–3 that we have omitted the graphs for economy. For example, if $p(s, \bar{a})$ is changed from a constant value 0.305 to expression (4.42), the scenario of multiple co-existing equilibria shown in Figure 2 can be recreated almost unchanged by simply increasing ϵ from 0.0001 to 0.000235. We also observed (results not shown here) that, with the change from constant to non-constant $p(s, \bar{a})$, the situation shown in Figure 3 can be recreated almost unchanged with a 50% increase in the value of ϵ .

The equilibria of (2.19), which are determined by (3.28), remain the same for any combinations of $p(s, \bar{a})$ and ϵ that leave the value of

$$\epsilon \int_0^\tau \int_0^\tau p(s, \bar{a}) e^{-\mu_1 \bar{a}} d\bar{a} ds \quad (4.43)$$

unchanged. Our simulations suggest that, for small ϵ , such combinations preserve not only the equilibria but also the stability of those equilibria and the general qualitative properties of solutions. But certainly the effect of larval competition on the actual equilibria of (2.19) is determined solely by the single parameter (4.43). We have spoken of ϵ as a parameter measuring the intensity of larval competition, and we may consider (4.43) as a more precise quantitative measure of that intensity. Note that, due to the exponential weighting factor in the integrand, the parameter (4.43) gives more weighting to competitive pressure exerted by younger larvae. In some species, it is primarily older larvae that exert competition, in the form of intimidatory tactics. In that scenario, if per-capita larval mortality (as measured by μ_1) is high then (4.43) is likely to be very small, so the overall effect of larval competition on the population is small.

Figure 5 shows, in the case when $b(A) = rA \exp(-A/K)$, the results of simulations that compare solutions of (2.19) with those of (2.8), the latter being the simplest model of this paper that claims to model larval competition. Panel (a) shows a situation in which (2.19) has just one positive equilibrium. Solutions of the two models are qualitatively very

similar in this case. For ease of comparison, parameter values were chosen so that this equilibrium would be the same as the positive equilibrium of (2.8). Panel (b) shows the principal difference between the two models, namely, that for some parameter values model (2.19) may have an additional small stable equilibrium (the refuge equilibrium) co-existing with the large (outbreak) equilibrium. In Section 5, we discuss further the implications of these findings.

5 Conclusion

In this paper, we have derived a very simple model, equation (2.8), for a population that experiences intra-specific competition in the larval life stage, on the assumption that a larva only competes with others at its own stage of development. We also derived a more complex model, equation (2.19), that allows for the possibility of a larva competing with larvae at other stages of development. In that way, model (2.19) addresses a deficiency with model (2.8) but its derivation assumes that competition among larvae (as measured by the parameter ϵ in (2.19)) is not too intense. Therefore, the conclusions we draw from the analysis and simulations of this paper are only valid in this case. It is remarkable that, even using (2.9) with its general kernel $p(a, \bar{a})$ as a starting point, we were still able to derive a delay differential equation (equation (2.19)) for the total number of adults $A(t)$. The derivation relies on smallness of ϵ and uses perturbation theory. The application of perturbation theory implies some loss of information, since one can never compute all the terms, but here we have a clear interpretation of how the perturbation procedure approximates the situation: it recognises that a maturing larva may experience competition pressure from all other larvae, but it fails to recognise that the older competing larvae experienced competition during their own development.

With the assumptions we have made in this paper, our modelling is likely to be most appropriate for insect and amphibian species that undergo metamorphosis. We assume that larvae compete only with larvae, and adults only with adults. This seems reasonable for such species because the adults and larvae often live in different kinds of habitats, have different diets and are in competition for different things. Larvae often compete with each other primarily for food, whereas in adults the competition is mainly for mates.

Our main finding with regard to (2.19) is that, for certain (non-monotone) birth functions including the Nicholson's blowflies birth function, the model exhibits properties similar to those of the spruce budworm model. In particular, for some parameter values two stable equilibria may co-exist including a small stable refuge equilibrium allowing the population to survive at low numbers by exploiting the fact that competition drops off as numbers decrease. These properties are not common in mechanistically derived scalar equations, with or without delay, for a single species that interacts only with itself. Recall that the spruce budworm model is actually a primitive model for a prey-predator system (budworm subject to predation by birds) that happens to reduce to a scalar differential equation, rather than a model specifically for a single species interacting only with itself. Models with an Allee effect have a small positive equilibrium, but that equilibrium is unstable in such models and is not comparable to the refuge equilibrium of (2.19) or of the spruce budworm model.

We also stress that model (2.19) admits unbounded (including linear) birth functions $b(\cdot)$. Even if $b(\cdot)$ is linear, (2.19) is still a non-linear differential equation and its solutions may still be bounded. It is common practice to assume that the birth rate function $b(\cdot)$ is bounded, to ensure solutions are bounded. For model (2.19), such an assumption is unnecessary, and we suggest that linear birth functions could in fact be quite reasonable for some species, especially those that experience intra-specific competition mainly at the larval stage.

We have compared solutions of (2.19) with those of the simplest model in this paper that claims to model larval competition, equation (2.8). The main difference, as noted above, is that (2.19) may have an additional (small) equilibrium, the refuge equilibrium. However, the existence of the additional equilibrium depends on parameter values, and in some situations the solutions of (2.19) are very similar to those of (2.8), even though the former aims to address an unrealistic assumption in the derivation of the latter (the idea that a larva only competes with others of its own age). In fact, for small ϵ , solutions of (2.19) do not depend strongly on the functional form of the kernel $p(s, \bar{a})$. This observation is very important because it implies that, even though there is an unrealistic assumption in the modelling leading to (2.8), if larval competition is not too intense then (2.8) might still be a reasonable simple approach to the modelling of larval competition in general. We emphasise, however, that the derivation of the more complex model (2.19) relies on the assumption that ϵ is small. If larval competition, as measured by ϵ , is very intense then equation (2.19) will lose its validity and a different approach will be required. This will be the subject of further research.

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