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EXISTENCE AND UNIQUENESS OF GLOBAL SOLUTIONS FOR A SIZE-STRUCTURED MODEL OF AN INSECT POPULATION WITH VARIABLE INSTAR DURATION

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Dedicated to Paul Waltman on the occasion of his 60th birthday

In [**12**], R.M. Nisbet and W.S.C. Gurney show how to construct mathematical models of the population dynamics of an insect which has an arbitrary number of instars (life stages) the duration of each of which is dependent on the insect achieving a threshold weight gain. Based on the general theory of size (mass)-structured population dynamics, see, e.g., [**11**], they obtain a system of delay differential equations of threshold-type for the number (density) of individuals in each instar as a function of time. By a threshold-type delay we mean a delay $\tau = \tau_i(t)$, which is determined by a threshold condition

$$\int_{t-\tau_i}^{t} g_i(s)\,ds = m_2 - m_1 \tag{0.1}$$

where the rate of increase of weight

$$\frac{dm}{dt} = g_i(t)$$

is given by a prescribed function or by a dynamical variable $g_i(t)$. The meaning of (0.1) is that an individual emerging (graduating) from the i'th instar at time t must have spent time $\tau_i = \tau_i(t)$ in the i'th instar, the instar being characterized by insect weight belonging to the interval (m_1, m_2). The rate of weight gain $g_i(t)$ may, for example, be given by

$$g_i(t) = G_i(F(t))$$

where $F(t)$ is the food density which might also be included in the system as a dynamically changing variable.

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The goal of the modeling in [**12**] was to explore the effect of varying instar duration on population dynamics. A special "strategic model" was formulated with the damselfly in mind, in which a single larval stage has variable duration. No mathematical analysis of the resulting system of equations was performed. Numerical simulations described in [**12**] appear to support the conclusion of "the stabilizing effect of the variable duration of the larval stage".

The aim of this paper is to begin a mathematical analysis of the strategic model formulated by Nisbet and Gurney. These authors, concerned with a numerical simulation of the model, were led to a system of equations which allowed for the possibility of nonbiologically meaningful solutions. We begin by deriving the model equations in such a way as to exclude these nonmeaningful solutions. This more restrictive set of equations is then shown to possess a unique global solution. Estimates of the exponential growth rate of the population are provided. The key tool in this analysis is a change of variables to a "physiological time" variable as used in [**13, 14**]. It has the effect of transforming a system of threshold delay differential equations to a standard system of functional differential equations. As the later equations describe the long time behavior of solutions of the model, the transformation provides a means of studying the asymptotic behavior of the system. This will be pursued in future work by the author. We also establish a precise connection between the original model equations, a mixed system of ordinary differential equations and a coupled hyperbolic partial differential equation, and the "reduced" system of threshold-type delay differential equations as well as the further reduced set of functional differential equations.

My interest in the study of differential delay equations and integral equations with threshold-type delays has been largely stimulated by the work of Paul Waltman. Threshold-type delays were first introduced by Ken Cooke in [**2**]. They were later used by Hoppensteadt and Waltman [**9, 10**] to model a threshold dose of infection in models of the dynamics of infectious diseases. The monograph [**15**] contains most of this work and as one of Paul Waltman's graduate students at roughly the time of its publication, I became interested in threshold delays. Later, Hoppensteadt and Waltman [**8**] formulated a model of respiration using threshold-delays. In [**16**], Butz and Waltman used threshold-delays as a triggering device in the modeling of the immune response to an antigen. The analysis of this model has been carried out in a series of papers by Gatica and Waltman [**4, 5, 6**].

Now it appears that threshold-type differential delay equations arise quite naturally in the reduction of certain systems of structured population models, for which some of the populations are unstructured, to simpler systems of equations. This was already recognized by W. Alt in [**1**] and by Metz and Diekmann [**11**]. In the present paper and in our earlier work [**14**], it is shown that these threshold-type delay equations can be transformed to standard functional differential equations. This allows the application of the large body of theory for functional differential equations to the problem of determining the asymptotic behavior of the systems of equations which result from certain structured population models.

1. The model and main results.

The strategic model of Nisbet and Gurney [**12**] is described by the following system of equations, the meaning of which will be described below,

$$\begin{aligned}
\frac{dF}{dt} &= G - \varepsilon^{-1}Q(F(t))L(t), \qquad F(0) = F_0\\
\frac{\partial \rho}{\partial t} + Q(F(t))\frac{\partial \rho}{\partial m} &= -\delta_L \rho, m_1 \le m \le m_2, \qquad t > 0,\\
Q(F(t))\rho(m_1, t) &= qN(t), \qquad t > 0,\\
\rho(m, 0) &= \rho_0(m), \qquad m_1 \le m \le m_2\\
\frac{dN}{dt} &= \alpha Q(F(t))\rho(m_2, t) - \delta_A N(t), \qquad N(0) = N_0,
\end{aligned}$$

where F_0, N_0 and $\rho_0(m)$ are nonnegative and the constants $G, \varepsilon, \delta_L, \delta_A$, q, α are positive.

Food density, $F(t)$, is supplied to the environment at a constant rate G and consumed by larvae at a per larvae rate $\varepsilon^{-1}Q(F(t))$. The larval population size, $L(t)$, is given by

$$L(t) = \int_{m_1}^{m_2} \rho(m, t)\, dm$$

where $\rho(\cdot, t)$ is the larval mass-density function. The larval population is characterized by individual body mass in the interval (m_1, m_2). A larvae is assumed to grow at a rate

$$\frac{dm}{dt} = Q(F(t))$$

which is proportional to the food consumption rate and it is assumed to experience mortality at a constant (weight-independent) rate δ_L. A fraction α, $0 < \alpha \leq 1$, of the larvae reaching mass m_2 is assumed to undergo a successful moult to become adults. Adults lay eggs at per capita rate q which immediately become larvae of mass m_1. Thus, larvae begin as eggs of mass m_1 and must gain mass $m_2 - m_1$ to be eligible to become adults of weight m_2. Finally, adult food consumption is neglected and they are assumed to experience mortality at rate δ_A. The function Q will be assumed to vanish when $F = 0$, be continuously differentiable with $Q'(F) > 0$ and be bounded. In [**12**], Q is taken to be of Michaelis-Menten type

$$Q(F) = \frac{\varepsilon A_{\max} F}{K + F}.$$

It is useful to scale variables in the equations above as follows

$$\begin{aligned}
\overline{F}(t) &= F(t)/G \\
\overline{\rho}(\overline{m}, t) &= \frac{(m_2 - m_1)^2}{\varepsilon G}\rho(m_1 + \overline{m}(m_2 - m_1), t), \qquad 0 \leq \overline{m} \leq 1, \\
\overline{N}(t) &= \frac{m_2 - m_1}{\varepsilon G} N(t) \\
\overline{Q}(\overline{F}) &= \frac{Q(G\overline{F})}{m_2 - m_1}, \qquad \overline{F} \geq 0.
\end{aligned}$$

With this scaling, the equations become

$$\begin{aligned}
\frac{dF}{dt} &= 1 - Q(F(t))L(t), \qquad F(0) = F_0 \\
\frac{\partial \rho}{\partial t} + Q(F(t))\frac{\partial \rho}{\partial m} &= -\delta_L \rho, \qquad 0 \leq m \leq 1,\ t > 0 \\
Q(F(t))\rho(0, t) &= qN(t), \qquad t > 0 \\
\rho(m, 0) &= \rho_0(m), \qquad 0 \leq m \leq 1 \\
\frac{dN}{dt} &= \alpha Q(F(t))\rho(1, t) - \delta_A N(t), \qquad N(0) = N_0.
\end{aligned} \tag{1.1}$$

In (1.1), we have dropped the bars over variables and of course the initial data F_0, N_0, ρ_0 have been scaled accordingly. The definition of L becomes

$$L(t) = \int_0^1 \rho(m,t)\, dm. \tag{1.2}$$

Hereafter, the equation (1.1) will be the focus of our attention.

By a global solution of (1.1), we mean a set of continuous functions:

$$\begin{gathered} F, N : [0,\infty) \to \mathbf{R} \\ \rho : [0,1] \times [0,\infty) \to \mathbf{R} \end{gathered}$$

which satisfy

(i) F and N are differentiable on $[0,\infty)$.

(ii) $F(0) = F_0$, $N(0) = N_0$ and $\rho(m,0) = \rho_0(m)$, $0 \le m \le 1$.

(iii) $Q(F(t))\rho(0,t) = qN(t)$, $t \ge 0$.

(iv) For each $(m,t) \in [0,1) \times [0,\infty)$

$$\lim_{h\to 0+} h^{-1}\left[\rho\left(m + \int_t^{t+h} Q(F(s))\, ds, t+h\right) - \rho(m,t)\right] = -\delta_L \rho(m,t).$$

(v) The first and last equation in (1.1) hold for $t \ge 0$ where $L(t)$ is given by (1.2).

The requirement (iv) implies that ρ is differentiable along characteristic curves corresponding to the second equation of (1.1), the characteristic curves being described by

$$\frac{dt}{ds} = 1, \qquad \frac{dm}{ds} = Q(F(s)),$$

and that the derivative of ρ at (m,t) along such a characteristic curve is given by $-\delta_L \rho(m,t)$. It is in this sense that the second equation of (1.1) is assumed to be satisfied.

We introduce the notation S for the strip $[0,1] \times [0,\infty)$ in the (m,t) plane. Our main result is the following theorem.

Theorem 1.1. *Assume that ρ_0 is continuous on $[0,1]$ and that the compatibility condition*

$$Q(F_0)\rho_0(0) = qN_0 \tag{1.3}$$

holds. Then there exists a unique global solution, (F,ρ,N) of (1.1). Moreover, F is positive for $t>0$ and ρ and N are nonnegative on their respective domains. If $\alpha q < \delta_A$ then this solution satisfies the estimate

$$\alpha L(t) + N(t) \leq Ce^{-\delta t}, \qquad t \geq 0 \tag{1.4}$$

where $\delta = \min\{\delta_A - \alpha q, \delta_L\} > 0$ and $C \geq 0$. If $\alpha q \geq \delta_A$ then the solution satisfies the estimate

$$\alpha L(t) + N(t) \leq Ce^{(\alpha q - \delta_A)t}, \qquad t \geq 0. \tag{1.5}$$

It is easy to see that the compatibility condition (1.3) is necessary in order for ρ to be continuous on S. If in our definition of a solution, the continuity of ρ is not required, then (1.3) could be dropped.

We note that if $\alpha q > \delta_A$ then a positive steady state solution of (1.1), given by

$$\begin{aligned} &\tau_0 = \delta_L^{-1}\ln(\alpha q/\delta_A), \qquad Q(F) = \tau_0^{-1}, \qquad L = \tau_0 \\ &N = \frac{\alpha\delta_L}{\alpha q - \delta_A}\tau_0, \qquad \rho(m) = qN\tau_0 e^{-\delta_L \tau_0 m}, \qquad 0 \leq m \leq 1 \end{aligned}$$

is defined provided τ_0^{-1} belongs to the range of Q. The number τ_0 denotes the length of the larval stage at steady state. As Q is monotone increasing, only one such steady state can exist. In future work, we will examine the stability of this steady state solution.

We begin the proof of Theorem 1.1 by assuming the existence of a global solution of (1.1) in order to derive simpler equations and ultimately a candidate for a solution of (1.1). In the following, we will use the notation

$$P_0(m) = \int_0^m \rho_0(u)\,du, \qquad 0 \leq m \leq 1.$$

The results to follow contain much information about the solution of (1.1) which is not contained in Theorem 1.1.

Proposition 1.2. *Let the hypotheses of Theorem* 1.1 *hold and assume that there exists a global solution* F, ρ, N *of* (1.1). *Then* F, ρ *and* N *are nonnegative on their respective domains. There exists a unique positive number* $t_0 = t_0(F_0, N_0, \rho_0)$ *which is the solution of*

$$1 = m(t) \equiv \int_0^t Q(F(s))\, ds.$$

On the interval $0 \le t \le t_0$, *the functions* F, N *and* L *must satisfy*

$$\begin{aligned}
&\frac{dF}{dt} = 1 - Q(F(t))L(t), \qquad F(0) = F_0 \\
&\frac{dN}{dt} = -\delta_A N(t) \\
&\qquad\qquad + \alpha Q(F(t))\rho_0\left(1 - \int_0^t Q(F(s))\, ds\right)e^{-\delta_L t}, \qquad N(0) = N_0 \\
&L(t) = e^{-\delta_L t} P_0\left(1 - \int_0^t Q(F(s))\, ds\right) + q\int_0^t e^{-\delta_L (t-s)} N(s)\, ds, \\
&\qquad\qquad L(0) = P_0(1).
\end{aligned} \tag{1.6}$$

The characteristic curve $\Gamma = \{(m, t) : m = m(t), 0 \le t \le t_0\}$ *divides the strip* S *into two components*

$$S_1 = \{(m, t) \in S : 0 < t < t_0 \text{ and } m > m(t)\}$$

and

$$S_2 = S - S_1.$$

For $t > t_0$, F, L *and* N *must satisfy*

$$\begin{aligned}
&\frac{dF}{dt} = 1 - Q(F(t))L(t), \\
&L(t) = q\int_{t-\tau_0}^t e^{-\delta_L (t-s)} N(s)\, ds, \\
&\frac{dN}{dt} = -\delta_A N(t) + \alpha q \frac{Q(F(t))}{Q(F(t-\tau_0))} N(t-\tau_0) e^{-\delta_L \tau_0},
\end{aligned} \tag{1.7}$$

where $\tau_0 = \tau_0(t)$ *is defined implicitly by*

$$\int_{t-\tau_0}^{t} Q(F(s))\,ds = 1. \tag{1.8}$$

The density ρ *is given by*

$$\rho(m,t) = \begin{cases} \rho_0\big(m - \int_0^t Q(F(s))\,ds\big)e^{-\delta_L t}, & (m,t) \in S_1 \\ \dfrac{qN(t-\tau)e^{-\delta_L \tau}}{Q(F(t-\tau))}, & (m,t) \in S_2 \end{cases} \tag{1.9}$$

where $\tau = \tau(m,t)$ *is defined implicitly by*

$$m = \int_{t-\tau}^{t} Q(F(s))\,ds. \tag{1.10}$$

The function τ has the biological meaning that a larvae of mass m at time t was an egg at time $t-\tau$. Thus $\tau(m,t)$ is the chronological age of a larvae of mass m at time t. Similarly, (1.8) expresses the fact that a larvae that becomes an adult at time t must have entered the larval stage at time $t-\tau_0$ and, during the interval $(t-\tau_0, t)$, accumulated a (scaled) weight gain of one unit. Thus, $\tau_0 = \tau_0(t)$ is the length of the larval stage for larvae maturing to adults at time t. It varies dynamically with the density of food, being longer when food supplies are uniformly scarce and shorter when food supplies are uniformly higher.

The positive number, t_0, described in Proposition 1.2, is the time at which the eggs (larvae with mass m_1) present at $t=0$ reach adult weight m_2.

We note that (1.7) differs from the corresponding system (A10)–(A13) of [**12**] in that our equation for L is an integrated version of (A11). The integrated form of the equation for L makes biological sense since the larval population at time t is simply the sum of the eggs laid from the time when the currently maturing larvae were eggs $(t-\tau_0)$ until the present (t) weighted by the probability of survival. The equation (A11) in [**12**] must be interpreted with care since an inappropriate choice of initial data could lead to negative larval population size.

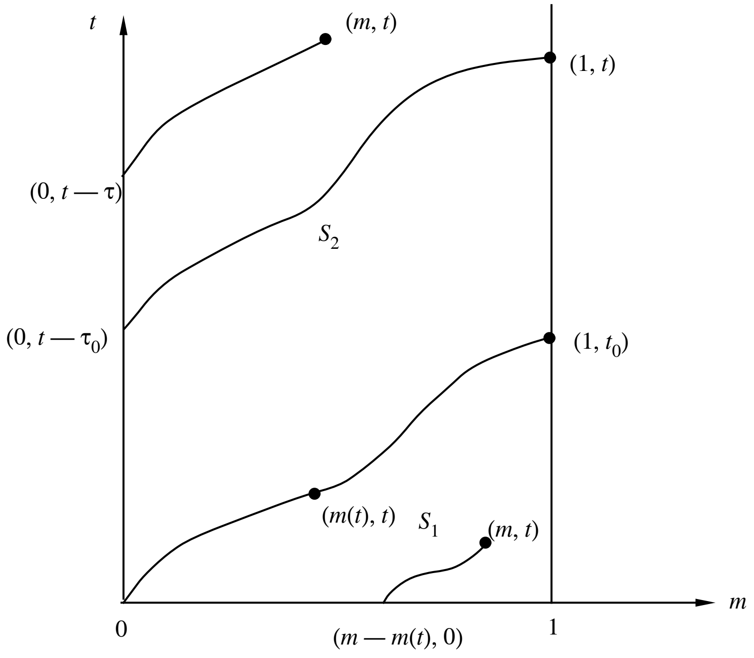

FIGURE 1. Characteristic curves.

In Figure 1, some characteristic curves are depicted and the numbers t_0, τ and τ_0 are implicitly described.

Proof. Assume that a global solution F, ρ, N of (1.1) exists and L is given by (1.2). Either $F_0 > 0$ or $F_0 = 0$ and $(dF/dt)(0) = 1$ and in either case F is positive in some interval $(0, t_1)$ for some $t_1 > 0$. The form of the equation for F is easily seen to imply that $t_1 = +\infty$ and $F(t) > 0$ for $t > 0$. Define $m(t) = \int_0^t Q(F(s))\, ds$ for $t > 0$ and let t_0 be defined as the unique solution of $m(t_0) = 1$ or $t_0 = \infty$ if no such solution exists. Define Γ as in the proposition but where we now allow for the possibility that Γ may not meet the vertical line $m = 1$; also let S_1 and S_2 be as defined in the proposition. Then the expression

(1.9) follows immediately on integrating the third equation of (1.1) along characteristic curves and using the prescribed values of ρ on the boundary. Note that τ, defined by (1.10) is a well-defined, smooth, nonnegative function in S_2. As $\rho_0 \geq 0$, we see immediately from (1.9) that $\rho \geq 0$ in S_1 and so $\rho(1,t) \geq 0$ on $0 \leq t \leq t_0$. It follows from the equation for N in (1.1) that $N(t) \geq 0$ for $0 \leq t \leq t_0$. This and the expression for ρ in S_2 given by (1.9) implies that $\rho \geq 0$ on $[0,1] \times [0,t_0]$ and so $L(t) \geq 0$ for $0 \leq t \leq t_0$. For $0 < t < t_0$, $L(t)$ may be computed as

$$L(t) = \int_0^{m(t)} \rho(m,t)\,dm + \int_{m(t)}^1 \rho(m,t)\,dm.$$

Putting $Q(t) = Q(F(t))$ and using (1.9), we obtain

$$= \int_0^{m(t)} e^{-\delta_L \tau} \frac{qN(t-\tau)}{Q(t-\tau)}\,dm + \int_{m(t)}^1 \rho_0\biggl(m - \int_0^t Q(s)\,ds\biggr) e^{-\delta_L t}\,dm$$

where $\tau = \tau(m,t)$ is determined by (1.10). Note that $(\partial\tau/\partial m)(m,t) = Q(t-\tau)^{-1}$ so that we may make the change of variables from m to τ in the first integral above to obtain the expression (1.6) for $L(t)$ on $0 \leq t \leq t_0$.

The expression (1.9) immediately yields the equation for N in (1.6). Thus, we have shown that F, N and L must satisfy (1.6) on $0 \leq t \leq t_0$. The equation for N can be integrated once to obtain
(1.11)

$$\begin{aligned} N(t) &= [N_0 + \alpha L(0)]e^{-\delta_A t} - \alpha e^{-\delta_L t} P_0\biggl(1 - \int_0^t Q(s)\,ds\biggr) \\ &\quad + e^{-\delta_A t} \int_0^t \alpha(\delta_A - \delta_L) e^{(\delta_A - \delta_L)s} P_0\biggl(1 - \int_0^s Q(r)\,dr\biggr)\,ds. \end{aligned}$$

We now show that t_0 is finite. If $t_0 = +\infty$ then (1.6) holds for $0 \leq t < \infty$. It is not hard to see from (1.11) that N is bounded. As N is nonnegative, one need only show that the last integral is bounded in case $\delta_A > \delta_L$. But this is clear since P_0 is bounded. Since N is bounded, so is L from (1.6) and we let $L_{\max} = \sup_{t\geq 0} L(t)$. Then F satisfies

$$F'(t) \geq 1 - \mu F, \qquad F(0) = F_0$$

where $\mu \equiv L_{\max}\mathrm{Lip}\,(Q)$. If $\mu > 0$, then

$$\begin{aligned} F(t) &\geq F_0 e^{-\mu t} + \frac{1}{\mu}(1 - e^{-\mu t}), \\ &\geq \min\left\{F_0, \frac{1}{\mu}\right\} > 0. \end{aligned}$$

If $\mu = 0$ then $F(t) \equiv t + F_0$. In either case, we see that $Q(F(t))$ is bounded below by a positive constant for $t > \varepsilon$, for every $\varepsilon > 0$, and therefore $\int_0^\infty Q(F(s))\,ds = +\infty$. But this immediately contradicts our assumption that $t_0 < \infty$, or $\int_0^t Q(F(s))\,ds < 1$ for all $t > 0$. Hence, we have established that $t_0 < \infty$.

Now consider F, N and L for $t > t_0$. The equation for dN/dt in (1.7) follows immediately from (1.1), (1.9) and the fact that $\tau(1,t) = \tau_0(t)$ as defined in (1.8). Note that $\tau_0(t_0) = t_0$. By the form of the equation for N in (1.7), it is clear that $N(t) \geq 0$ for $t \geq t_0$. Hence $\rho \geq 0$ on S. The equation for L in (1.7) follows exactly as the corresponding expression in (1.6), by using (1.9). As N is nonnegative, it is apparent that L is as well. This establishes Proposition 1.2. □

Now we show that (1.6) has a unique solution.

Lemma 1.3. *There exists a unique positive number* t_0 *and unique continuous functions* F, N, L *defined on* $[0, t_0]$ *satisfying*

(a) $F(0) = F_0$, $N(0) = N_0$, $L(0) = P_0(1)$,

(b) F *and* N *are differentiable on* $[0, t_0]$,

(c) *The inequality*

$$0 \leq \int_0^t Q(F(s))\,ds \leq 1$$

holds for $0 \leq t \leq t_0$ *with equality holding at* $t = t_0$ *in the second inequality.*

(d) (1.6) *holds on* $[0, t_0]$.

In addition, the solution of (a)–(d) *satisfies* $F(t) > 0$ *and* $N(t), L(t) \geq 0$ *on* $0 < t \leq t_0$.

Proof. It will be convenient to extend the domain of ρ_0 by defining $\rho_0(m) = \rho_0(0)(\rho_0(1))$ for $m < 0$ $(m > 1)$. With this extended ρ_0, we can extend P_0 to be defined for all $m \in \mathbf{R}$ by $P_0(m) = \int_0^m \rho_0(u)\, du$ but note that P_0 is negative if $m < 0$.

In order to show the existence of a solution of (1.6), recall

$$m(t) = \int_0^t Q(F(s))\, ds$$

and differentiate the expression for L to obtain the system of ordinary differential equations

$$\begin{aligned}
&\frac{dF}{dt} = 1 - Q(F(t))L(t), \qquad F(0) = F_0,\\
&\frac{dm}{dt} = Q(F(t)), \qquad m(0) = 0,\\
&\frac{dL}{dt} = -\delta_L L(t) + qN(t) - e^{-\delta_L t}\rho_0(1-m(t))Q(F(t)), \qquad L(0) = P_0(1),\\
&\frac{dN}{dt} = \alpha Q(F(t))\rho_0(1-m(t))e^{-\delta_L t} - \delta_A N(t), \qquad N(0) = N_0.
\end{aligned} \tag{1.12}$$

By the Peano existence theorem, there exists a solution of (1.12) which can be extended to a maximal interval of existence $[0, t_1)$ where $0 < t_1 \leq \infty$. It is easy to argue, as in the previous proposition, since $F_0 \geq 0$, that $F(t) > 0$ for $0 < t < t_1$. Obviously, $m(t) > 0$ on this interval as well. Let $t_2 = t_1$ if $m(t) < 1$ on $[0, t_1)$, otherwise let t_2 be the smallest positive solution of $m(t) = 1$. Then for $0 \leq t < t_2$, $0 < 1 - m(t) \leq 1$. It follows immediately that $N(t) \geq 0$ on $0 \leq t < t_2$. The equation for L in (1.12) can be integrated once to obtain the expression for L in (1.6). Thus, $L(t) \geq 0$ on $0 \leq t < t_2$. If $t_2 < t_1$, then we are done as it is easy to see that F, N and L satisfy (a)–(d). If $t_2 = t_1$, then we may argue as in the previous proposition that N and L are bounded and so if $t_1 < \infty$ then F is bounded and this contradicts the fact that $[0, t_1)$ is the maximal interval of existence of the solution. If $t_1 = +\infty$, then we argue a contradiction to $m(t) < 1$ exactly as in the previous proposition. Hence, we see that there exists $t_0 > 0$ and a solution F, N, L of (1.6) and $[0, t_0]$ satisfying (a)–(d). In addition, $F(t) > 0$ and $N(t), L(t) \geq 0$ on $(0, t_0]$.

We now consider the question of uniqueness of solutions for the initial value problem (1.12). As ρ_0 is only assumed to be continuous, standard results do not apply directly. It is easily seen that for any solution F, m, L, N of (1.12), L must satisfy the integral equation in (1.6) and N must satisfy the integral equation (1.11). Hence, (1.12) is equivalent to the system of integral equations

$$\begin{aligned} F(t) &= F_0 + t - \int_0^t Q(F(s))L(s)\,ds \\ m(t) &= \int_0^t Q(F(s))\,ds \\ L(t) &= e^{-\delta_L t}P_0(1-m(t)) + q\int_0^t e^{-\delta_L(t-s)}N(s)\,ds \\ N(t) &= [N_0 + \alpha L(0)]e^{-\delta_A t} - \alpha e^{-\delta_L t}P_0(1-m(t)) \\ &\quad + \alpha(\delta_A - \delta_L)\int_0^t e^{-\delta_A(t-s)}e^{-\delta_L s}P_0(1-m(s))\,ds. \end{aligned}$$

Now, suppose there are two solutions of (1.12), (F, m, L, N) and $(\overline{F}, \overline{m}, \overline{L}, \overline{N})$ on a common interval $[0, T]$, for some $T > 0$ such that $m(T)$, $\overline{m}(T) \le 1$. Then an estimate yields

$$\begin{aligned} |F(t) - \overline{F}(t)| &\le \overline{Q}\int_0^t |L(s) - \overline{L}(s)|\,ds + K\int_0^t |F(s) - \overline{F}(s)|\,ds \\ |m(t) - \overline{m}(t)| &\le \mathrm{Lip}\,(Q)\int_0^t |F(s) - \overline{F}(s)|\,ds \\ |L(t) - \overline{L}(t)| &\le ||\rho_0||_\infty |m(t) - \overline{m}(t)| + q\int_0^t |N(s) - \overline{N}(s)|\,ds \\ |N(t) - \overline{N}(t)| &\le \alpha||\rho_0||_\infty |m(t) - \overline{m}(t)| + R\int_0^t |m(s) - \overline{m}(s)|\,ds \end{aligned}$$

where

$$\begin{aligned} K &= \max_{0\le s\le T}\{L(s), \overline{L}(s)\}\cdot \mathrm{Lip}\,(Q), \\ ||\rho_0||_\infty &= \sup_{0\le m\le 1} \rho_0(m), \\ \mathrm{Lip}\,(Q) &= \sup_{0\le F'\le F} \frac{Q(F) - Q(F')}{F - F'}, \\ \overline{Q} &= \sup_{F\ge 0} Q(F), \\ R &= \alpha|\delta_A - \delta_L|\,||\rho_0||_\infty. \end{aligned}$$

Putting $\tilde{F}(t) = \int_0^t |F(s) - \overline{F}(s)|\, ds$ and similarly defining $\tilde{m}, \tilde{L}$ and $\tilde{N}$, the above integral estimates imply that

$$\begin{aligned}
\frac{d\tilde{F}}{dt} &\le \overline{Q}\tilde{L} + K\tilde{F}, \qquad \tilde{F}(0) = 0\\
\frac{d\tilde{m}}{dt} &\le \mathrm{Lip}\,(Q)\tilde{F}, \qquad \tilde{m}(0) = 0\\
\frac{d\tilde{L}}{dt} &\le \mathrm{Lip}\,(Q)||\rho_0||_\infty \tilde{F} + q\tilde{N}, \qquad \tilde{L}(0) = 0\\
\frac{d\tilde{N}}{dt} &\le \alpha||\rho_0||_\infty \mathrm{Lip}\,(Q)\tilde{F} + R\tilde{m}, \qquad \tilde{N}(0) = 0.
\end{aligned}$$

By the Kamke comparison theorem [**3**], it follows that

$$\tilde{F}(t), \tilde{m}(t), \tilde{L}(t), \tilde{N}(t) \le 0, \qquad 0 \le t \le T,$$

and hence $F = \overline{F}$, $m = \overline{m}$, $L = \overline{L}$ and $N = \overline{N}$. This establishes the uniqueness of solutions of (1.12) and hence (1.6). Our proof is complete. □

Now we focus on the threshold delay differential equations (1.7) and (1.8). It can be viewed as an equation for F and N since L and τ_0 can be regarded as determined, explicitly in the case of L, implicitly in the case of τ_0, by F and N. By a solution of (1.7), we will mean continuous functions $F(t)$ and $N(t)$ defined for $t \in [0, t_1)$, where $t_0 < t_1 \le \infty$, such that $F(t)$ and $N(t)$ agree on $[0, t_0]$ with the functions described in Lemma 1.3, $F(t)$ and $N(t)$ are differentiable on (t_0, t_1) and (1.7) holds in the sense that $L(t)$ and $\tau_0(t)$ are defined by the second and fourth equation, respectively.

Temporarily assuming that (1.7) defines functions $F(t), L(t), N(t)$ and $\tau_0(t)$ for $t \ge t_0$, we set

$$\begin{aligned}
\eta = m(t) &= \int_0^t Q(F(s))\, ds, \qquad t \ge 0,\\
x(\eta) = F(t), \qquad y(\eta) &= L(t), \qquad z(\eta) = N(t).
\end{aligned} \tag{1.13}$$

Since an individual larvae gains mass at the rate $Q(F(t))$ at time t, the new independent variable η may be regarded as the accumulated mass of an imaginary larvae present as an egg at $t = 0$ which is forced to remain in the larval class. Note that $t = t_0$ corresponds to $\eta = 1$ in the above transformation since $\tau(t_0) = t_0$ in the threshold condition (1.8). The latter can be rewritten as

$$\int_0^t Q(F(s))\,ds - \int_0^{t-\tau_0} Q(F(s))\,ds = 1$$

in order to see that

$$\eta - 1 = \int_0^{t-\tau_0} Q(F(s))\,ds.$$

This is the key point of making the transformation (1.13) since it transforms a variable delay $t - \tau_0(t)$ to a constant delay $\eta - 1$. Furthermore,

$$\begin{aligned} \tau_0(t) = t - (t - \tau_0(t)) &= \int_{\eta-1}^{\eta} \frac{dt}{d\bar{\eta}}\,d\bar{\eta} \\ &= \int_{\eta-1}^{\eta} Q(x(\bar{\eta}))^{-1}\,d\bar{\eta} \\ &= \int_{-1}^{0} Q(x_\eta(s))^{-1}\,ds \equiv \tau(x_\eta), \qquad t \geq t_0, \end{aligned} \tag{1.14}$$

where we have used the usual notation x_η for the element of $C \equiv C([-1,0],\mathbf{R})$ defined by $x_\eta(s) = x(\eta + s)$ for $-1 \leq s \leq 0$. The calculation above shows that the variable delay has been converted to a nonlinear functional on C. A straightforward calculation shows that x, y, z must satisfy

$$\begin{aligned} \frac{dx}{d\eta} &= Q(x(\eta))^{-1} - y(\eta) \\ y(\eta) &= q\int_{-1}^{0} z_\eta(r) Q(x_\eta(r))^{-1} \exp\Big[-\delta_L \int_r^0 Q(x_\eta(u))^{-1}\,du \Big]\,dr \\ \frac{dz}{d\eta} &= \alpha q Q(x(\eta-1))^{-1} z(\eta-1) e^{-\delta_L \tau(x_\eta)} - \delta_A Q(x(\eta))^{-1} z(\eta) \end{aligned} \tag{1.15}$$

for $\eta > 1$. This is simply a functional differential equation for x and z as y is determined by x and z. The initial data for (1.15) are given by

$$x(\eta) = F(t), \qquad z(\eta) = N(t), \qquad 0 \leq \eta \leq 1, \tag{1.16}$$

where $F(t)$ and $N(t)$ are given on $0 \le t \le t_0$ by Lemma 1.3 and η is given in (1.13).

Our next result makes precise the formal arguments above by establishing the existence and uniqueness of a solution of (1.7) and by describing the relationship between a solution of (1.7) and a solution of (1.15).

Proposition 1.4. *The equation* (1.7)*, with initial data* $F|_{[0,t_0]}$*,* $L|_{[0,t_0]}$*,* $N|_{[0,t_0]}$ *given by Lemma* 1.3*, has a unique solution defined on* (t_0, ∞)*. This solution satisfies* $F(t) > 0$ *and* $L(t)$*,* $N(t) \ge 0$*. If* $\alpha q < \delta_A$ *then*

$$\alpha L(t) + N(t) \le C e^{-\delta(t-t_0)}, \qquad t \ge t_0 \tag{1.17}$$

where $\delta = \min\{\delta_A - \alpha q, \delta_L\} > 0$ *and* $C = \alpha L(t_0) + N(t_0)$*. If* $\alpha q \ge \delta_A$ *then*

$$\alpha L(t) + N(t) \le C e^{(\alpha q - \delta_A)(t-t_0)}, \qquad t \ge t_0. \tag{1.18}$$

The solution $(F(t), L(t), N(t))$ *and* $\tau_0(t)$ *can be expressed in terms of the unique maximally extended solution* $(x(\eta), y(\eta), z(\eta))$ *of the functional differential equation* (1.15) *corresponding to the initial data* (1.16) *as*

$$\begin{gathered} F(t) = x(\eta), \qquad L(t) = y(\eta), \qquad N(t) = z(\eta), \qquad t \ge 0 \\ t = \int_0^\eta Q(x(s))^{-1}\, ds, \end{gathered} \tag{1.19}$$

with $\tau_0(t)$ *defined by* (1.14) *for* $t \ge t_0$*.*

In view of (1.19), the solution of (1.7) is determined by the corresponding solution of (1.15) and (1.16). Properties of the solution of (1.7) can be investigated by studying the solutions of (1.15), a functional differential equation for which there are many available techniques.

It must be noted that the maximally extended solution of (1.15), (1.16) is defined for $1 \le \eta < \infty$ as we will show in Proposition 1.5 below.

Proof of Proposition 1.4. Observe that (1.15) is a functional differential equation for $x(\eta)$ and $z(\eta)$, $\eta > 1$, with nonnegative initial data given by (1.16). By standard results in the theory of such equations [**7**], there is a unique solution of (1.15) which can be extended to a maximal interval of existence, $[1, \eta_0)$, for some η_0 satisfying $1 < \eta_0 \leq \infty$. The form of (1.15) immediately implies that $x(\eta) > 0$, $z(\eta) \geq 0$ on $[1, \eta_0)$. Indeed, the domain of the definition of the right side of (1.15) is the set $D = \{(\phi, \psi) \in C \times C : \phi(\theta) > 0, 0 \leq \theta \leq 1\}$; $(x_\eta, z_\eta) \in D$, $1 \leq \eta < \eta_0$.

Let $u(\eta) = \alpha y(\eta)$. A straightforward computation gives

$$\begin{aligned}\frac{du}{d\eta} &= \alpha q z(\eta) Q(x(\eta))^{-1} - \alpha q z(\eta - 1) Q(x(\eta - 1))^{-1} e^{-\delta_L \tau(x_\eta)} \\ &\quad - \delta_L u(\eta) Q(x(\eta))^{-1}.\end{aligned}$$

Hence, $w(\eta) = u(\eta) + z(\eta)$ satisfies

$$\frac{dw}{d\eta} = Q(x(\eta))^{-1}[(\alpha q - \delta_A) z(\eta) - \delta_L u(\eta)].$$

If $\alpha q < \delta_A$ then, as z and u are positive,

$$\frac{dw}{d\eta} \leq -\delta Q(x(\eta))^{-1} w(\eta)$$

where $\delta = \min\{\delta_A - \alpha q, \delta_L\} > 0$. In this case,

$$w(\eta) \leq w(1) \exp\left(-\delta \int_1^\eta Q(x(s))^{-1}\, ds\right), \qquad 1 < \eta < \eta_0. \tag{1.20}$$

If $\alpha q \geq \delta_A$ then

$$\frac{dw}{d\eta} \leq (\alpha q - \delta_A) Q(x(\eta))^{-1} w(\eta)$$

and hence

$$w(\eta) \leq w(1) \exp\left((\alpha q - \delta_A) \int_1^\eta Q(x(s))^{-1}\, ds\right), \qquad 1 < \eta < \eta_0. \tag{1.21}$$

The inequalities (1.20) and (1.21) lead immediately to (1.17) and (1.18) as we will show later. For now, we observe that

$$\int_1^{\eta_0} Q(x(s))^{-1}\, ds = +\infty. \tag{1.22}$$

For, if this integral were finite then w, and hence both y and z, would be bounded on $[1, \eta_0)$. Hence there would exist a positive constant E such that

$$\frac{dx}{d\eta} \geq Q(x(\eta))^{-1} - E.$$

As $Q(x)^{-1}$ is strictly decreasing and becomes unbounded as $x \to 0+$, it is easy to see from the differential inequality that there exists $x_m > 0$ such that $x(\eta) \geq x_m$ for $1 \leq \eta < \eta_0$. Also, as

$$\frac{dx}{d\eta} \leq Q(x(\eta))^{-1}$$

we have

$$x(\eta) \leq x(1) + \int_1^\eta Q(x(s))^{-1}\, ds$$

and so $x(\eta)$ would also be bounded from above by a positive constant. Hence we see that if the integral in (1.22) were finite then $x(\eta)$ belongs to a compact subset of $(0, \infty)$ on its domain $[1, \eta_0)$. But this precludes the possibility that $\eta_0 < \infty$ since, in this case, we could extend the solution (x, z) to the right of $\eta = \eta_0$ contradicting our assumption that (x, z) was maximally extended. We conclude that if $\eta_0 < \infty$, then (1.22) must hold. In case $\eta_0 = +\infty$, then the fact that $x(\eta)$ would be bounded above and below by positive constants if (1.22) were violated, together with the properties of Q, immediately imply a contradiction to the finiteness of the integral. Hence, (1.22) holds in this case as well.

Now, using the maximally extended solution $(x(\eta), z(\eta))$ of (1.15) defined on $0 \leq \eta < \eta_0$, define $F(t), L(t), N(t)$ and $\tau_0(t)$ by (1.19) and (1.14). By (1.22), these functions are defined for all $t \geq 0$.

As $(x(\eta), y(\eta), z(\eta))$ are given on $0 \leq \eta \leq 1$ by (1.16) with $(F(t), L(t), N(t))$ given by Lemma 1.3, it is easily seen that the new definition of $(F(t), L(t), N(t))$ agrees with the old one for $0 \leq t \leq t_0$ and that $t_0 = \int_0^1 Q(x(s))^{-1}\, ds$ (see the calculation (1.14) and recall that $\tau(t_0) = t_0$).

We now show that $F(t), L(t), N(t)$ and

$$\tau_0(t) = \tau(x_\eta) = \int_0^\eta Q(x(r))^{-1}\, dr - \int_0^{\eta - 1} Q(x(r))^{-1}\, dr$$

satisfy (1.7) for $t > t_0$. From the definition of $\tau_0(t)$ we see that $\tau_0(t_0) = t_0$ and for $t > t_0$

$$\begin{aligned}\int_{t-\tau_0(t)}^{t} Q(F(s))\,ds &= \int_{\eta-1}^{\eta} Q(x(\bar\eta))Q(x(\bar\eta))^{-1}\,d\bar\eta \\ &= 1\end{aligned}$$

where we made the change of variable $s = \int_0^{\bar\eta} Q(x(r))^{-1}\,dr$ in the first integral and used the fact that $s = t$ when $\bar\eta = \eta$ and $s = t - \tau_0(t)$ when $\bar\eta = \eta - 1$. In fact, by the definition of $\tau_0(t)$

$$\begin{aligned}\tau_0(t) &= \int_0^{\eta} Q(x(r))^{-1}\,dr - \int_0^{\eta-1} Q(x(r))^{-1}\,dr \\ &= t - \int_0^{\eta-1} Q(x(r))^{-1}\,dr\end{aligned}$$

which implies that $t - \tau_0(t)$ corresponds to $\eta - 1$ under the change of independent variable. It now requires only a straightforward calculation to see that $F(t), L(t)$ and $N(t)$ satisfy (1.7) for $t > t_0$. Moreover, the estimates (1.17) and (1.18) follow from the estimates (1.20) and (1.21) since $\int_1^{\eta} Q(x(s))^{-1}\,ds = t - t_0$. We have now established the existence of a solution of (1.7) for $t > t_0$ satisfying the estimates (1.20) or (1.21).

In order to conclude the uniqueness of the solution of the initial value problem associated with (1.7), we seek a contradiction to the assumption that there are two distinct solutions corresponding to the given initial data on $0 \le t \le t_0$. The transformation (1.13) applied to each of these two distinct solutions must yield (1.15) with the same initial data (1.16). By uniqueness of solutions of initial value problems associated with (1.15), we may conclude that the transformation (1.13) applied to each of the two distinct solutions yields the same solution (x, y, z) of (1.15) corresponding to the initial data (1.16). It is easy to see that for a given solution of (1.7), the application of transformation (1.13) followed by the transformation (1.19) leads back to the given solution of (1.7). It follows that we have a contradiction to our assumption of nonuniqueness. This establishes the uniqueness of solutions of (1.7) as asserted. □

Proposition 1.5. *Let* $\delta_0 = \min\{\delta_L, \delta_A\}$. *Then we have*

$$N(t) \leq N(t_0)e^{-\delta_A(t-t_0)} + \alpha q \int_0^{t-\tau_0(t)} N(r)e^{-\delta_0(t-r)}\,dr, \qquad t > t_0, \tag{1.23}$$

and

$$\int_0^{+\infty} Q(F(s))\,ds = +\infty. \tag{1.24}$$

Before proving the assertions (1.23) and (1.24), we remark that (1.24) has an immediate consequence that $\eta_0 = +\infty$ in Proposition 1.4, that is, the maximally extended solution of (1.15), (1.16) is defined for all $\eta \geq 0$. In fact, since F, N and L are defined for all $t \geq 0$ by Proposition 1.4, x, y and z are defined by (1.13) for all $\eta \geq 0$ and satisfy (1.15). A further consequence of (1.24) is that

$$\lim_{t \to +\infty} t - \tau_0(t) = +\infty.$$

This follows immediately from (1.24) and (1.8) since the latter implies that $t - \tau_0(t)$ is strictly increasing so the limit exists and both (1.8) and (1.24) imply that the limit cannot be finite.

The estimate (1.23), which is an equality when $\delta_A = \delta_L = \delta_0$, is easier to describe in this special case. It says that the adult population at time $t > t_0$ is the sum of two terms, one representing those members of the adult population present at $t = t_0$ which are still alive at time t and the other representing the total number of "births" from time zero to the time when the currently (time t) maturing larvae were eggs, which have survived to time t and successfully moulted. Observe that individuals are not counted twice in the sum since adults present at time t_0 were eggs prior to time zero.

Proof of Proposition (1.5). Integrate the equation for N in (1.7) once to obtain

$$\begin{aligned}N(t) &= N(t_0)e^{-\delta_A(t-t_0)} \\ &\quad + \alpha q \int_{t_0}^{t} N(s-\tau_0)e^{-\delta_L \tau_0} e^{-\delta_A(t-s)} \frac{Q(F(s))}{Q(F(s-\tau_0))}\, ds \\ &\leq N(t_0)e^{-\delta_A(t-t_0)} \\ &\quad + \alpha q \int_{t_0}^{t} N(s-\tau_0)e^{-\delta_0 \tau_0} e^{-\delta_0(t-s)} \frac{Q(F(s))}{Q(F(s-\tau_0))}\, ds.\end{aligned}$$

Equation (1.8) implies the relation

$$\frac{d}{dt}(t-\tau_0(t)) = \frac{Q(F(t))}{Q(F(t-\tau_0(t))}.$$

This suggests a change of variable in the integral term from s to $r = s - \tau_0(s)$ which yields the estimate

$$N(t) \leq N(t_0)e^{-\delta_A(t-t_0)} + \alpha q \int_0^{t-\tau_0(t)} N(r)e^{-\delta_0(t-r)}\, dr$$

where we have used $\tau(t_0) = t_0$. This is (1.23).

Now suppose that (1.24) does not hold. Choose $T > t_0$ such that $\int_T^\infty Q(F(s))\, ds \leq 1/2$. It is easy to see that this implies $t - \tau_0(t) \leq T$ for $t \geq T$ or larvae maturing at time t were eggs before time T. The estimate (1.23) implies that

$$N(t) \leq N(t_0)e^{-\delta_A(t-t_0)} + \alpha q \int_0^{T} N(r)e^{-\delta_0(t-r)}\, dr$$

for $t \geq T$, and hence there exists $M > 0$ such that

$$N(t) \leq Me^{-\delta_0 t}, \qquad t \geq 0.$$

The integral equation for L in (1.7) implies that

$$\begin{aligned}L(t) &= q \int_{t-\tau_0}^{t} e^{-\delta_L(t-s)} N(s)\, ds \\ &\leq qM \int_{t-\tau_0}^{t} e^{-\delta_0 t}\, ds \leq qMe^{-\delta_0 t} t\end{aligned}$$

so $L(t) \to 0$ as $t \to 0+$. In particular, L is bounded and we may argue that (1.24) holds exactly as in the proof of Proposition 1.2, thus obtaining a contradiction to our assumption that the integral is finite. $\square$

Proof of Theorem 1.1. Lemma 1.3 gives F, N and L on $[0, t_0]$ and Proposition 1.4 defines F, N and L on $[t_0, \infty)$. These definitions together with ρ defined by (1.9) give a candidate (F, ρ, N) for the solution of (1.1). The continuity of F and N holds by definition and the compatibility condition (1.3) is easily seen to imply the continuity of ρ on S. Obviously, F, ρ, and N are nonnegative on their respective domains.

It is immediately clear from (1.9) that F and N satisfy the equations for these variables in (1.1). Similarly, the boundary and initial data for F, N and ρ are easily checked. It only remains to check that (iv) of the definition of a global solution holds.

In S_1, we use (1.9) to evaluate

$$\begin{aligned} h^{-1}&\left[\rho\left(m + \int_t^{t+h} Q(F(r))\,dr, t+h\right) - \rho(m,t)\right] \\ &= h^{-1}\left[e^{-\delta_L(t+h)}\rho_0\left(m + \int_t^{t+h} Q(F(r))\,dr - \int_0^{t+h} Q(F(r))\,dr\right)\right. \\ &\qquad\qquad\qquad\qquad \left. - e^{-\delta_L t}\rho_0\left(m - \int_0^t Q(F(r))\,dr\right)\right] \\ &= \rho_0\left(m - \int_0^t Q(F(r))\,dr\right)\frac{e^{-\delta_L(t+h)} - e^{-\delta_L t}}{h}. \end{aligned}$$

Letting $h \to 0+$ in this expression leads to the limit $-\delta_L\rho(m,t)$ as desired.

In S_2, ρ is differentiable by (1.9) and the fact that N, τ, Q and F are differentiable. The verification of (1.1) is straightforward but tedious. Using

$$\frac{\partial \tau}{\partial m} = Q(F(t-\tau))^{-1}$$

and

$$1 - \frac{\partial \tau}{\partial t} = \frac{Q(F(t))}{Q(F(t-\tau))},$$

we obtain the expressions

$$\begin{aligned}Q(F(t))\frac{\partial\rho}{\partial m} &= -qN'(t-\tau)\frac{Q(F(t))}{Q^2(F(t-\tau))}e^{-\delta_L\tau}\\ &\quad - \delta_L qN(t-\tau)\frac{Q(F(t))}{Q^2(F(t-\tau))}e^{-\delta_L\tau}\\ &\quad + qN(t-\tau)e^{-\delta_L\tau}\frac{Q'(F(t-\tau))F'(t-\tau)Q(F(t))}{Q^3(F(t-\tau))},\end{aligned}$$

and

$$\begin{aligned}\frac{\partial\rho}{\partial t} &= qN'(t-\tau)e^{-\delta_L\tau}\frac{Q(F(t))}{Q^2(F(t-\tau))}\\ &\quad - qN(t-\tau)e^{-\delta_L\tau}\frac{Q'(F(t-\tau))F'(t-\tau)Q(F(t))}{Q^3(F(t-\tau))}\\ &\quad - \frac{qN(t-\tau)}{Q(F(t-\tau))}\delta_L e^{-\delta_L\tau} + \delta_L qN(t-\tau)e^{-\delta_L\tau}\frac{Q(F(t))}{Q^2(F(t-\tau))}.\end{aligned}$$

Adding the expressions above gives $-\delta_L\rho$ and completes the proof that (F,ρ,N) is a solution of (1.1).

The uniqueness assertion of Theorem 1.1 holds by Proposition 1.2 and the uniqueness assertions of Lemma 1.3 and Proposition 1.4. The estimates (1.4) and (1.5) follow from (1.17) and (1.18). □

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