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Existence of solutions for a host–parasite model[☆]

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Abstract

The sea bass *Dicentrarchus labrax* has several gill ectoparasites. *Diplectanum aequans* (Plathelminth, Monogenea) is one of these species. Under certain demographic conditions, this flat worm can trigger pathological problems, in particular in fish farms. The life cycle of the parasite is described and a model for the dynamics of its interaction with the fish is described and analyzed. The model consists of a coupled system of ordinary differential equations and one integro-differential equation. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

There is an abundance of host–parasite systems that occur in nature. In this work, we consider one that is of interest because of a problem noticed in aquaculture. We present a new mathematical model of the host–parasite system and we prove the existence of solutions. The ideas we present are not all limited to this specific host–parasite system but could be used to model many other host–parasite systems as well.

For the host–parasite system we will consider, the symptoms the host experiences due to the parasitism are determined by the number of parasites it carries. Because of this, we will consider *density models* — models that take into account the number of parasites that a host has [1,6,7,9]. This is in contrast with *prevalence models* such as S-I-R models where the mere presence of the parasite

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is most important. An age-structured model of this host–parasite dynamics has been considered, subdivided into a countable number of classes depending on how many parasites a host has [6,7,9]. That is, there is a countable number of partial differential equations: one for hosts having no parasites, one for hosts having one parasite, one for hosts having two parasites, and so on. Elsewhere, a deterministic model without age–structure — consisting of a countable number of ordinary differential equations, one for each class of host, is examined [1]. It is suggested that one may wish to try taking the number of parasites that a host carries to be a continuous variable [1]. We followed this idea in a previous paper [11], and we now elaborate and analyze the continuous model here.

The host we look at is the sea-bass, *Dicentrarchus labrax*. The parasite in the system is the macroparasite, *Diplectanum aequans*. The parasite attaches itself to the gills of the sea-bass. If enough parasites are on the gills, the fish suffocates, and the parasites die along with the fish.

The life cycle of *Diplectanum aequans* consists of three distinct phases: eggs, larvae, and parasites. Eggs live outside the host in the sea or water basin. This stage lasts approximately four days. Eggs that survive the four days become larvae. The larva stage lasts about 2 days. During this time, the larvae must adhere to a host or die from lack of nourishment. Once a larva attaches to a host, it becomes a parasite. The average lifetime of a parasite is approximately 90 days and consists of two stages: juvenile and adult stages. The first 20 days are the juvenile stage, the last 70 — the adult stage. Juvenile parasites can fecundate an adult partner, but they are unable to procreate. Once a parasite is an adult, it can both fecundate another adult parasite and procreate [10].

Eggs laid by the adult parasites go into the water and fall to the bottom of the sea or basin. There, if they survive, they develop into larvae in about four days. Next, the larvae try to attach to a host. Many conditions influence parasite recruitment by hosts. We consider two important ones. First, the more hosts present, the more recruitment can take place assuming some given number of larvae available. Second, hosts that carry many parasites will recruit more larvae than hosts that carry few or no parasites. This is because hosts with few or no parasites are healthy and spend their time swimming around actively while highly parasitized hosts are unhealthy. This causes them to spend much of their time near the bottom of the sea or basin in an inactive state making it easier for more larvae to attach themselves to these fish [10].

The basin's water is renewed by piping in water from a nearby sea. This results in an exterior supply of eggs and larvae. Tanks in fish farms tend to contain fish of roughly the same size, so we will not need to take into account the fact that larger fish can tolerate more parasites than smaller ones. The ages of the fish and time spans we consider allow us to ignore reproduction of hosts, since sea-bass males require about two years to mature sexually and females require about three years to do so [12]. The fish farmers are concerned with a time span more along the lines of one to two years. A discrete model for this system with Poisson distributions of deaths and recruitment was originally proposed by Langlais and Silan [10] and extended by Bouloux [2,3]. Our continuous model described in this paper is similar to that one in many ways.

The organization of this paper is as follows. In the next section we present a continuous mathematical model for the host–parasite system described above. In this model, we try to incorporate some of the features that appear in the discrete model mentioned above [2,10]. In particular, the recruitment process is modeled in a similar way. In Section 3, we will show that a solution exists to these equations. The idea will be to construct a mapping using the equations and then show that the mapping has a fixed point. Finally, in Section 4, we shall present the results of some numerical simulations obtained using this model and draw some conclusions.

2. A continuous mathematical model

2.1. Dynamics of the egg and larva populations

We begin by describing the dynamics for the first two stages in the life cycle of the parasite population: the egg and larva stages. We will use the same variable to represent the egg and larva populations, $E(a, t)$, where a represents age and t represents time. $E(a, t)$ is the age-density distribution at time t of eggs and larvae. Ages between 0 and 4 correspond to eggs and ages between 4 and 6 correspond to larvae. We let $L(t)$ be the total number of larvae at time t , so

$$L(t) = \int_4^6 E(a, t) da.$$

We assume E satisfies simple linear dynamics of McKendrick type [8]:

$$\begin{aligned} \frac{\partial E}{\partial t} + \frac{\partial E}{\partial a} &= -\mu_E(a)E + \Lambda(a, t), \\ E(0, t) &= \beta \mathcal{A}(t), \\ E(a, 0) &= E_0(a), \quad 0 \leq a \leq 6. \end{aligned} \tag{1}$$

Here $\mu_E(a)$ denotes the mortality rate at age a . For ages between 0 and 4, it equals the mortality rate of eggs, for ages between 4 and 6, it equals the mortality rate of larvae, and for ages greater than 6, it is assumed to be infinite since larvae are either dead by age 6 or have attached themselves to hosts and are parasites. $\Lambda(a, t)$ denotes an exterior supply of both eggs and larvae. β is the birth rate of adult parasites, and $\mathcal{A}(t)$ is the number of adult parasites at time t . Finally, $E_0(a)$ gives the initial age distribution of eggs and larvae.

If $\mathcal{A}(t)$ is a known function, we can solve (1) along characteristics. The characteristic equations are

$$\frac{dt}{ds} = 1, \quad \frac{da}{ds} = 1, \quad \frac{dE}{ds} = -\mu_E E + \Lambda.$$

Integrating these we obtain $t = s + t_0$, $a = s + a_0$, and

$$E = C e^{-\int_0^s \mu_E(\sigma + a_0) d\sigma} + \int_0^s \Lambda(\tau + a_0, \tau + t_0) e^{-\int_0^\tau \mu_E(\sigma + a_0) d\sigma} d\tau.$$

For $a \geq t$ we have the boundary condition when $s = 0$, $t = 0$, $a = a_0$, and $E = E_0(a_0)$. So $t_0 = 0$, $a_0 = a - t$, and

$$E(a, t) = E_0(a - t) e^{-\int_0^t \mu_E(\sigma + a - t) d\sigma} + \int_0^t \Lambda(\tau + a - t, \tau) e^{-\int_{\tau+a-t}^a \mu_E(\sigma) d\sigma} d\tau.$$

For $a < t$ we have the boundary condition when $s = 0$, $t = t_0$, $a = 0$, and $E = \beta \mathcal{A}(t_0)$. So $a_0 = 0$, $t_0 = t - a$, and

$$E(a, t) = \beta \mathcal{A}(t - a) e^{-\int_0^a \mu_E(\sigma) d\sigma} + \int_0^a \Lambda(\tau, \tau + t - a) e^{-\int_\tau^a \mu_E(\sigma) d\sigma} d\tau.$$

In summary, if $\mathcal{A}(t)$ is known, we can solve for $E(a, t)$ explicitly and get

$$E(a, t) = \begin{cases} E_0(a - t) e^{-\int_{a-t}^a \mu_E(\sigma) d\sigma} + \int_0^t \Lambda(\tau + a - t, \tau) e^{-\int_{\tau+a-t}^a \mu_E(\sigma) d\sigma} d\tau, & a \geq t, \\ \beta \mathcal{A}(t - a) e^{-\int_0^a \mu_E(\sigma) d\sigma} + \int_0^a \Lambda(\tau, \tau + t - a) e^{-\int_{\tau}^a \mu_E(\sigma) d\sigma} d\tau, & a < t. \end{cases} \quad (2)$$

2.2. Dynamics of the parasite and host populations

We let $H(p, t)$ be the parasite-density distribution of hosts at time t . This means if $0 \leq p_1 < p_2 \leq p^* < +\infty$

$$\int_{p_1}^{p_2} H(p, t) dp = \text{the number of hosts having between } p_1 \text{ and } p_2 \text{ parasites at time } t.$$

The total number of hosts at time t , $\mathcal{H}(t)$, is then given by

$$\mathcal{H}(t) = \int_0^{p^*} H(p, t) dp,$$

while the total number of parasites at time t , $\mathcal{P}(t)$, is then given by

$$\mathcal{P}(t) = \int_0^{p^*} pH(p, t) dp.$$

We have assumed that no host can have more than $p^* < \infty$ parasites and survive.

In order to keep the structure of the hosts more manageable, we make the following hypothesis

(H1) At time $t = 0$ all parasites in all hosts are juvenile parasites of age 0.

This will allow us to track the number of juvenile and adult parasites without adding any type of age structure to this portion of the model. At the end of this section we explain how we do this.

We describe the dynamics of the parasites within a host of type $H(p_0, t_0)$ by the following initial value problem:

$$\begin{aligned} \frac{dp}{dt} = v(p, t) &= -\mu(t)p + \rho \frac{\mathcal{H}(t)}{\mathcal{H}(t) + C} f(\mathcal{F}(H)(t), p, t) L(t), \\ p(t_0) &= p_0. \end{aligned} \quad (3)$$

The first term on the right side of (3), $-\mu(t)p$, is a death term. Here $\mu(t)$ is the mortality rate of parasites, and we take it to be

$$\mu(t) = \frac{\mu_j[\mathcal{P}(t) - \mathcal{A}(t)] + \mu_a \mathcal{A}(t)}{\mathcal{P}(t)} \quad \text{if } t \geq 0,$$

where μ_j and μ_a are the mortality rates for juvenile and adult parasites, respectively, and $0 < \mu_j < \mu_a$. Recall that $\mathcal{P}(t)$ is the total number of parasites, and $\mathcal{A}(t)$ is the total number of adult parasites at time t . Notice that because of (H1), $\mu(t) = \mu_j$ for $t \in [0, 20]$. The second term of $v(p, t)$ has to do with the recruitment of new larvae by the host. Since the parasites lay eggs that fall into the water, so new parasites come from a host recruiting them. $L(t)$ is the total number of larvae available for recruitment. $\rho \in [0, 1]$ is the probability that a larva adheres to a host when there is an

unlimited supply of hosts, and $\mathcal{H}(t)/(\mathcal{H}(t) + C)$ with $C > 0$, constant, is a scaling factor for this probability. When there are few hosts, this factor is close to zero, and when there are many hosts, this factor is close to one. Finally $f(\mathcal{F}(H)(t), p, t)$ is a function related to the probability that a larva that will attach itself to a host will do so to one that already has p parasites. This function is meant to model the field observation that highly parasitized hosts recruit more new parasites than less highly parasitized hosts [10]. The total number of larvae recruited by all hosts during the time t to $t + dt$ is

$$\rho \frac{\mathcal{H}(t)}{\mathcal{H}(t) + C} L(t) dt,$$

but from the form of $v(p, t)$ it also must be equal to

$$\int_0^{p^*} \rho \frac{\mathcal{H}(t)}{\mathcal{H}(t) + C} f(\mathcal{F}(H)(t), p, t) L(t) H(p, t) dp.$$

This puts the following restriction on $f(\mathcal{F}(H)(t), p, t)$

$$\int_0^{p^*} f(\mathcal{F}(H)(t), p, t) H(p, t) dp = 1. \quad (4)$$

If we were to choose f to be of the simple form mp , for example, (4) requires us to have $1/\mathcal{P}(t)$ for the slope.

The growth of the host population is given by the following problem

$$\begin{aligned} \frac{\partial H}{\partial t} + \frac{\partial}{\partial p}(vH) &= -\mu_H(p)H, \\ H(p, 0) &= H_0(p), \\ H(0, t) &= 0, \end{aligned} \quad (5)$$

where $\mu_H(p)$ denotes the parasite-induced mortality rate of the hosts and $H_0(p)$ is the initial distribution of hosts. We take the mortality rate of the hosts to be constant for values of p between 0 and some critical level. Then for values of p between the critical level and what we call a lethal level $\mu_H(p)$ is positive and increasing. Finally for values of p greater than the lethal level, $\mu_H(p)$ continues to increase but more rapidly and goes to infinity as p approaches p^* .

2.3. Computing the total number of adult and juvenile parasites

We now explain how to compute the total number of adult parasites at time t , $\mathcal{A}(t)$. If $t \in [0, 20)$, then $\mathcal{A}(t) = 0$ because of (H1). Otherwise, suppose $p = G(t; p_0, t_0)$ is the solution of the initial value problem (3). If we let $k(t)$ be the number of adult parasites in a host of type $H(p, t)$, then

$$k(t) = e^{-\int_{t-20}^t \mu(\sigma) d\sigma} G(t - 20; p, t).$$

These are the parasites that were present 20 days ago and have survived the last 20 days. That means

$$\mathcal{A}(t) = \int_0^{p^*} e^{-\int_{t-20}^t \mu(\sigma) d\sigma} G(t - 20; p, t) H(p, t) dp.$$

If we let $j(t)$ denote the number of juvenile parasites in a host of type $H(p, t)$ and we let $\mathcal{J}(t)$ denote the total number of juvenile parasites at time t , then obviously we have $j(t) = p - k(t)$ and $\mathcal{J}(t) = \mathcal{P}(t) - \mathcal{A}(t)$.

We can compute $j(t)$ without first computing $k(t)$ by figuring out how many parasites were recruited and survived during the last 20 days. This gives us

$$j(t) = \int_{t-20}^t e^{-\int_{\tau}^t \mu(\sigma) d\sigma} \rho \frac{\mathcal{H}(\tau)}{\mathcal{H}(\tau) + C} L(\tau) f(\mathcal{F}(H)(\tau), G(\tau; p, t), \tau) d\tau.$$

$j(t)$ defined this way should still satisfy $j(t) = p - k(t)$. We check this now. We know that $G(\tau; p, t)$ satisfies (3), so

$$\frac{d}{d\tau} G(\tau; p, t) + \mu(\tau) G(\tau; p, t) = \rho \frac{\mathcal{H}(\tau)}{\mathcal{H}(\tau) + C} f(\mathcal{F}(H)(\tau), G(\tau; p, t), \tau) L(\tau).$$

We can rewrite this in the form

$$\frac{d}{d\tau} [e^{\int_0^{\tau} \mu(\sigma) d\sigma} G(\tau; p, t)] = \rho \frac{\mathcal{H}(\tau)}{\mathcal{H}(\tau) + C} L(\tau) f(\mathcal{F}(H)(\tau), G(\tau; p, t), \tau) e^{\int_0^{\tau} \mu(\sigma) d\sigma}.$$

Integrating both sides from $t - 20$ to t we get

$$\begin{aligned} e^{\int_0^t \mu(\sigma) d\sigma} G(t; p, t) - e^{\int_0^{t-20} \mu(\sigma) d\sigma} G(t-20; p, t) \\ = \int_{t-20}^t \rho \frac{\mathcal{H}(\tau)}{\mathcal{H}(\tau) + C} L(\tau) f(\mathcal{F}(H)(\tau), G(\tau; p, t), \tau) e^{\int_0^{\tau} \mu(\sigma) d\sigma} d\tau. \end{aligned}$$

Solving for $G(t; p, t)$ and noting that $p = G(t; p, t)$ we see that

$$\begin{aligned} p &= \int_{t-20}^t \rho \frac{\mathcal{H}(\tau)}{\mathcal{H}(\tau) + C} L(\tau) f(\mathcal{F}(H)(\tau), G(\tau; p, t), \tau) e^{-\int_{\tau}^t \mu(\sigma) d\sigma} d\tau + e^{-\int_{t-20}^t \mu(\sigma) d\sigma} G(t-20; p, t) \\ &= j(t) + k(t), \end{aligned}$$

as we need.

In the next section, we will show that a solution exists to these equations after making some assumptions on such functions as μ_H , f , and H_0 . In Section 3.1 we handle the case $t \in [0, 20)$, in Section 3.2 we take care of the case $t \in [20, 24)$, and in Section 3.3 we take care of the case $t \in [24, 44)$. The reason we break things up into these time blocks is because there are some discontinuities that occur at $t = 20, 24, 44, 64, 84, \dots$. Because of (H1), there is a discontinuity in $\mathcal{A}(t)$ at $t = 20$ — there are no adult parasites during the first 20 days, but then at day 20 all parasites that are present at $t = 0$ and survive become adults. This causes a discontinuity in $\mu(t)$ at $t = 20$ too. Then at $t = 24$, the eggs that were laid by the new adults at $t = 20$ and have survived hatch into larvae. This causes a jump in $L(t)$ which also causes a jump in $\mathcal{P}(t)$ at $t = 24$. This jump in $\mathcal{P}(t)$ results in another jump in $\mathcal{A}(t)$ at $t = 44, 64, \dots$, and the whole process continues.

3. Existence of a solution

In this section, we show that solutions $E(a, t)$ and $H(p, t)$ exist for (1) and (5), respectively.

3.1. Existence for $t \in [0, T]$, $0 < T < 20$

In this section, we take $t \in [0, T]$, where $0 < T < 20$. We will say more about T later. Since $t < 20$, $\mathcal{A}(t) = 0$. So we can solve (1) explicitly and get

$$E(a, t) = \begin{cases} E_0(a - t) e^{-\int_{a-t}^a \mu_E(\sigma) d\sigma} + \int_0^t \Lambda(\tau + a - t, \tau) e^{-\int_{\tau+a-t}^a \mu_E(\sigma) d\sigma} d\tau, & a \geq t, \\ \int_0^a \Lambda(\tau, \tau + t - a) e^{-\int_{\tau}^a \mu_E(\sigma) d\sigma} d\tau, & a < t. \end{cases} \quad (6)$$

We assume E_0 is continuous and $E_0(0) = 0$. We also assume μ_E is nonnegative and $\Lambda(a, t)$ is bounded and nonnegative. Then the total number of larvae, $L(t)$, is a bounded, nonnegative, continuous function for $t \in [0, T]$. Let $L_\infty = \|L\|$ ($< +\infty$), where $\|\cdot\|$ denotes the sup norm. Throughout this work $\|\cdot\|$ will denote the sup norm.

In (3) $v(p, t)$ was defined to be

$$v(p, t) = -\mu(t)p + \rho \frac{\mathcal{H}(t)}{\mathcal{H}(t) + C} f(\mathcal{F}(H)(t), p, t) L(t).$$

Because of (H1) and the fact that $t < 20$, $\mu(t) = \mu_j$ here. We now make the following assumptions on $v(p, t)$:

$$\mathcal{F} : C([0, p^*] \times [0, T]) \rightarrow C([0, T]) \quad \text{is continuous,} \quad (7)$$

$$f(x, p, t) \geq 0 \quad \text{is bounded, and is Lipschitz continuous in } p, \quad (8)$$

$$\frac{\partial f}{\partial p} \text{ exists} \quad \text{is uniformly continuous, and is bounded.} \quad (9)$$

We also assume

$$\mu_H(p) \geq 0, \text{ continuous, increasing and } \int_0^{p^*} \mu_H(p) dp = \infty. \quad (10)$$

Further, we make the following assumptions about H_0 :

$$H_0 \in C([0, p^*]),$$

$$H_0(0) = H_0(p^*) = 0,$$

$$H_0 \geq 0,$$

$$\|H_0\| \leq C_0 < \infty,$$

$$\mathcal{H}(0) = \int_0^{p^*} H_0(p) dp \geq \delta_0,$$

where C_0 and δ_0 are positive constants.

Our goal is to convert problem (5) into that of finding a fixed point of a mapping and then to show that the mapping indeed does have a fixed point. Since $E(a, t)$ is known for $t \in [0, T]$, this will

mean that a solution to the equations presented in Section 2 exists for $t \in [0, T]$. We now construct our mapping.

Suppose we are given $H_i(p, t)$ defined for $p \in [0, p^*]$ and $t \in [0, T]$ with the following properties:

$$\begin{aligned} H_i &\in C([0, p^*] \times [0, T]), \\ H_i(p, 0) &= H_0(p), \\ H_i &\geq 0, \\ \|H_i\| &\leq c_0 < \infty, \\ \mathcal{H}_i(t) &= \int_0^{p^*} H_i(p, t) \, dp \geq \varepsilon_0, \end{aligned} \tag{11}$$

where c_0 and ε_0 are given positive constants. The domain of our mapping will consist of functions that satisfy properties (11). Set

$$v_i(p, t) = -\mu_j p + \rho \frac{\mathcal{H}_i(t)}{\mathcal{H}_i(t) + C} L(t) f(\mathcal{F}(H_i)(t), p, t).$$

Now, we consider the first-order partial differential equation

$$\frac{\partial H}{\partial t} + \frac{\partial}{\partial p}(v_i H) = -\mu_H(p)H,$$

$$H(p, 0) = H_0(p),$$

$$H(0, t) = 0.$$

This is the same as (5) except $v_i(p, t)$ does not depend on the solution to the problem. In (5), $v(p, t)$ does depend on the solution. We can now solve this problem along characteristics in the same manner that we solved (1) for $E(a, t)$. Here the characteristic differential equations are

$$\frac{dt}{ds} = 1, \tag{12}$$

$$\frac{dp}{ds} = v_i(p, t) \tag{13}$$

and

$$\frac{dH}{ds} = \left[-\mu_H(p) - \frac{\partial v_i}{\partial p} \right] H. \tag{14}$$

From (12)

$$t = s + t_0.$$

For (13) we consider the initial value problem

$$\begin{aligned} \frac{dp}{dt} &= v_i(p, t), \\ p(t_0) &= p_0. \end{aligned} \tag{15}$$

We extend $v_i(p, t)$, that is, we extend $H_i(p, t)$, $\mathcal{H}_i(t)$, $\mathcal{F}(H_i)(t)$, and $L(t)$, so that $v_i \in C([- \eta, p^* + \eta] \times [- \eta, T + \eta])$, where $\eta > 0$. Then v_i is Lipschitz continuous in p in the set $[- \eta, p^* + \eta] \times [- \eta, T + \eta]$ with Lipschitz constant M ,

$$M \leq \left| -\mu_j + \frac{c_0 p^* L_\infty \|\partial f / \partial p\|}{\varepsilon_0 + C} \right|.$$

From ordinary differential equation theory, we know that a solution $p = G_i(t; p_0, t_0)$ to (15) exists in a neighborhood of (t_0, p_0) , and this solution can be extended forward and backward in time as long as $0 \leq G_i(t; p_0, t_0) \leq p^*$ and $0 \leq t \leq T$. If $G_i(t^*; p_0, t_0) = p^*$ for some t^* , $0 < t^* < T$, we will define $G_i(t; p_0, t_0) = p^*$ for $t^* \leq t \leq T$. And if $G_i(t^z; p_0, t_0) = 0$ for some t^z , $0 < t^z \leq t_0$, we will define $G_i(t; p_0, t_0) = 0$ for $0 \leq t \leq t^z$. Later we will need to look at (15) and $p = G_i(t; p_0, t_0)$ more closely, but for now we move onto (14).

Integrating (14) we get

$$H = K e^{\mu_j s} e^{-\int_0^{s+t_0} [\mu_H(G_i(\sigma; p_0, t_0)) + \rho[\mathcal{H}_i(\sigma)/(\mathcal{H}_i(\sigma) + C)]L(\sigma)(\partial f / \partial p)(\mathcal{F}(H_i)(\sigma), G_i(\sigma; p_0, t_0), \sigma)] d\sigma}.$$

Next, we use the initial condition $H(p, 0) = H_0(p)$ and the boundary condition $H(0, t) = H(p^*, t) = 0$ to get for $(t, p) \in [0, T] \times [0, p^*]$

$$H(p, t) = \begin{cases} H_0(G_i(0; p, t)) e^{\mu_j t} e^{-\int_0^t [\mu_H(G_i(\sigma; p, t)) + \rho[\mathcal{H}_i(\sigma)/(\mathcal{H}_i(\sigma) + C)]L(\sigma)(\partial f / \partial p)(\mathcal{F}(H_i)(\sigma), G_i(\sigma; p, t), \sigma)] d\sigma} & \text{for } 0 \leq t \leq T, \quad G_i(t; 0, 0) \leq p \leq G_i(t; p^*, 0), \\ 0 & \text{otherwise.} \end{cases} \quad (16)$$

We now define the mapping we have been looking for, Φ , by $\Phi(H_i) = H$, where H is given by (16). Our goal is to show that Φ has a fixed point. To do this we will use the following theorem [5].

Theorem 1 (Schauder). *If S is a convex closed subset of a Banach space and R is a relatively compact subset of S , then every continuous mapping of S into R has a fixed point.*

For our situation set

$$S = \{H : H \text{ has the properties (11)}\}.$$

It is not hard to see that S is a convex closed subset of $C([0, p^*] \times [0, T])$. Let

$$R = \{\Phi(H) : H \in S\}.$$

We need to show that $R \subseteq S$ and that R is relatively compact. First we show that $R \subseteq S$.

Suppose $H \in S$. Looking at (16) we see that $\Phi(H)(p, 0) = H_0(p)$, $\Phi(H) \geq 0$, and $\|\Phi(H)\| \leq C_0 e^{\mu_j T}$. Assuming $C_0 \leq c_0 e^{-20\mu_j}$, we will have $\|\Phi(H)\| \leq c_0$. We still must show that $\Phi(H) \in C([0, p^*] \times [0, T])$ and that $\int_0^{p^*} \Phi(H)(p, t) dp \geq \varepsilon_0$. We will look at the latter first.

Because $\int_0^{p^*} H_0(p) dp \geq \delta_0$, we can find p_1 and p_2 such that $0 < p_1 < p_2 < p^*$ and $\int_{p_1}^{p_2} H_0(p) dp \geq \delta_1$, where $\frac{1}{2}\delta_0 \leq \delta_1 \leq \delta_0$.

Notice that $-\mu_j p \leq v(p, t) \leq -\mu_j p + k$, where $k = (\rho c_0 p^* L_\infty \|f\|)/(\varepsilon_0 + C)$. Thus,

$$G(t; p_1, 0) \geq p_1 e^{-\mu_j t}$$

and

$$G(t; p_2, 0) \leq \frac{k}{\mu_j} + \left(p_2 - \frac{k}{\mu_j}\right) e^{-\mu_j t}.$$

Fix $\eta > 0$ such that $p_2 < p^* - \eta$. If $k/\mu_j > p^* - \eta$, define T_2 by $p^* - \eta = k/\mu_j + (p_2 - k/\mu_j)e^{-\mu_j T_2}$. In this case,

$$T_2 = \frac{1}{\mu_j} \ln \frac{k/\mu_j - p_2}{k/\mu_j - p^* + \eta}.$$

If $k/\mu_j \leq p^* - \eta$, let $T_2 = 20 - \varepsilon$, where ε is some small positive number. Now we define T by $T = \min\{T_2, 20 - \varepsilon\}$. Then

$$\begin{aligned} \int_0^{p^*} \Phi(H)(p, t) \, dp &\geq e^{-T[\mu_H(p^* - \eta) + \rho c_0 p^* L_\infty \|\partial f / \partial p\| / (\varepsilon_0 + C)]} \int_{p_1}^{p_2} H_0(p) \, dp \\ &\geq \delta_1 e^{-T[\mu_H(p^* - \eta) + \rho c_0 p^* L_\infty \|\partial f / \partial p\| / (\varepsilon_0 + C)]} \\ &\geq \frac{\delta_0}{2} e^{-T[\mu_H(p^* - \eta) + \rho c_0 p^* L_\infty \|\partial f / \partial p\| / (\varepsilon_0 + C)]} \\ &\geq \varepsilon_0, \end{aligned}$$

if we have chosen δ_0 such that

$$\delta_0 \geq 2\varepsilon_0 e^{T[\mu_H(p^* - \eta) + \rho c_0 p^* L_\infty \|\partial f / \partial p\| / (\varepsilon_0 + C)]}.$$

Finally, to show that $R \subseteq S$, we must verify that $\Phi(H) \in C([0, p^*] \times [0, T])$. We partition $[0, p^*] \times [0, T]$ into the disjoint sets

$$A_1 = \{(t, p) : 0 \leq t \leq T, G(t; p^*, 0) < p \leq p^*\},$$

$$A_2 = \{(t, p) : 0 \leq t \leq T, G(t; 0, 0) \leq p \leq G(t; p^*, 0)\},$$

$$A_3 = \{(t, p) : 0 \leq t \leq T, 0 \leq p < G(t; 0, 0)\}.$$

Notice that $A_1 \cup A_2 \cup A_3 = [0, T] \times [0, p^*]$. If we examine (16), we see that $\Phi(H)$ is continuous in each A_i , $i = 1, 2, 3$, separately. We have to verify that it is continuous across the boundaries between the sets.

Let $(t_1, p_1) \in A_1$ and $(t_2, p_2) \in A_2$, and suppose $[(t_1 - t_2)^2 + (p_1 - p_2)^2]^{1/2} < \delta$, where $\delta > 0$. We can find a point $(t_{12}, p_{12}) \in \partial A_1 \cap \partial A_2$ such that $[(t_{12} - t_i)^2 + (p_{12} - p_i)^2]^{1/2} < \delta$, $i = 1, 2$. If we set

$$\begin{aligned} V &= \max_{(t, p) \in A_1 \cup A_2 \cup A_3} |v(p, t)| \\ &\leq \mu_j p^* + \frac{\rho c_0 p^* L_\infty \|f\|}{\varepsilon_0 + C}, \end{aligned}$$

then

$$-V|t - t_2| + p_2 \leq G(t; p_2, t_2) \leq V|t - t_2| + p_2.$$

Thus,

$$\begin{aligned} |G(t_{12}; p_2, t_2) - G(t_{12}; p_{12}, t_{12})| &= |G(t_{12}; p_2, t_2) - p_{12}| \\ &\leq |t_2 - t_{12}|V + |p_2 - p_{12}| \\ &\leq \delta(V + 1). \end{aligned} \quad (17)$$

We now state a theorem from ordinary differential equation theory that we will use a number of times. For a reference, see [4] for example.

Theorem 2. Suppose g is a continuous function of two variables in a domain D , and it is Lipschitz continuous in its second argument in D with Lipschitz constant k . Let ϕ_1 and ϕ_2 be ε_1 - and ε_2 -approximate solutions of

$$\frac{dx}{dt} = g(t, x)$$

of class $(C \cap \text{piecewise } C^1)$ on some interval (a, b) , satisfying for some τ , $a < \tau < b$,

$$|\phi_1(\tau) - \phi_2(\tau)| \leq \delta,$$

where δ is a nonnegative constant. If $\varepsilon = \varepsilon_1 + \varepsilon_2$, then for all $t \in (a, b)$,

$$|\phi_1(t) - \phi_2(t)| \leq \delta e^{k|t-\tau|} + \frac{\varepsilon}{k}(e^{k|t-\tau|} - 1).$$

Using Theorem 2 and (17) we see that

$$|G(0; p_2, t_2) - G(0; p_{12}, t_{12})| \leq \delta(V + 1)e^{MT}.$$

But since $(t_{12}, p_{12}) \in \partial A_1 \cap \partial A_2$, $G(0; p_{12}, t_{12}) = p^*$. So

$$|G(0; p_2, t_2) - p^*| \leq \delta(V + 1)e^{MT}.$$

Because $(t_1, p_1) \in A_1$, $\Phi(H)(p_1, t_1) = 0$, so

$$\begin{aligned} &|\Phi(H)(p_2, t_2) - \Phi(H)(p_1, t_1)| \\ &= \Phi(H)(p_2, t_2) \\ &= H_0(G(0; p_2, t_2))e^{\mu_j t} e^{-\int_0^{t_2} [\mu_H(G(\sigma; p_2, t_2)) + \rho[\mathcal{H}(\sigma)/(\mathcal{H}(\sigma) + C)]L(\sigma)(\partial f/\partial p)(\mathcal{F}(H)(\sigma), G(\sigma; p_2, t_2), \sigma)] d\sigma} \\ &\leq H_0(G(0; p_2, t_2))e^{\mu_j T}. \end{aligned}$$

Since H_0 is continuous and $H_0(p^*) = 0$, by taking δ small enough, we can make $H_0(G(0; p_2, t_2))$ and hence $|\Phi(H)(p_2, t_2) - \Phi(H)(p_1, t_1)|$ as small as we please. Thus, $\Phi(H)$ is continuous across the boundary between A_1 and A_2 . The same idea can be used to show that $\Phi(H)$ is continuous across the boundary between A_2 and A_3 . So $\Phi(H) \in C([0, p^*] \times [0, T])$. We have shown that $R \subseteq S$.

In order to apply Theorem 1 to Φ , we need to show that R is relatively compact. We will use the Arzelà–Ascoli Theorem to do this. So we will need to show that R is uniformly bounded and equicontinuous.

Since $\|\Phi(H)\| \leq c_0$ for all $H \in S$, R is uniformly bounded. Now we verify that R is equicontinuous.

Suppose $(t_1, p_1), (t_2, p_2) \in [0, p^*] \times [0, T]$ and $[(p_1 - p_2)^2 + (t_1 - t_2)^2]^{1/2} < \delta$ where $\delta > 0$. We just saw that if $(t_1, p_1) \in A_1$ and $(t_2, p_2) \in A_2$, then we can make $|\Phi(H)(p_1, t_1) - \Phi(H)(p_2, t_2)|$ as small as we want by taking δ sufficiently small. Notice that this was independent of our choice of $H \in S$. We can do the same for $(t_1, p_1) \in A_3$ and $(t_2, p_2) \in A_2$. Recall that $\Phi(H)(p, t) = 0$ for all $(t, p) \in A_1 \cup A_3$, so to show equicontinuity, it only remains to show we can do this for $(t_1, p_1), (t_2, p_2) \in A_2$.

Suppose $(t_1, p_1), (t_2, p_2) \in A_2$. Then by the same argument as (17),

$$|G(t_1; p_1, t_1) - G(t_1; p_2, t_2)| \leq \delta(V + 1).$$

This and Theorem 2 imply that for $0 \leq t \leq T$

$$|G(t; p_1, t_1) - G(t; p_2, t_2)| \leq \delta(V + 1)e^{MT}.$$

We have a few cases to consider.

First suppose $p_1 = p^*$. Then $e^{-\int_0^{t_1} \mu_H(G(\sigma; p_1, t_1)) d\sigma} = 0$, so $\Phi(H)(p_1, t_1) = 0$. Also $|p^* - p_2| < \delta$, so $e^{-\int_0^{t_2} \mu_H(G(\sigma; p_2, t_2)) d\sigma}$ is as small as we want by taking δ sufficiently small. This means $\Phi(H)(p_2, t_2)$ is small, and hence, so is $|\Phi(H)(p_1, t_1) - \Phi(H)(p_2, t_2)|$. All this is independent of our choice of $H \in S$. The case where $p_2 = p^*$ is the same.

Second, suppose $p_1 \neq p^*$, $p_2 \neq p^*$, but $G(0; p_1, t_1) = p^*$. Then, because $H_0(p^*) = 0$, $\Phi(H)(p_1, t_1) = 0$. From Theorem 2, we know that we will have $G(0; p_2, t_2) = p^* - \eta$ where $\eta \geq 0$ is as small as we want (by taking δ sufficiently small). Then,

$$\Phi(H)(p_2, t_2) \leq H_0(G(0; p_2, t_2))e^{\mu_j t_2}$$

is small since H_0 is continuous and $H_0(p^*) = 0$. Thus $|\Phi(H)(p_1, t_1) - \Phi(H)(p_2, t_2)|$ is small. All this is again independent of our choice of $H \in S$. The case where $G(0; p_2, t_2) = p^*$ is the same.

Third suppose $p_1 \neq p^*$, $p_2 \neq p^*$, $G(0; p_1, t_1) \neq p^*$, and $G(0; p_2, t_2) \neq p^*$. Then $G(\sigma; p_i, t_i) \neq p^*$ for $0 \leq \sigma \leq t_i$, $i = 1, 2$, and $\mu_H(G(\sigma; p_i, t_i))$ will be uniformly continuous for $0 \leq \sigma \leq t_i$, $i = 1, 2$. Now, given $\varepsilon > 0$, taking δ sufficiently small, the continuity of H_0 implies

$$|H_0(G(0; p_1, t_1)) - H_0(G(0; p_2, t_2))| < \varepsilon. \quad (18)$$

Also, for $0 \leq \sigma \leq t_1$, the uniform continuity of $\partial f / \partial p$ implies

$$\left| \frac{\partial f}{\partial p}(\mathcal{F}(H)(\sigma), G(\sigma; p_1, t_1), \sigma) - \frac{\partial f}{\partial p}(\mathcal{F}(H)(\sigma), G(\sigma; p_2, t_2), \sigma) \right| < \varepsilon \quad (19)$$

and the uniform continuity of $\mu_H(G(\sigma; p_i, t_i))$ for $0 \leq \sigma \leq t_i$, $i = 1, 2$, implies

$$|\mu_H(G(\sigma; p_1, t_1)) - \mu_H(G(\sigma; p_2, t_2))| < \varepsilon. \quad (20)$$

These bounds are all independent of our choice of $H \in S$. Looking back at (16) we see that conditions (18)–(20) along with the continuity of the exponential function imply we can make $|\Phi(H)(p_1, t_1) - \Phi(H)(p_2, t_2)|$ as small as we please independently of our choice of $H \in S$ by taking δ small enough. Therefore, R is equicontinuous. The Arzelà–Ascoli Theorem then tells us that R is relatively compact.

Before we can use Theorem 1 to say Φ has a fixed point, the last condition we need to verify is that Φ is continuous. Suppose $H_1, H_2 \in S$ and $\|H_1 - H_2\| < \delta$, where $\delta > 0$. Instead of looking

immediately at $\|\Phi(H_1) - \Phi(H_2)\|$, we obtain a few preliminary bounds. First,

$$\left| \frac{\mathcal{H}_1(t)}{\mathcal{H}_1(t) + C} - \frac{\mathcal{H}_2(t)}{\mathcal{H}_2(t) + C} \right| = \left| \frac{C(\mathcal{H}_1(t) - \mathcal{H}_2(t))}{(\mathcal{H}_1(t) + C)(\mathcal{H}_2(t) + C)} \right| < \frac{\delta C p^*}{\varepsilon_0^2}. \quad (21)$$

Second,

$$\begin{aligned} & (\mathcal{H}_1(t) + C)(\mathcal{H}_2(t) + C) \left[\frac{\mathcal{H}_1(t)}{\mathcal{H}_1(t) + C} f(\mathcal{F}(H_1)(t), p, t) - \frac{\mathcal{H}_2(t)}{\mathcal{H}_2(t) + C} f(\mathcal{F}(H_2)(t), p, t) \right] \\ &= \mathcal{H}_1(t)\mathcal{H}_2(t)[f(\mathcal{F}(H_1)(t), p, t) - f(\mathcal{F}(H_2)(t), p, t)] \\ &+ C[\mathcal{H}_1(t)f(\mathcal{F}(H_1)(t), p, t) - \mathcal{H}_1(t)f(\mathcal{F}(H_2)(t), p, t) \\ &+ \mathcal{H}_1(t)f(\mathcal{F}(H_2)(t), p, t) - \mathcal{H}_2(t)f(\mathcal{F}(H_2)(t), p, t)] \\ &= \mathcal{H}_1(t)[\mathcal{H}_2(t) + C][f(\mathcal{F}(H_1)(t), p, t) - f(\mathcal{F}(H_2)(t), p, t)] \\ &+ Cf(\mathcal{F}(H_2)(t), p, t)[\mathcal{H}_1(t) - \mathcal{H}_2(t)], \end{aligned}$$

so

$$\begin{aligned} |v_1(p, t) - v_2(p, t)| &= \rho L(t) \left| \frac{\mathcal{H}_1(t)}{\mathcal{H}_1(t) + C} f(\mathcal{F}(H_1)(t), p, t) - \frac{\mathcal{H}_2(t)}{\mathcal{H}_2(t) + C} f(\mathcal{F}(H_2)(t), p, t) \right| \\ &\leq \rho L_\infty \left[\frac{c_0 p^*}{\varepsilon_0} |f(\mathcal{F}(H_1)(t), p, t) - f(\mathcal{F}(H_2)(t), p, t)| + \frac{\delta \|f\| C p^*}{\varepsilon_0^2} \right]. \end{aligned}$$

The continuity of \mathcal{F} and the uniform continuity of f tell us given $\delta_2 > 0$, if we choose δ sufficiently small, $|v_1(p, t) - v_2(p, t)| < \delta_2$. Theorem 2 then tells us

$$|G_1(t; p_0, t_0) - G_2(t; p_0, t_0)| \leq \frac{\delta_2}{M} (e^{MT} - 1). \quad (22)$$

Let A_{i1}, A_{i2}, A_{i3} , $i = 1, 2$, correspond to the sets A_1, A_2, A_3 defined earlier. That is, for $i = 1, 2$

$$A_{i1} = \{(t, p) : 0 \leq t \leq T, G_i(t; p^*, 0) < p \leq p^*\},$$

$$A_{i2} = \{(t, p) : 0 \leq t \leq T, G_i(t; 0, 0) \leq p \leq G_i(t; p^*, 0)\},$$

$$A_{i3} = \{(t, p) : 0 \leq t \leq T, 0 \leq p < G_i(t; 0, 0)\}.$$

We will look at $|\Phi(H_1)(p, t) - \Phi(H_2)(p, t)|$ for $(t, p) \in A_{1j} \cap A_{2k}$, $j, k = 1, 2, 3$.

If $(t, p) \in A_{11} \cap A_{21}, A_{11} \cap A_{23}, A_{13} \cap A_{21}, A_{13} \cap A_{23}$,

$$|\Phi(H_1)(p, t) - \Phi(H_2)(p, t)| = 0.$$

If $(t, p) \in A_{13} \cap A_{22}$,

$$|\Phi(H_1)(p, t) - \Phi(H_2)(p, t)| = \Phi(H_2)(p, t) \leq H_0(G_2(0; p, t))e^{\mu_j T}.$$

First using the fact that $(t, p) \in A_{13} \cap A_{22}$ and then using (22) we see that

$$\begin{aligned} |G_2(t; p, t) - G_2(t; 0, 0)| &= |p - G_2(t; 0, 0)| \\ &\leq |G_1(t; 0, 0) - G_2(t; 0, 0)| \\ &\leq \frac{\delta_2}{M}(e^{MT} - 1). \end{aligned}$$

Now, Theorem 2 tells us

$$G_2(0; p, t) = |G_2(0; p, t) - G_2(0; 0, 0)| \leq \frac{\delta_2}{M}(e^{MT} - 1)e^{MT}.$$

Since H_0 is continuous and $H_0(0) = 0$, we can make $|\Phi(H_1)(p, t) - \Phi(H_2)(p, t)|$ as small as we want by taking δ sufficiently small.

If $(t, p) \in A_{12} \cap A_{23}$, we have the same situation as $(t, p) \in A_{13} \cap A_{22}$. Actually, $(t, p) \in A_{12} \cap A_{21}$, $A_{11} \cap A_{22}$ also puts us in basically the same situation. We will omit the details for these cases.

It only remains to consider $(t, p) \in A_{12} \cap A_{22}$. Here

$$\begin{aligned} &|\Phi(H_1)(p, t) - \Phi(H_2)(p, t)| \\ &= \left| H_0(G_1(0; p, t))e^{\mu_H t} - \int_0^t [\mu_H(G_1(\sigma; p, t)) + \rho[\mathcal{H}_1(\sigma)/(\mathcal{H}_1(\sigma) + C)]L(\sigma)(\partial f/\partial p)(\mathcal{F}(H_1)(\sigma), G_1(\sigma; p, t), \sigma)] d\sigma \right. \\ &\quad \left. - H_0(G_2(0; p, t))e^{\mu_H t} - \int_0^t [\mu_H(G_2(\sigma; p, t)) + \rho[\mathcal{H}_2(\sigma)/(\mathcal{H}_2(\sigma) + C)]L(\sigma)(\partial f/\partial p)(\mathcal{F}(H_2)(\sigma), G_2(\sigma; p, t), \sigma)] d\sigma \right|. \end{aligned}$$

We will consider a few cases.

First suppose $G_1(t^*; p, t) = p^*$ for some $t^* \in (0, t]$. Then $e^{-\int_0^t \mu_H(G_1(\sigma; p, t)) d\sigma} = 0$, so $\Phi(H_1)(p, t) = 0$. Also (22) tells us $|G_2(t^*; p, t) - p^*| \leq (\delta_2/M)(e^{MT} - 1)$. So we can make $e^{-\int_0^t \mu_H(G_2(\sigma; p, t)) d\sigma}$ as small as we want by taking δ sufficiently small. Thus, we can make $|\Phi(H_1)(p, t) - \Phi(H_2)(p, t)|$ as small as we want. The case where $G_2(t^*; p, t) = p^*$ for some $t^* \in (0, t]$ is the same.

Next, suppose $G_1(0; p, t) = p^*$. Then, $H_0(G_1(0; p, t)) = 0$, so $\Phi(H_1)(p, t) = 0$. Also (22) tells us $|G_2(0; p, t) - p^*| \leq (\delta_2/M)(e^{MT} - 1)$. Since, H_0 is continuous and $H_0(p^*) = 0$, we can make $\Phi(H_2)(p, t)$ as small as we want by taking δ sufficiently small. Thus, we can make $|\Phi(H_1)(p, t) - \Phi(H_2)(p, t)|$ as small as we want. The case where $G_2(0; p, t) = p^*$ is the same.

Finally suppose $G_i(\sigma; p, t) \neq p^*$ for $\sigma \in [0, t]$, $i = 1, 2$. By taking δ sufficiently small, (21), (22), and the continuity of H_0 , μ_H , $\partial f/\partial p$, \mathcal{F} , and the exponential function tell us we can make $|\Phi(H_1)(p, t) - \Phi(H_2)(p, t)|$ as small as we want. Therefore, Φ maps S into R continuously. Theorem 1 guarantees that Φ has a fixed point. That means that (5) has a solution $H(p, t)$. As mentioned above, since we already know $E(a, t)$, we have shown that a solution exists to the equations presented in the previous section, for $t \in [0, T]$, $0 < T < 20$.

3.2. Existence for $t \in [20, T]$, $20 < T < 24$

In this section, we take $t \in [20, T]$ where $20 < T < 24$. Assumptions (7)–(10) concerning \mathcal{F} , f , and μ_H still hold with T now being the T used here. We can assume we have solutions for $t \in [0, 20]$. We need to show now that (1) and (5) have solutions for $t \in [20, T]$.

Since $t < 24$, looking back at (2) we see that

$$L(t) = \int_4^6 \int_0^a \Lambda(\tau, \tau + t - a) e^{-\int_\tau^a \mu_E(\sigma) d\sigma} d\tau da.$$

So $L(t)$ is a bounded, nonnegative, and continuous function for $t \in [20, T]$. We again let $L_\infty = \|L\|$.

Now we consider (5) except in place of the initial condition $H(p, 0) = H_0(p)$, we have $H(p, 20) = H_{20}(p, 20)$ where H_{20} is the solution to (5) for $t \in [0, 20]$. We shall label this problem (5'). We assume H_{20} satisfies the following conditions

$$H_{20} \in C([0, p^*] \times [0, 20]),$$

$$H_{20}(0, t) = H_{20}(p^*, t) = 0,$$

$$H_{20} \geq 0,$$

$$\|H_{20}\| \leq C_{20} < \infty,$$

$$\mathcal{H}_{20}(t) = \int_0^{p^*} H_{20}(p, t) dp \geq \delta_{20},$$

$$\mathcal{P}_{20}(t) = \int_0^{p^*} pH_{20}(p, t) dp \geq \delta_{20},$$

where C_{20} and δ_{20} are positive constants. Also suppose $p = G_{20}(t; p_0, t_0)$ is the solution of

$$\begin{aligned} \frac{dp}{dt} &= v_{20}(p, t) = -\mu_j p + \rho[\mathcal{H}_{20}(t)/(\mathcal{H}_{20}(t) + C)]L(t)f(\mathcal{F}(H_{20})(t), p, t), \\ p(t_0) &= p_0 \end{aligned} \quad (23)$$

for $0 \leq t, t_0 \leq 20$.

To show that (5') has a solution, we will follow the procedure used in the previous subsection. Here, though, $\mu(t)$, the mortality rate of the parasites, is not known. So we shall define a mapping $\Phi(H_i, \mu_i) = (H, \mu)$ and show that this mapping has a fixed point meaning that (5') has a solution, $H(p, t)$. Then we will be able to define $\mathcal{A}(t)$ for $t \in [20, T]$. Using this in (2) will give us a solution to (1), $E(a, t)$, for $a \in [0, 6]$ and $t \in [20, T]$, and this will mean a solution to the equations presented in Section 2 exists for $t \in [20, T]$. We now construct our mapping.

Just as in the last subsection, suppose we are given $H_i(p, t)$ defined for $p \in [0, p^*]$ and $t \in [20, T]$ with the following properties:

$$H_i \in C([0, p^*] \times [20, T]),$$

$$H_i(p, 20) = H_{20}(p, 20),$$

$$H_i \geq 0,$$

$$\|H_i\| \leq c_{20} < \infty,$$

(24)

$$\mathcal{H}_i(t) = \int_0^{p^*} H_i(p, t) dp \geq \varepsilon_{20},$$

$$\int_0^{p^*} pH_i(p, t) dp \geq \varepsilon_{20},$$

where c_{20} and ε_{20} are given positive constants. Also suppose we are given $\mu_i(t)$ defined for $t \in [20, T]$ such that

$$\begin{aligned}\mu_i(t) &\in C([20, T]), \\ \mu_j &\leq \mu_i(t) \leq \mu_a.\end{aligned}\tag{25}$$

Set

$$v_i(p, t) = -\mu_i(t)p + \rho[\mathcal{H}_i(t)/(\mathcal{H}_i(t) + C)]L(t)f(\mathcal{F}(H_i)(t), p, t).$$

We now consider the first-order partial differential equation

$$\frac{\partial H}{\partial t} + \frac{\partial}{\partial p}(v_i H) = -\mu_H(p)H,$$

$$H(p, 20) = H_{20}(p, 20),$$

$$H(0, t) = 0$$

for $20 \leq t \leq T$. We can solve this along characteristics. The characteristic differential equations are again (12)–(14) with respective solutions $t = s + t_0$, $p = G_i(t; p_0, t_0)$, and

$$H = Ke^{-\int_{t_0}^{s+t_0} [\mu_H(G_i(\sigma; p_0, t_0)) - \mu_i(\sigma) + \rho[\mathcal{H}_i(\sigma)/(\mathcal{H}_i(\sigma) + C)]L(\sigma)(\partial f/\partial p)(\mathcal{F}(H_i)(\sigma), G_i(\sigma; p_0, t_0), \sigma)] d\sigma}.$$

Using the initial and boundary conditions we get for $(t, p) \in [20, T] \times [0, p^*]$

$$H(p, t) = \begin{cases} H_{20}(G_i(20; p, t), 20) \\ \quad \times e^{-\int_{20}^t [\mu_H(G_i(\sigma; p, t)) - \mu_i(\sigma) + \rho[\mathcal{H}_i(\sigma)/(\mathcal{H}_i(\sigma) + C)]L(\sigma)(\partial f/\partial p)(\mathcal{F}(H_i)(\sigma), G_i(\sigma; p, t), \sigma)] d\sigma} \\ \quad \text{for } 20 \leq t \leq T, \quad G_i(t; 0, 0) \leq p \leq G_i(t; p^*, 0), \\ 0 \quad \text{otherwise.} \end{cases}\tag{26}$$

We let

$$S_H = \{H : H \text{ satisfies properties (24)}\},$$

$$S_\mu = \{\mu : \mu \text{ satisfies properties (25)}\},$$

$$S = S_H \times S_\mu$$

and we define a mapping on S, Φ^H , by $\Phi^H(H_i, \mu_i) = H$, where $H(p, t)$ is given by (26). Next we define three more mappings on $S, \Phi^{\mathcal{P}}, \Phi^{\mathcal{A}}$, and Φ^μ , by

$$\Phi^{\mathcal{P}}(H, \mu)(t) = \int_0^{p^*} p \Phi^H(H, \mu)(p, t) dp,$$

$$\Phi^{\mathcal{A}}(H, \mu)(t) = \int_0^{p^*} e^{(t-40)\mu_j} e^{-\int_{20}^t \mu(\sigma) d\sigma} G_{20}(t-20; G(20; p, t), 20) \Phi^H(H, \mu)(p, t) dp$$

and

$$\Phi^\mu(H, \mu)(t) = \frac{\mu_a \Phi^{\mathcal{A}}(H, \mu)(t) + \mu_j [\Phi^{\mathcal{P}}(H, \mu)(t) - \Phi^{\mathcal{A}}(H, \mu)(t)]}{\Phi^{\mathcal{P}}(H, \mu)(t)} \quad (27)$$

for $t \in [20, T]$. Finally, we define the mapping on S that we wish to show has a fixed point, Φ , by $\Phi(H, \mu) = (\Phi^H(H, \mu), \Phi^\mu(H, \mu))$. Now let

$$R_H = \{\Phi^H(H, \mu) : (H, \mu) \in S\},$$

$$R_\mu = \{\Phi^\mu(H, \mu) : (H, \mu) \in S\},$$

$$R = \{\Phi(H, \mu) : (H, \mu) \in S\} = R_H \times R_\mu.$$

Notice that S is a closed convex set. We want to show that $R \subseteq S$. To do this we will show that $R_H \subseteq S_H$ and $R_\mu \subseteq S_\mu$.

To show $R_H \subseteq S_H$ we follow the same procedure used in Section 3.1 to show that $R \subseteq S$. The major difference is that there $\mu(t)$ was constant, so we did not have $\mu_i(t)$ to concern us. But $\mu_i(t)$ is continuous and bounded above and below by μ_j and μ_a respectively, so the arguments from Section 3.1 are easily modified to take care of this. The other difference is that here we also need to verify that $\Phi^{\mathcal{P}}(H, \mu)(t) \geq \varepsilon_{20}$. But the argument to show that $\int_0^{p^*} p \Phi^H(H, \mu)(p, t) dp \geq \varepsilon_{20}$ is the same as the one to show $\int_0^{p^*} \Phi^H(H, \mu)(p, t) dp \geq \varepsilon_{20}$, so the details from Section 3.1 should suffice to handle this difference too. We will omit the details of showing that $R_H \subseteq S_H$ and move on to showing that $R_\mu \subseteq S_\mu$.

Suppose $(H, \mu) \in S$. Since $\Phi^{\mathcal{A}}(H, \mu)(t)$ and $\Phi^{\mathcal{P}}(H, \mu)(t)$ are continuous for $t \in [20, T]$, $\Phi^\mu(H, \mu) \in C([20, T])$. It remains to show that $\mu_j \leq \Phi^\mu(H, \mu) \leq \mu_a$. This amounts to verifying that $\Phi^{\mathcal{P}}(H, \mu)(t) - \Phi^{\mathcal{A}}(H, \mu)(t) \geq 0$ for $t \in [20, T]$.

We have

$$\begin{aligned} & \Phi^{\mathcal{P}}(H, \mu)(t) - \Phi^{\mathcal{A}}(H, \mu)(t) \\ &= \int_0^{p^*} [p - e^{-(40-t)\mu_j} e^{-\int_{20}^t \mu(\sigma) d\sigma} G_{20}(t-20; G(20; p, t), 20)] \Phi^H(H, \mu)(p, t) dp. \end{aligned} \quad (28)$$

Thus, we need to verify that for any $p \in [0, p^*]$ and $t \in [20, T]$ the expression inside the square brackets in (28) is nonnegative.

First, recall that $p = G_{20}(s; p_{20}, 20)$ is the solution of (23). Let

$$K = \frac{\rho C_{20} P^* L_\infty \|f\|}{(\delta_{20} + C)}.$$

Because $v_{20}(p, t) \leq -\mu_j p + K$,

$$G_{20}(s; p_{20}, 20) \leq \frac{K}{\mu_j} + \left(p_{20} - \frac{K}{\mu_j} \right) e^{-(s-20)\mu_j}. \quad (29)$$

Second, recall that $p = G(s; p_0, t_0)$ is the solution of

$$\frac{dp}{dt} = v(p, t) = -\mu(t)p + \rho[\mathcal{H}(t)/(\mathcal{H}(t) + C)]L(t)f(\mathcal{F}(H)(t), p, t),$$

$$p(t_0) = p_0.$$

Because $v(p, t) \geq \mu_j p$,

$$G(s; p_0, t_0) \geq p_0 e^{-(s-t_0)\mu_j}. \quad (30)$$

Using (29), (30), and the fact that $p = G(t; p, t)$ we get

$$\begin{aligned} p - e^{-(40-t)\mu_j} e^{-\int_{20}^t \mu(\sigma) d\sigma} G_{20}(t-20; G(20; p, t), 20) \\ &= G(20; G(20; p, t), 20) - e^{-(40-t)\mu_j} e^{-\int_{20}^t \mu(\sigma) d\sigma} G_{20}(t-20; G(20; p, t), 20) \\ &\geq G(20; p, t) e^{-(t-20)\mu_j} - e^{-(40-t)\mu_j} e^{-\int_{20}^t \mu(\sigma) d\sigma} \left[\frac{K}{\mu_j} + \left(G(20; p, t) - \frac{K}{\mu_j} \right) e^{-(t-40)\mu_j} \right] \\ &= G(20; p, t) [e^{-(t-20)\mu_j} - e^{-\int_{20}^t \mu(\sigma) d\sigma}] + \frac{K}{\mu_j} e^{-\int_{20}^t \mu(\sigma) d\sigma} [1 - e^{-(40-t)\mu_j}] \\ &\geq 0. \end{aligned}$$

The last inequality is due to fact that $0 \leq \mu_j \leq \mu(\sigma)$ and $t \leq T < 40$ so that both terms in the previous line are nonnegative. Thus, $R_\mu \subseteq S_\mu$.

We have shown $R \subseteq S$. Now we will show that R is relatively compact by showing that R_H and R_μ are each relatively compact. We will use the Arzelà–Ascoli Theorem to do this.

The verification that R_H is uniformly bounded and equicontinuous is basically the same as the verification that R in Section 3 is uniformly bounded and equicontinuous. Again the difference is with $\mu(t)$, but this difference causes no great difficulties, so we omit the details of showing that R_H is relatively compact and move on to looking at R_μ .

Let (H, μ) be in S . Since $\|\Phi^\mu(H, \mu)\| \leq \mu_a$, R_μ is uniformly bounded. Now choose $t_1, t_2 \in [20, T]$ such that $|t_1 - t_2| < \delta$. Then

$$\begin{aligned} |\Phi^\mu(H, \mu)(t_1) - \Phi^\mu(H, \mu)(t_2)| &= \left| \frac{\mu_a \Phi^{\mathcal{A}}(H, \mu)(t_1) + \mu_j [\Phi^{\mathcal{P}}(H, \mu)(t_1) - \Phi^{\mathcal{A}}(H, \mu)(t_1)]}{\Phi^{\mathcal{P}}(H, \mu)(t_1)} \right. \\ &\quad \left. - \frac{\mu_a \Phi^{\mathcal{A}}(H, \mu)(t_2) + \mu_j [\Phi^{\mathcal{P}}(H, \mu)(t_2) - \Phi^{\mathcal{A}}(H, \mu)(t_2)]}{\Phi^{\mathcal{P}}(H, \mu)(t_2)} \right| \\ &= \frac{\mu_a - \mu_j}{\Phi^{\mathcal{P}}(H, \mu)(t_1) \Phi^{\mathcal{P}}(H, \mu)(t_2)} |\Phi^{\mathcal{A}}(H, \mu)(t_1) \Phi^{\mathcal{P}}(H, \mu)(t_2) \\ &\quad - \Phi^{\mathcal{A}}(H, \mu)(t_2) \Phi^{\mathcal{P}}(H, \mu)(t_1)| \\ &\leq \frac{\mu_a - \mu_j}{\Phi^{\mathcal{P}}(H, \mu)(t_1) \Phi^{\mathcal{P}}(H, \mu)(t_2)} [\Phi^{\mathcal{P}}(H, \mu)(t_2) |\Phi^{\mathcal{A}}(H, \mu)(t_1) \end{aligned}$$

$$\begin{aligned}
& -\Phi^{\mathcal{A}}(H, \mu)(t_2)| + \Phi^{\mathcal{A}}(H, \mu)(t_2)|\Phi^{\mathcal{P}}(H, \mu)(t_1) - \Phi^{\mathcal{P}}(H, \mu)(t_2)|] \\
& \leq \frac{\mu_a - \mu_j}{\Phi^{\mathcal{P}}(H, \mu)(t_1)} [|\Phi^{\mathcal{A}}(H, \mu)(t_1) - \Phi^{\mathcal{A}}(H, \mu)(t_2)| \\
& \quad + |\Phi^{\mathcal{P}}(H, \mu)(t_1) - \Phi^{\mathcal{P}}(H, \mu)(t_2)|] \\
& \leq \frac{\mu_a - \mu_j}{\varepsilon_{20}} [|\Phi^{\mathcal{A}}(H, \mu)(t_1) - \Phi^{\mathcal{A}}(H, \mu)(t_2)| \\
& \quad + |\Phi^{\mathcal{P}}(H, \mu)(t_1) - \Phi^{\mathcal{P}}(H, \mu)(t_2)|].
\end{aligned}$$

Note that we used the fact that $\Phi^{\mathcal{P}}(H, \mu)(t) - \Phi^{\mathcal{A}}(H, \mu)(t) \geq 0$ in order to say $\Phi^{\mathcal{A}}(H, \mu)(t)/\Phi^{\mathcal{P}}(H, \mu)(t) \leq 1$.

We now look at the two terms in the last inequality one at a time and show that each can be made small independent of our choice of $(H, \mu) \in S$. We consider the second term first. Since R_H is equicontinuous and

$$|\Phi^{\mathcal{P}}(H, \mu)(t_1) - \Phi^{\mathcal{P}}(H, \mu)(t_2)| \leq \int_0^{p^*} p |\Phi^H(H, \mu)(p, t_1) - \Phi^H(H, \mu)(p, t_2)| \, dp,$$

we can make $|\Phi^{\mathcal{P}}(H, \mu)(t_1) - \Phi^{\mathcal{P}}(H, \mu)(t_2)|$ as small as we please by taking δ small enough. This is independent of our choice of $(H, \mu) \in S$.

Second, we consider

$$\begin{aligned}
& |\Phi^{\mathcal{A}}(H, \mu)(t_1) - \Phi^{\mathcal{A}}(H, \mu)(t_2)| \\
& = \left| \int_0^{p^*} \left[e^{(t_1-40)\mu_j} e^{-\int_{20}^{t_1} \mu(\sigma) \, d\sigma} G_{20}(t_1 - 20; G(20; p, t_1), 20) \Phi^H(H, \mu)(p, t_1) \right. \right. \\
& \quad \left. \left. - e^{(t_2-40)\mu_j} e^{-\int_{20}^{t_2} \mu(\sigma) \, d\sigma} G_{20}(t_2 - 20; G(20; p, t_2), 20) \Phi^H(H, \mu)(p, t_2) \right] \, dp \right|. \tag{31}
\end{aligned}$$

Using the Mean Value Theorem we easily see that

$$|e^{(t_1-40)\mu_j} - e^{(t_2-40)\mu_j}| \leq |t_1 - t_2| \mu_j \leq \delta \mu_j \tag{32}$$

and

$$|e^{-\int_{20}^{t_1} \mu(\sigma) \, d\sigma} - e^{-\int_{20}^{t_2} \mu(\sigma) \, d\sigma}| \leq |t_1 - t_2| \mu_a \leq \delta \mu_a. \tag{33}$$

We define V as we did in the previous section:

$$\begin{aligned}
V &= \max_{(t,p) \in [20,T] \times [0,p^*]} |v(p, t)| \\
&\leq \mu_a p^* + \frac{\rho c_0 p^* L_{\infty} \|f\|}{\varepsilon_0 + C}.
\end{aligned}$$

Then, since

$$\begin{aligned}
|G(t_2; p, t_1) - G(t_2; p, t_2)| &= |G(t_2; p, t_1) - p| \\
&= |G(t_2; p, t_1) - G(t_1; p, t_1)|
\end{aligned}$$

$$\begin{aligned} &\leq |t_1 - t_2|V \\ &\leq \delta V. \end{aligned}$$

Theorem 2 tells us

$$|G(20; p, t_1) - G(20; p, t_2)| \leq \delta V e^{(T-20)M}.$$

Using this and Theorem 2 again, we see that for all $p \in [0, p^*]$

$$\begin{aligned} &|G_{20}(t_1 - 20; G(20; p, t_1), 20) - G_{20}(t_2 - 20; G(20; p, t_2), 20)| \\ &\leq |G_{20}(t_1 - 20; G(20; p, t_1), 20) - G_{20}(t_2 - 20; G(20; p, t_1), 20)| \\ &\quad + |G_{20}(t_2 - 20; G(20; p, t_1), 20) - G_{20}(t_2 - 20; G(20; p, t_2), 20)| \\ &\leq |t_1 - t_2|V + \delta V e^{(T-20)M} e^{(T-20)M} \\ &\leq \delta V [1 + e^{2(T-20)M}]. \end{aligned} \tag{34}$$

Again because R_H is equicontinuous, $|\Phi^H(H, \mu)(p, t_1) - \Phi^H(H, \mu)(p, t_2)|$ can be made small for all $p \in [0, p^*]$. This fact and (32)–(34) are independent of our choice of $(H, \mu) \in S$, and looking back at (31), we see that they imply we can make $|\Phi^{\mathcal{A}}(H, \mu)(t_1) - \Phi^{\mathcal{A}}(H, \mu)(t_2)|$ small independently of our choice of $(H, \mu) \in S$. Thus R_μ is also equicontinuous, and by the Arzelà–Ascoli Theorem, it is relatively compact. It follows that R is relatively compact.

Before we can use Schauder’s Theorem to say Φ has a fixed point, we need to verify that Φ is continuous. The argument that Φ^H is continuous is again about the same as the argument that Φ in Section is continuous, and we omit the details. We only need to verify the continuity of Φ^μ .

Suppose $(H_1, \mu_1), (H_2, \mu_2) \in S$ and $\|H_1 - H_2\|, \|\mu_1 - \mu_2\| < \delta$ where $\delta > 0$. Instead of looking immediately at $\|\Phi^\mu(H_1, \mu_1) - \Phi^\mu(H_2, \mu_2)\|$, we obtain a few preliminary bounds. First,

$$\left| \frac{\mathcal{H}_1(t)}{\mathcal{H}_1(t) + C} - \frac{\mathcal{H}_2(t)}{\mathcal{H}_2(t) + C} \right| < \frac{\delta C p^*}{\varepsilon_{20}^2}.$$

Second,

$$\begin{aligned} &|v_1(p, t) - v_2(p, t)| \\ &= \left| \left[-\mu_1(t)p + \rho \frac{\mathcal{H}_1(t)}{\mathcal{H}_1(t) + C} L(t) f(\mathcal{F}(H_1)(t), p, t) \right] \right. \\ &\quad \left. - \left[-\mu_2(t)p + \rho \frac{\mathcal{H}_2(t)}{\mathcal{H}_2(t) + C} L(t) f(\mathcal{F}(H_2)(t), p, t) \right] \right| \\ &\leq \delta p^* + \rho L_\infty \left[\frac{c_0 p^*}{\varepsilon_{20}^2} |f(\mathcal{F}(H_1)(t), p, t) - f(\mathcal{F}(H_2)(t), p, t)| + \frac{\delta \|f\| C p^*}{\varepsilon_{20}^2} \right]. \end{aligned}$$

The continuity of \mathcal{F} and the uniform continuity of f tell us given $\delta_2 > 0$, if we choose δ sufficiently small, $|v_1(p, t) - v_2(p, t)| < \delta_2$. Theorem 2 then tells us

$$|G_1(t; p_0, t_0) - G_2(t; p_0, t_0)| \leq \frac{\delta_2}{M} (e^{(T-20)M} - 1). \tag{35}$$

We have

$$\begin{aligned}
 & |\Phi^\mu(H_1, \mu_1)(t) - \Phi^\mu(H_2, \mu_2)(t)| \\
 &= \left| \frac{\mu_a \Phi^{\mathcal{A}}(H_1, \mu_1)(t) + \mu_j(\Phi^{\mathcal{P}}(H_1, \mu_1)(t) - \Phi^{\mathcal{A}}(H_1, \mu_1)(t))}{\Phi^{\mathcal{P}}(H_1, \mu_1)(t)} \right. \\
 &\quad \left. - \frac{\mu_a \Phi^{\mathcal{A}}(H_2, \mu_2)(t) + \mu_j(\Phi^{\mathcal{P}}(H_2, \mu_2)(t) - \Phi^{\mathcal{A}}(H_2, \mu_2)(t))}{\Phi^{\mathcal{P}}(H_2, \mu_2)(t)} \right| \\
 &= \frac{\mu_a - \mu_j}{\Phi^{\mathcal{P}}(H_1, \mu_1)(t) \Phi^{\mathcal{P}}(H_2, \mu_2)(t)} |\Phi^{\mathcal{P}}(H_2, \mu_2)(t) \Phi^{\mathcal{A}}(H_1, \mu_1)(t) - \Phi^{\mathcal{P}}(H_1, \mu_1)(t) \Phi^{\mathcal{A}}(H_2, \mu_2)(t)| \\
 &\leq \frac{\mu_a - \mu_j}{\varepsilon_{20}} [|\Phi^{\mathcal{P}}(H_1, \mu_1)(t) - \Phi^{\mathcal{P}}(H_2, \mu_2)(t)| + |\Phi^{\mathcal{A}}(H_1, \mu_1)(t) - \Phi^{\mathcal{A}}(H_2, \mu_2)(t)|]. \quad (36)
 \end{aligned}$$

Notice that $|\Phi^{\mathcal{P}}(H_1, \mu_1)(t) - \Phi^{\mathcal{P}}(H_2, \mu_2)(t)|$ can be made small by taking δ small enough since the mapping Φ^H is continuous. We need to verify that we can make the second term of (36) small.

From the definition of $\Phi^{\mathcal{A}}(H, \mu)$ we get

$$\begin{aligned}
 & |\Phi^{\mathcal{A}}(H_1, \mu_1) - \Phi^{\mathcal{A}}(H_2, \mu_2)| \\
 &\leq e^{(t-40)\mu_j} \int_0^{p^*} |e^{-\int_{20}^t \mu_1(\sigma) d\sigma} G_{20}(t-20; G_1(20; p, t), 20) \Phi^H(H_1, \mu_1)(p, t) \\
 &\quad - e^{-\int_{20}^t \mu_2(\sigma) d\sigma} G_{20}(t-20; G_2(20; p, t), 20) \Phi^H(H_2, \mu_2)(p, t)| dp.
 \end{aligned}$$

Using the Mean Value Theorem we see that

$$|e^{-\int_{20}^t \mu_1(\sigma) d\sigma} - e^{-\int_{20}^t \mu_2(\sigma) d\sigma}| \leq \delta(T-20). \quad (37)$$

Using (35) and Theorem 2 we see that

$$|G_{20}(t-20; G_1(20; p, t), 20) - G_{20}(t-20; G_2(20; p, t), 20)| \leq \frac{\delta_2}{M} (e^{(T-20)M} - 1) e^{(T-20)M}. \quad (38)$$

We already know that $|\Phi^H(H_1, \mu_1)(p, t) - \Phi^H(H_2, \mu_2)(p, t)|$ can be made small because Φ^H is continuous. Thus, (37), and (38) imply that the second term of (36), $|\Phi^{\mathcal{A}}(H_1, \mu_1) - \Phi^{\mathcal{A}}(H_2, \mu_2)|$, will be small if δ is sufficiently small. This is what we need to conclude that Φ^μ maps S into R_μ continuously.

So Φ is a continuous mapping of a closed convex set S into a relatively compact subset of S , R . Schauder's Theorem tells us that Φ has a fixed point.

Finally, if (H, μ) is a fixed point of Φ , we define

$$\begin{aligned}
 \mathcal{A}(t) &= \Phi^{\mathcal{A}}(H, \mu)(t) \\
 &= \int_0^{p^*} e^{(t-40)\mu_j} e^{\int_{20}^t \mu(\sigma) d\sigma} G_{20}(t-20; G(20; p, t), 20) \Phi^H(H, \mu)(p, t) dp.
 \end{aligned}$$

Then $E(a, t)$ is given by (2), and we have shown that there is a solution to the equations presented in Section 2 for $t \in [20, T]$.

3.3. Existence for $t \in [24, T]$, $24 < T < 44$

In this section we take $t \in [24, T]$, where $24 < T < 44$. Actually, we need to first restrict T to be less than or equal to 28. If we can show existence for values of t up to $T \leq 28$, then we try for values of T less than or equal to 32, and so on until we reach $T < 44$. If it is not clear now why we go in steps of 4, it will soon become clear.

The difference between this case and that of Section 3.2 is that here $L(t)$ is not known. This causes no great difficulty though. We proceed in the same way. We suppose we are given $H_i(p, t)$ defined for $p \in [0, p^*]$ and $t \in [24, T]$ with properties similar to those of (24) with the t range suitably altered. We also suppose we are given $\mu_i(t)$ with properties similar to (25) again with the t range suitably altered. Let H_{24} be the solution of (5) for $t \in [0, 24]$. We then set

$$\mathcal{H}_i(t) = \int_0^{p^*} H_i(p, t) \, dp,$$

$$\mathcal{P}_i(t) = \begin{cases} \int_0^{p^*} pH_i(p, t) \, dp & \text{if } t > 24, \\ \int_0^{p^*} pH_{24}(p, t) \, dp & \text{if } 0 \leq t \leq 24, \end{cases}$$

$$\mathcal{A}_i(t) = \frac{\mu_i(t) - \mu_j}{\mu_a - \mu_j} \mathcal{P}_i(t),$$

$$L_i(t) = \int_4^6 \left[\beta \mathcal{A}_i(t-a) e^{-\int_0^a \mu_E(\sigma) \, d\sigma} + \int_0^a \Lambda(\tau, \tau+t-a) e^{-\int_\tau^a \mu_E(\sigma) \, d\sigma} \, d\tau \right] da,$$

$$v_i(p, t) = -\mu_i(t)p + \rho \frac{\mathcal{H}_i(t)}{\mathcal{H}_i(t) + C} L_i(t) f(\mathcal{F}(H_i)(t), p, t).$$

Notice that for $4 \leq a \leq 6$, since $24 \leq t \leq T \leq 28$,

$$\begin{aligned} \mathcal{A}_i(t-a) &\leq \mathcal{P}_i(t-a) \\ &= \int_0^{p^*} pH_{24}(p, t-a) \, dp \\ &\leq \|H_{24}\| \int_0^{p^*} p \, dp \\ &= \frac{\|H_{24}\| (p^*)^2}{2}. \end{aligned}$$

This means that $L_i(t)$ is a bounded, nonnegative, and continuous function. So we can follow the exact same steps we took in Section 3.2 to show that a solution exists for the equations from Section 2 for $t \in [24, T]$.

If a solution exists for $t \in [0, 28]$, we set H_{28} to be a solution of (5) for that range of t and repeat the same argument except with $T \leq 32$ this time. We continue until we have shown a solution exists for $t \in [24, T]$ with $24 < T < 44$.

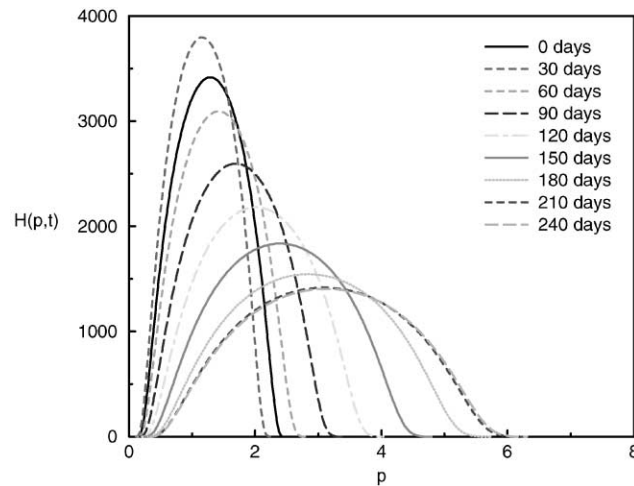


Fig. 1. Snapshots of $H(p, t)$ for $0 \leq t \leq 240$ using the linear f ; $\rho = 0.005$; μ_H with $n = 1$.

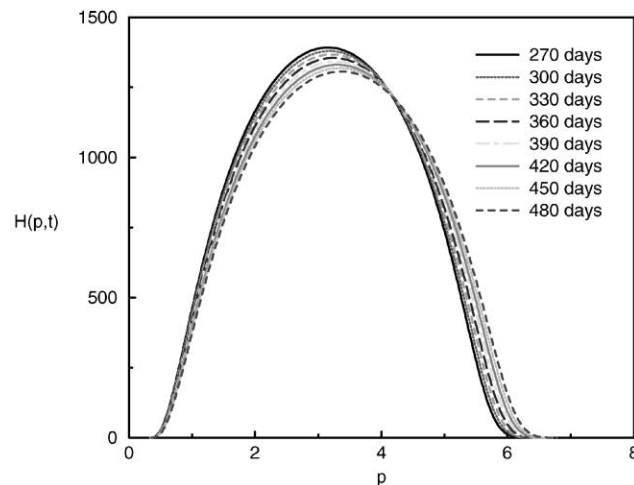


Fig. 2. Snapshots of $H(p, t)$ for $270 \leq t \leq 480$ using the linear f ; $\rho = 0.005$; μ_H with $n = 1$.

Remark. Clearly, the method of this subsection can be used iteratively to yield a solution for $t \in [0, T]$, for any $T > 0$.

4. Numerical simulations

We present in this section the results from some numerical simulations. We shall discuss the numerical methods employed elsewhere. Here we shall focus on the qualitative and quantitative results they yield.

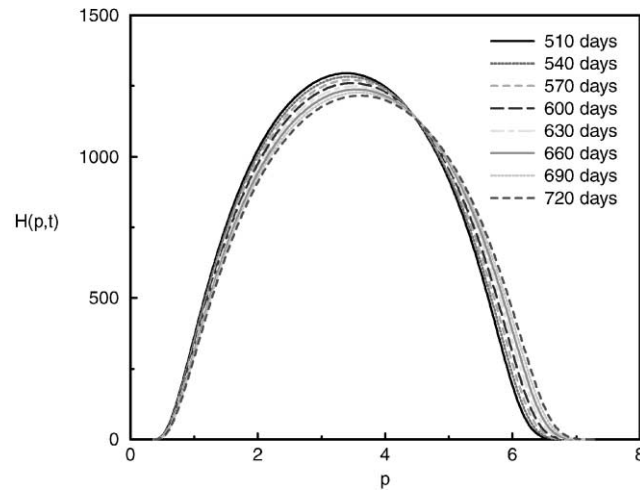


Fig. 3. Snapshots of $H(p, t)$ for $510 \leq t \leq 720$ using the linear f ; $\rho = 0.005$; μ_H with $n = 1$.

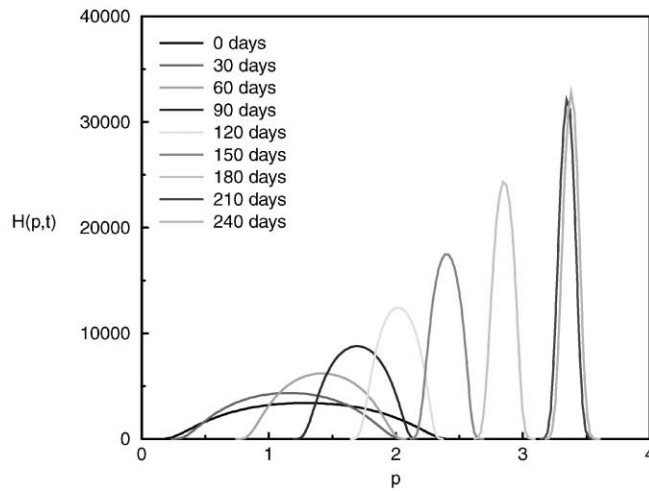


Fig. 4. Snapshots of $H(p, t)$ for $0 \leq t \leq 240$ using the f of Langlais and Silan; $\rho = 0.005$; μ_H with $n = 1$.

We use parameter values largely based on those of Langlais and Silan [10].

- Death rates are

$$\mu_e = 1/10,$$

$$\mu_l = 1/2 \text{ (continuous models),}$$

$$\mu_j = \ln(10/9)/20,$$

$$\mu_a = 1/70.$$

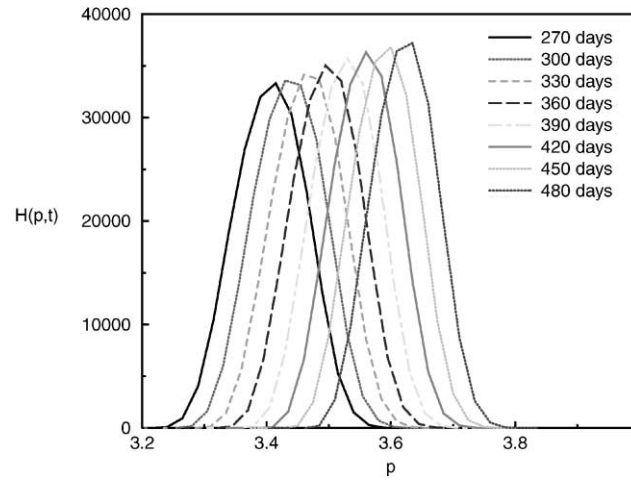


Fig. 5. Snapshots of $H(p,t)$ for $270 \leq t \leq 480$ using the f of Langlais and Silan; $\rho = 0.05$; μ_H with $n = 1$.

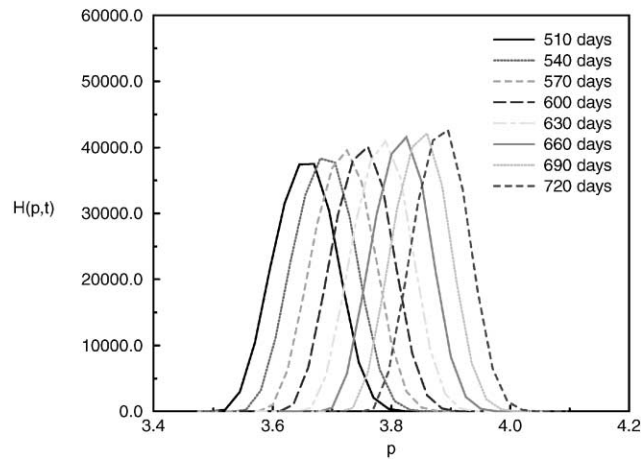


Fig. 6. Snapshots of $H(p,t)$ for $510 \leq t \leq 720$ using the f of Langlais and Silan; $\rho = 0.05$; μ_H with $n = 1$.

- Egg-laying rate is

$$\beta = 7.$$

- Special p values used are

$$p_{\text{thresh}} = 30,$$

$$p_{\text{crit}} = 300,$$

$$p_{\text{leth}} = 800,$$

$$p^* = 1500.$$

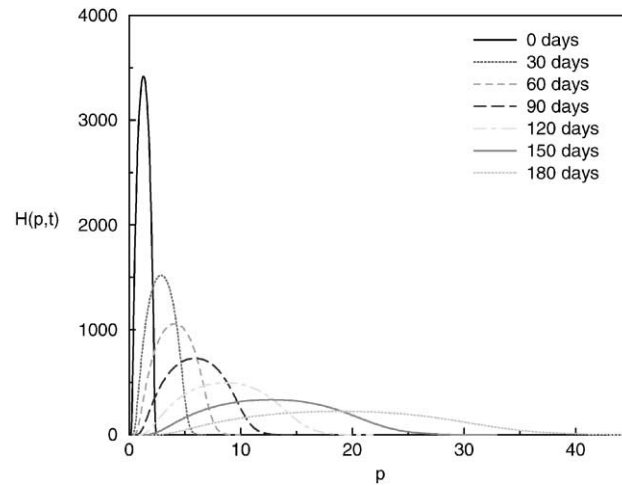


Fig. 7. Snapshots of $H(p, t)$ for $0 \leq t \leq 180$ using the linear f ; $\rho = 0.5$; μ_H with $n = 1$.

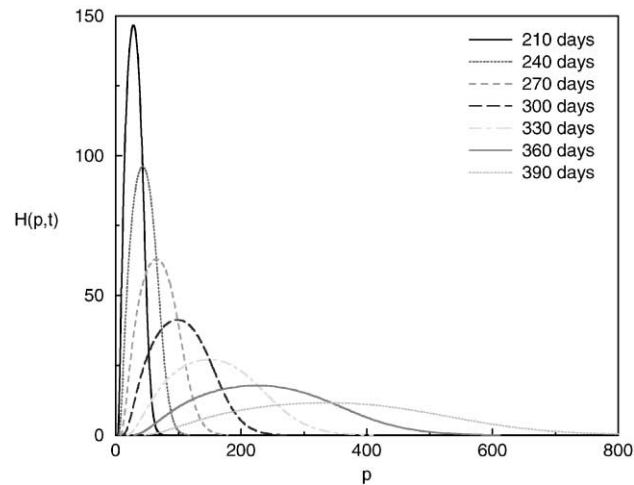


Fig. 8. Snapshots of $H(p, t)$ for $210 \leq t \leq 390$ using the linear f ; $\rho = 0.5$; μ_H with $n = 1$.

- Parameters affecting larvae recruitment include

$$\rho \in [0, 1] \quad (\text{various values used}),$$

$$C = 1000.$$

- For the exterior supply of eggs and larvae we use

$$A(a, t) = \begin{cases} 100 & \text{if } 0 \leq \text{mod}(t, 360) \leq 180, \\ 0 & \text{otherwise.} \end{cases}$$

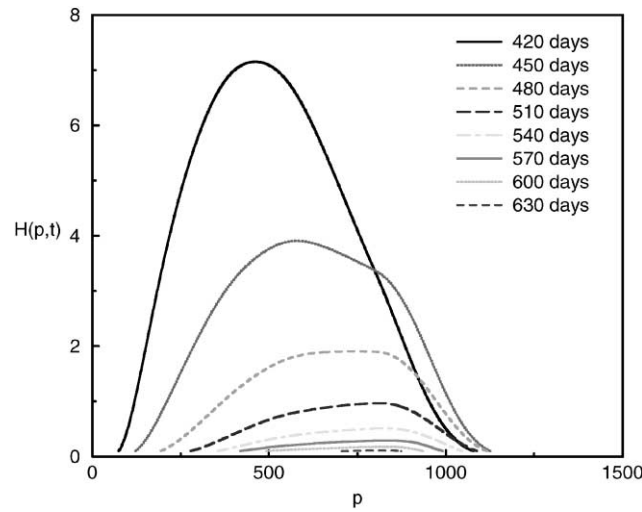


Fig. 9. Snapshots of $H(p, t)$ for $420 \leq t \leq 630$ using the linear f ; $\rho = 0.5$; μ_H with $n = 1$.

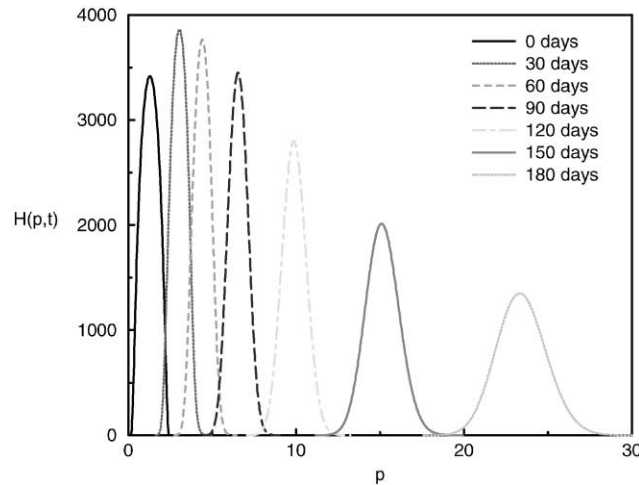


Fig. 10. Snapshots of $H(p, t)$ for $0 \leq t \leq 180$ using the f of Langlais and Silan; $\rho = 0.5$; μ_H with $n = 1$.

- For the recruitment functions $f(p, t)$ we first use the following:

$$f(p, t) = f_0(t) + \lambda(t)[(p - p_{\text{thresh}})_+]^2,$$

where

$$(p - p_{\text{thresh}})_+ = \begin{cases} p - p_{\text{thresh}} & \text{if } p > p_{\text{thresh}}, \\ 0 & \text{otherwise.} \end{cases}$$

This was first proposed by Langlais and Silan [10]. The goal is to model the fact that hosts with less than p_{thresh} parasites act the same as far as recruiting new parasites goes, but for hosts with more parasites, parasite recruitment increases.

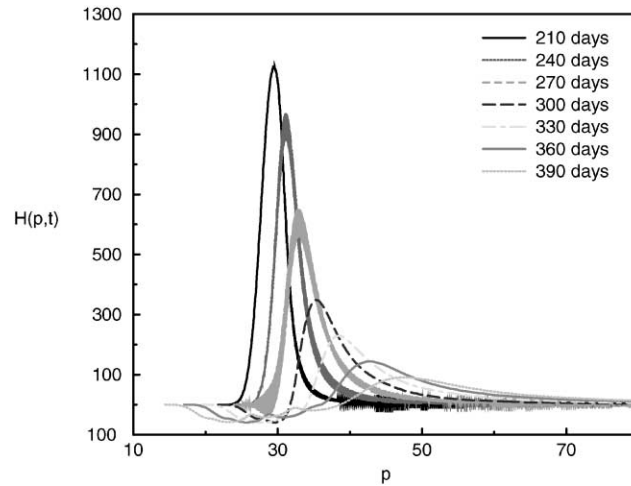


Fig. 11. Snapshots of $H(p, t)$ for $210 \leq t \leq 390$ using the f of Langlais and Silan; $\rho = 0.5$; μ_H with $n = 1$.

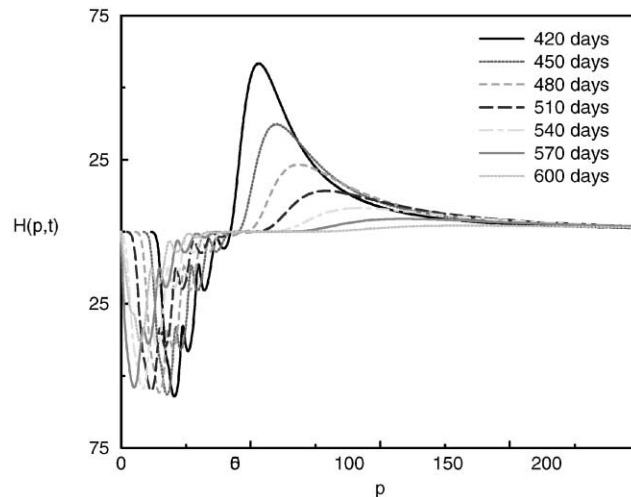


Fig. 12. Snapshots of $H(p, t)$ for $420 \leq t \leq 600$ using the f of Langlais and Silan; $\rho = 0.5$; μ_H with $n = 1$.

One determines $f_0(t)$ and $\lambda(t)$ for our continuous model exactly as for the discrete model [10], except integrations are replaced for summations.

It is unclear how good of choice this f is in the first place. Moreover, for the continuous models there is the problem that $\lambda(t)$ may not remained bounded at all times. For the existence proof in Section 3 we required that it remained bounded. We used this f and — as long as $i_{\text{up}}^n \Delta p$ remained less than p_{thresh} — there were no problems as is to be expected. But if $i_{\text{up}}^n \Delta p$ crept above p_{thresh} , it would not take long before i_{up}^n would shoot up to i_{max} (a couple days of simulated time while it might take over 100 days for $i_{\text{up}}^n \Delta p$ to reach p_{thresh}). When one looks at graphs of $H(p, t)$ versus p

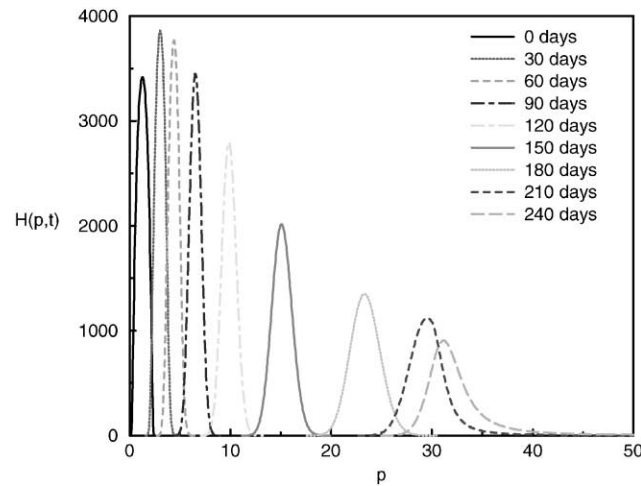


Fig. 13. Snapshots of $H(p, t)$ for $0 \leq t \leq 240$ using the f of Langlais and Silan; $\rho = 0.5$; μ_H with $n = 4$.

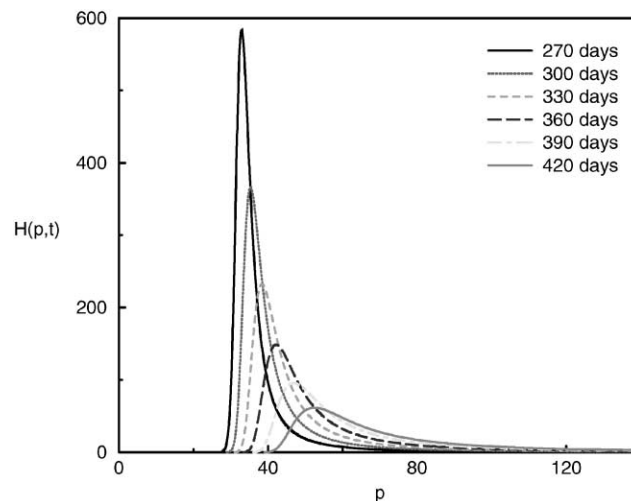


Fig. 14. Snapshots of $H(p, t)$ for $270 \leq t \leq 420$ using the f of Langlais and Silan; $\rho = 0.5$; μ_H with $n = 4$.

for fixed values of t after $i_{\text{up}}^n \Delta p$ passes p_{thresh} , one notices oscillations appearing. When presenting numerical results, we shall refer to this f as “the f of Langlais and Silan”.

Because of the problems we experienced with the f of Langlais and Silan, we tried a simpler form for f . We took $f(p, t) = m(t)p$. For mass balance, we need $m(t) = 1/\mathcal{P}(t)$. This f , which we shall refer to as “the linear f ”, has the advantages that it is easy to compute, and it does not seem to cause the numeric difficulties that the other form of f does. We ran simulations of the continuous models using the linear f along with using the f of Langlais and Silan.

The mortality rate of hosts, $\mu_H(i)$, was defined exactly as for the discrete model [10], with the continuous variable p replacing the discrete variable i . Only in one situation did we modify $\mu_H(p)$

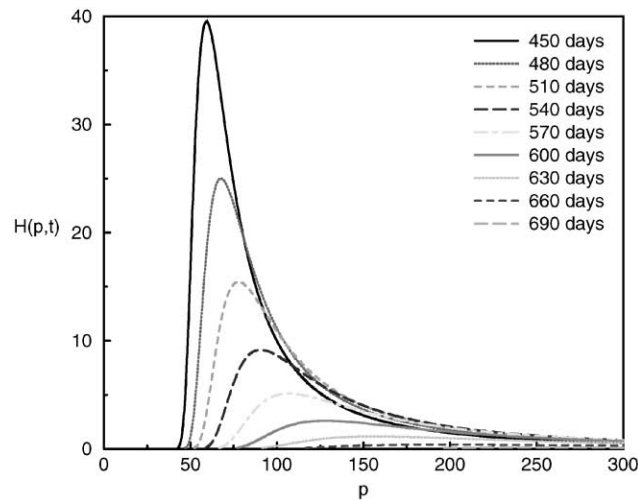


Fig. 15. Snapshots of $H(p, t)$ for $450 \leq t \leq 690$ using the f of Langlais and Silan; $\rho = 0.5$; μ_H with $n = 4$.

slightly. That is when there is heavy parasite recruitment. If ρ is large, in an attempt to eliminate the oscillations that appear in our graphs of $H(p, t)$, for the continuous model with heavy parasite recruitment, we tried modifying $\mu_H(p)$ for values of p in the interval (p_{leth}, p^*) . We took for these values of p

$$\mu_H(i) = -\frac{S'(p_{\text{leth}})}{S(p_{\text{leth}})} + C \frac{(i - p_{\text{leth}})^2}{(p^* - i)^n},$$

where $n \geq 1$. From a modeling viewpoint, we are not sure if $n = 1$ or $n = 15$ is a better choice. But from a numerical analysis viewpoint, a larger value of n is better. When there is heavy parasite recruitment and $f(p, t) \approx Cp^2$, where C depends on the parasite recruitment, the off-diagonal terms in the tridiagonal system we must solve to find H_i^n may become quite large for p close to p^* . Taking a larger n will make the diagonal terms larger for p close to p^* and hopefully make the linear system easier to solve. Numerical simulations indicate that this choice of $\mu_H(p)$ indeed helped.

The initial number of hosts was 5000, with a smooth initial distribution of parasites supported in the interval $[0, 2]$.

We have run simulations from 0 to 720 days of the model with the linear f and $\rho = 0.005$ (Figs. 1–3), with the f of Langlais and Silan and $\rho = 0.005$ (Figs. 4–6), with the linear f and $\rho = 0.5$ (Figs. 7–9), with the f of Langlais and Silan and $\rho = 0.5$ (Figs. 10–12), and with the f of Langlais and Silan, $n = 4$ in $\mu_H(p)$, and $\rho = 0.5$ (Figs. 13–15). If not otherwise mentioned, we had $n = 1$ in $\mu_H(p)$.

For the smaller value of ρ we see that little recruitment takes place, as is to be expected. The difference between using the linear f or that of Langlais and Silan is that the former leads to a smooth distribution of parasites in the hosts with a small support located near $p = 0$, while the latter leads to a unimodal distribution of parasites with a load of roughly 4 parasites per host for all hosts. The former results are much more realistic, albeit still quite unrealistic due to the support being to the right of $p = 0$. The area under any of these curves represents the total number of hosts, which remains almost constant at 5000 (since at these low parasite loads there is no host mortality).

For the larger value of ρ , we see that much parasite recruitment takes place and that the host population dies out as a result. For the run with the f of Langlais and Silan and $\rho = 0.5$ (Figs. 10–12), we notice the oscillations in the graphs when $i_{\max} \Delta p > 30 = p_{\text{leth}}$. Negative values of H even appear, which is definitely undesirable. But when we increase n to 4 (Figs. 13–15), those problems do not appear to be there. The results of these last simulations resemble, after 200–300 days, those of the discrete model [10], both qualitatively and quantitatively.

We notice that in all cases here, we have no hosts free of parasites. Again, biologically, this does not seem reasonable. However, the mathematical model we use here forces that to be the case. A correction to this problem will be addressed in a forthcoming paper by the authors.

References

- [1] R.M. Anderson, Mathematical models of host–helminth parasite interactions, in: M.B. Usher, M.H. Williamson (Eds.), *Ecological Stability*, Chapman & Hall, London, 1974, pp. 43–69.
- [2] C. Bouloux, M. Langlais, P. Silan, A marine host–parasite model with direct biological cycle and age structure, *Ecol. Modeling* 107 (1997) 73–86.
- [3] C. Bouloux, *Modélisation, simulations et analyse mathématique de systèmes, hôtes-parasites*, Ph.D. Thesis, Université de Bordeaux 1, Bordeaux, France, 1997.
- [4] E.A. Coddington, N. Levinson, in: *Theory of Ordinary Differential Equations*, International Series in Pure and Applied Mathematics, McGraw-Hill, New York, 1955.
- [5] D. Gilbarg, N.S. Trudinger, in: *Elliptic Partial Differential Equations of Second Order*, 2nd Edition, Grundlehren der Mathematischen Wissenschaften, Vol. 224, Springer, Berlin, 1983.
- [6] K.P. Hadeler, K. Dietz, Nonlinear hyperbolic partial differential equations for the dynamics of parasite populations, *Comput. Math. Appl.* 9 (1983) 415–430.
- [7] K.P. Hadeler, K. Dietz, Population dynamics of killing parasites which reproduce in the host, *J. Math. Biol.* 21 (1984) 45–55.
- [8] F. Hoppensteadt, in: *Mathematical Theories of Populations: Demographics, Genetics and Epidemics*, Regional Conference Series in Applied Mathematics, Vol. 20, SIAM, Philadelphia, 1975.
- [9] M. Kretzschmar, A renewal equation with a birth–death process as a model for parasitic infections, *J. Math. Biol.* 27 (1989) 191–221.
- [10] M. Langlais, P. Silan, Theoretical and mathematical approach of some regulation mechanism in a marine host–parasite system, *J. Biol. Systems* 3 (1995) 559–568.
- [11] F.A. Milner, C.A. Patton, A new approach to mathematical modeling of host–parasite systems, *Comput. Math. Appl.* 37 (1999) 93–110.
- [12] P. Silan, C. Maillard, Biology of *Serranicotyle labracis*, ectoparasite of *Dicentrarchus labrax* (Teleostei): contribution to the study of its populations, *Marine Biol.* 103 (1989) 481–487.