



A New Approach to Mathematical Modeling of Host-Parasite Systems

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Abstract—We propose a new approach to mathematical modeling of host-parasite systems by using partial differential equations where the degree of parasitism in a host is represented by a continuous variable p . This contrasts with the standard approach found in the literature of using a countable number of ordinary differential equations, one for each nonnegative integer, corresponding to the class of hosts having exactly that number of parasites. The new model bears some similarity with size-structured models of population dynamics. We specialize the model to a specific pair of helminth macroparasites infecting sea bass. We show that the model is well posed and we study its asymptotic behavior. Finally, we present results from some simulations. © 1999 Elsevier Science Ltd. All rights reserved.

1. INTRODUCTION

Host-parasite systems are enormously varied. Differences occur mainly due to the environment in which the interaction of the species takes place, as well as to the type of parasite and host involved. Few quantitative studies of the joint dynamics of such populations have been made [1,2]. The gaps are particularly important in the case of metazoarian parasites and aquatic ecosystems, given that almost the entirety of the free organisms living in those environments are prone to be affected by parasitism. In many cases, synergical effects between the various mechanisms that take place in the dynamics of such populations have been very poorly identified. Most of the ideas in this realm are based on theoretical arguments, rarely on experimental ones, and very few studies have been done on natural populations [3–6].

The majority of biomathematical approaches used to model host-parasite systems [7–11] have concentrated on the infectious process. This is quite adequate when dealing with microparasites such as virus, bacteria, etc. However, they are completely inadequate for systems involving macroparasites such as the one we shall consider. These have the following specific property: their installation and survival in the host are essentially dependent on the *number* of parasites already affixed, not only on their mere presence. This gives rise to several density-dependent processes, among which we have intra- and/or inter-species competition, pathogenesis, immune response of the host [12]. Several related systems have been studied for human and other mam-

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mal hosts [13–20]. A few authors incorporated randomness in the dynamics [21,22], and others developed mathematical tools [23,24].

The theoretical implications of host population size regulation by their parasites have taken an increasing importance in the research of the last 20 years [4,25–28]. In particular, macroparasites (helminthic, crustacean, etc.) have been studied in [3,29–31], for example.

There was some pioneer work on host-parasite systems during the first half of this century [32,33]; but deterministic modeling of the propagation of infectious diseases was the object of most epidemic modeling and many papers appeared following the introduction of S-I-R models in [34]; see, for example [35]. More recently, the age structure of the population was considered [36]. This allows us to model birth and death processes which may be age and/or density dependent, as well as the vertical transmission of and the immunity to the disease [37]. Also, stochastic models were proposed [38].

Modeling of host-parasite systems in marine environment is almost nonexistent. Be it for mesoparasites [39,40] or for marine ectoparasites [41–43], great developments are needed. These developments are all the more important in view of some new problems of parasite pathology and epidemiology which appeared with the recent introduction of new methods of aquaculture [44,45].

The host population we shall consider is that of sea bass, (*dicentrarchus labrax*), and a helminth macroparasite which adheres to the branchiae of the fish, (*diplectanum aequans*) [12]. The parasite is oviparous and hermaphrodite and it reproduces after a cross-coupling with a partner. When enough parasites adhere to a host, they kill it by suffocation. The life cycle of *diplectanum aequans* consists of three distinct phases: eggs, larvae, and parasites. The eggs live outside the host and are found in the open waters as well as in farming basins. The egg stage lasts for about four days. After these four days the eggs become larvae, which are always found in farming basins. The larva stage lasts for about two days. Larvae become parasites when they adhere to a host. The parasite stage lasts approximately ninety days and is divided into two periods: α -immature stage, and β -adult stage. The former lasts for about 20 days during which the individual has only its male functions. It is, therefore, unable to procreate but is capable of fecundating an adult partner. The adult stage lasts for about 70 days during which the individual has both male and female functions, and is thus, capable of procreating as well as fecundating. When this stage ends, the individual dies.

Eggs are laid by parasites affixed to a host. Once the egg is laid, it falls to the bottom of the sea or basin where it may become a larva in about four days or it may die. If the individual lives as a larva, then it must adhere to a host within two days or die from lack of nourishment. The adherence to a host depends on several factors, among which we shall consider two essential ones: first, the probability of encountering a host is greater when the population of hosts increases and, second, the larva will attach itself more easily to an infected host than to an uninfected one. If the number of parasites in a host surpasses a certain threshold, the host will become ill and drift towards the bottom of the basin where the majority of the larvae live. A significant recruitment of larvae by that host will then take place, aggravating its illness and making its survival very difficult. This is effectively a lethal threshold phenomenon. In summary, the cycle has three phases:

- (a) the production of eggs and their mortality,
- (b) the passage through the larva stage, and
- (c) the attachment of larvae to hosts and the subsequent death of the parasites because of their own mortality and that of the host—which entails the death of the parasites attached to it.

Such a host-parasite system exists, for example, in aquaculture basins which are physically separated from the sea, but whose water is renewed by bringing in sea water which in turn brings in some number of larvae [45]. A discrete model with nonuniform distributions of deaths and recruitment has been recently proposed for this system [46].

The structure of this paper is as follows. We present in the next section a mathematical model describing this host-parasite interaction, and incorporating the essential feature of the lethal threshold mentioned above, as well as a recruitment function which is parasite-density dependent: larger fractions of new parasites adhere to hosts having already more parasites. In Section 3, we prove that the model is well posed in some simplified situations, and in Section 4, we present the results of some numerical simulations.

2. THE MATHEMATICAL MODEL

We shall use the same variable to represent the first two stages in the life cycle of the parasites, $E(a, t)$, where a represents the age and thus differentiates eggs from larvae: ages between 0 and 4 correspond to eggs, those between 4 and 6 to larvae. We assume simple linear dynamics of McKendrick type [18]:

$$\begin{aligned} \frac{\partial E}{\partial t} + \frac{\partial E}{\partial a} &= -\mu_E(a) E + \Lambda, \\ E(0, t) &= B(t), \\ E(a, 0) &= E_0(a), \quad 0 \leq a \leq 6. \end{aligned} \tag{2.1}$$

Here $\mu_E(a)$ denotes the mortality rate at age a , which equals the mortality rate of eggs for ages between 0 and 4, that of larvae for ages between 4 and 6, and it is infinite for ages greater than 6 so that larvae will not survive after two days in that stage (unless they attach to a host and become parasites). $\Lambda = \Lambda(a, t)$ denotes an external supply of both eggs and larvae, $B(t)$ denotes the egg-laying function, which is the product of the number of adult parasites times the mean fertility rate of adult parasites. Finally, E_0 gives the initial age distribution of eggs and larvae in the system.

Next let $H(p, t)$ be the parasite density distribution of hosts. This means that, for $0 \leq p_1 < p_2 < +\infty$,

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

The total number of hosts at time t is then given by

$$\mathcal{H}(t) = \int_0^\infty H(p, t) dp, \tag{2.2}$$

while the total number of parasites at time t is

$$\mathcal{P}(t) = \int_0^\infty pH(p, t) dp. \tag{2.3}$$

In order to keep the structure of the hosts more manageable, we shall make a simplifying assumption that will allow us to keep track of the division of parasites into juveniles and adults without knowing their ages. We shall make the following hypothesis.

HYPOTHESIS 1. *At time $t = 0$, all parasites in all hosts are newly attached, that is juvenile parasites of age 0.*

The dynamics of the parasites will be described within each host of type $H(p_0, 0)$ by the following initial value problem:

$$\begin{aligned} pt &= -\mu p + \rho \frac{\mathcal{H}}{\mathcal{H} + C} f(p)L(t), \quad t > 0, \\ p(0) &= p_0, \end{aligned} \tag{2.4}$$

where μ denotes the mean mortality rate of parasites, assumed to be constant in this description,

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

is the total number of larvae available for recruitment, ρ is the probability that a larva will adhere to a host when there is an unlimited supply of the latter, $\mathcal{H}(t)/(\mathcal{H}(t) + C)$ is a scaling factor for this probability, with value 0 when there are no hosts, and value 1 when there is an unlimited number of them. Finally, $f(p)$ is a monotone nondecreasing function related to the probability that larvae which will adhere to a host will do it to a host having already p parasites. More specifically, $f(p)H(p, t)$ will be the probability density function for adherence to hosts with respect to how parasitized these already are. During observations in the field, it was noticed that, for hosts having fewer parasites than a threshold value \bar{p} , the probability of attachment seems largely independent of the degree of parasitism. After that threshold, the probability of attachment increases quite noticeably with increasing numbers of parasites already attached [43]. Consequently, the following function was proposed in [46]:

$$f(p, t) = f_0(t) + \lambda(t) [(p - \bar{p})_+]^2, \quad (2.5)$$

where the $+$ denotes the positive part of the function, and $f_0(t)$ and $\lambda(t)$ must be determined from the consistency relation

$$\int_0^\infty f(p, t)H(p, t) dp = 1$$

together with another relation derived from field observations, giving the proportion of larvae that will adhere to highly parasitized hosts as a function F of the proportion of the latter among all hosts, with $F(x) \geq x$

$$\int_{\bar{p}}^\infty f(p, t)H(p, t) dp = F \left(\frac{\int_{\bar{p}}^\infty H(p, t) dp}{\mathcal{H}(t)} \right).$$

Finally, the dynamics of the host population is given by the following initial boundary value problem:

$$\begin{aligned} \frac{\partial H}{\partial t} + \frac{\partial}{\partial p}[v(t)H] &= -\mu_h H - \mu_p(p)H, \\ v(t) &= \frac{dp}{dt}, \\ H(0, t) &= 0, \\ H(p, 0) &= H_0(p), \end{aligned} \quad (2.6)$$

where μ_h denotes the natural mortality rate of hosts in the absence of parasites, $\mu_p(p)$ is the additional mortality of hosts due to a burden of p parasites, which should be infinite once the lethal threshold p^* is reached. The condition $H(0, t) = 0$ for $t > 0$ means that after the initial time, no hosts will be free of parasites. This is a necessary consequence of the type of recruitment we chose, which makes all hosts recruit some parasites, albeit possibly a very small number. In order to have compatibility between the boundary condition and the condition $H_0(p)$, we should require that

$$H_0(0) = 0, \quad (2.7)$$

otherwise, no continuous solution of the problem can exist. Also, for obvious biological reasons, H_0 must be compactly supported in the positive real line, and integrable on it.

We can describe now how to divide the parasites into juveniles and adults. Since juveniles are all parasites recruited during the past 20 days who are still alive (after this age parasites become adult), all we need to do is multiply the recruitment rate by the probability of survival

and integrate the product for the past 20 days. Let j denote the number of juveniles among the p parasites in a host of type $H(p, t)$. Then,

$$j(t) = \int_{t-20}^t e^{-\mu(t-\tau)} \rho L(\tau) \frac{\mathcal{H}(\tau)}{\mathcal{H}(\tau) + C} f(p(\tau)) d\tau, \quad t \geq 20. \quad (2.8)$$

For $t < 20$, we know that $j = p$, in view of Hypothesis 1. In order to count the adults, all we need to do is look at the total number of parasites 20 days earlier and multiply it by the probability that they survived. If we let k denote the number of adults among the p parasites in a host of type $H(p, t)$, then

$$k(t) = p(t - 20) e^{-20\mu}, \quad t \geq 20. \quad (2.9)$$

For $t < 20$, we know $k = 0$, in view of Hypothesis 1. Since for all $t \geq 0$ we must have $p = j + k$, we should verify the consistency of their defining relations (2.4), (2.8), and (2.9). Note that (2.4) can be rewritten in the following form:

$$\frac{d}{d\tau} [e^{\mu\tau} p(\tau)] = \rho \frac{\mathcal{H}(\tau)}{\mathcal{H}(\tau) + C} f(p(\tau)) L(\tau) e^{\mu\tau},$$

and integrating from $t - 20$ to t , we see that

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

whereby

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

as needed.

Finally, note that the egg-laying function $B(t)$ can be expressed now as

$$B(t) = \beta \mathcal{A}, \quad (2.10)$$

where β is the mean number of eggs laid by each adult parasite in the unit of time, and

$$\mathcal{A}(t) = \int_0^\infty e^{-20\mu} p(t - 20) H(p, t) dp \quad (2.11)$$

is the total number of adult parasites in all hosts.

3. WELL POSEDNESS OF THE MODEL

We shall make some simplifying assumptions that will allow us to solve the model explicitly, while preserving the qualitative features of its dynamics. These simplifications essentially amount to decoupling the host-parasite dynamics from that of eggs and larvae. The well posedness of the general model will be addressed elsewhere. Let us assume that the total number of larvae $L(t)$ is constant, and also that the coefficients f_0 and λ that define $f(p)$ in (2.5) are constant. This does not quite make (2.4) autonomous but it allows us to treat it that way, after observing that $\mathcal{H}(t)/\mathcal{H}(t) + C$ stays between 0 and 1, even if \mathcal{H} were to become infinite. Consequently, we shall solve (2.4)–(2.6) replacing $\rho(\mathcal{H}/\mathcal{H} + C)$ with ρ , $0 \leq \rho \leq 1$.

First note that, for $\rho = 0$ we have a linear and separable equation for p , with solution

$$p(\tau) = p_0 e^{-\mu\tau}.$$

Hence, the unique trajectory through a point (p, t) in the first quadrant is $p(\tau) = pe^{-\mu(\tau-t)}$, $\tau \geq 0$. Also, (2.6) is a first-order linear partial differential equation, which can be explicitly solved

$$H(p, t) = H_0(pe^{\mu t})e^{(\mu-\mu_h)t - \int_0^t \mu_p(pe^{\mu\tau})d\tau}.$$

Let now $p_0^{\max} = \max\{\text{supp } H_0\}$. Then, (2.2), (2.3), we have

$$\begin{aligned}\mathcal{H}(t) &= e^{-\mu_h t} \int_0^{p_0^{\max}} H_0(l) e^{-1/\mu \int_{l_0}^l (\mu_p(s)/s) ds} dl, \\ \mathcal{P}(t) &= e^{-(\mu+\mu_h)t} \int_0^{p_0^{\max}} l H_0(l) e^{-1/\mu \int_{l_0}^l (\mu_p(s)/s) ds} dl.\end{aligned}$$

Obviously, this leads to the extinction of parasites and hosts since there is in this case no recruitment of either.

Next let us assume $\rho > 0$, and define the total host mortality $\mu_H = \mu_H(p) = \mu_h + \mu_p(p)$. We shall study now the parasite dynamics within one host. Note that (2.4) can be rewritten as

$$\frac{dp}{dt} = \begin{cases} -\mu p + \rho L f_0, & 0 \leq p \leq \bar{p}, \\ \rho L \lambda \left[p^2 - 2 \left(\bar{p} + \frac{\mu}{2\rho L \lambda} \right) p + \left(\frac{f_0}{\lambda} + \bar{p}^2 \right) \right], & p > \bar{p}. \end{cases} \quad (3.1)$$

For simplicity, let us introduce

$$\alpha = \frac{\mu}{\rho L}.$$

Note that, for high levels of parasitism ($p > \bar{p}$), whether the number of parasites in the host increases or decreases is determined by the discriminant of the quadratic polynomial in (3.1). Let

$$\Delta = \frac{1}{\lambda} \left(\alpha \bar{p} - f_0 + \frac{\alpha^2}{4\lambda} \right).$$

Then, if $\Delta < 0$ it follows that $\frac{dp}{dt} > 0$ and p is necessarily monotone increasing, while, if $\Delta > 0$, the quadratic has two real distinct roots,

$$p_{\infty}^+ = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta}, \quad p_{\infty}^- = \bar{p} + \frac{\alpha}{2\lambda} - \sqrt{\Delta},$$

and p decreases as long as it is in the interval $(p_{\infty}^-, p_{\infty}^+)$, while it increases outside the closure of this interval.

We can solve (3.1) with the initial condition $p(0) = p_0$ in explicit form, since this is a first-order separable equation. We need to consider three cases according to how f_0 compares with $\alpha \bar{p}$, and in each case several situations according to the size of p_0 .

CASE I. $f_0/\alpha \leq \bar{p}$.

(a) $p_0 \in [0, \bar{p}]$ gives

$$p(t) = \frac{f_0}{\alpha} (1 - e^{-\mu t}) + p_0 e^{-\mu t} \xrightarrow{t \rightarrow +\infty} \frac{f_0}{\alpha}.$$

For any given pair (p, t) in the first quadrant with $(f_0/\alpha)(1 - e^{-\mu t}) < p < (f_0/\alpha)(1 - e^{-\mu t}) + \bar{p}e^{-\mu t}$, the unique trajectory passing through this point is

$$p(\tau) = \frac{f_0}{\alpha} (1 - e^{\mu(t-\tau)}) + pe^{\mu(t-\tau)}, \quad (3.2)$$

which originates at the point $((f_0/\alpha)[1 - e^{\mu t}] + pe^{\mu t}, 0)$ and approaches the line $p = f_0/\alpha$ as τ tends to infinity.

(b) $p_0 \in (\bar{p}, p_{\infty}^+)$ gives, with

$$t^* = \frac{1}{2\sqrt{\Delta\rho L\lambda}} \ln \left[\frac{(p_0 - p_{\infty}^-)(\sqrt{\Delta} + \alpha/2\lambda)}{(p_{\infty}^+ - p_0)(\sqrt{\Delta} - \alpha/2\lambda)} \right]$$

$$p(t) = \begin{cases} \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{p_0 - p_{\infty}^+ + (p_0 - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}t}}{p_{\infty}^+ - p_0 + (p_0 - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}t}}, & t \leq t^*, \\ \frac{f_0}{\alpha} [1 - e^{-\mu(t-t^*)}] + \bar{p}e^{-\mu(t-t^*)}, & t > t^*, \end{cases} \quad t \rightarrow +\infty \frac{f_0}{\alpha}. \quad (3.3)$$

(c) $p_0 = p_{\infty}^+$ gives $p(t) \equiv p_{\infty}^+$.

(d) $p_0 \in (p_{\infty}^+, +\infty)$ gives, for

$$t < t^{**} = \frac{1}{2\sqrt{\Delta\rho L\lambda}} \ln \frac{p_0 - p_{\infty}^-}{p_0 - p_{\infty}^+},$$

$$p(t) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{p_0 - p_{\infty}^+ + (p_0 - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}t}}{p_{\infty}^+ - p_0 + (p_0 - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}t}} \xrightarrow{t \rightarrow t^{**}-} +\infty. \quad (3.4)$$

In this case, for any given pair (p, t) in the first quadrant, with $p > p_{\infty}^+$, the unique trajectory passing through this point is

$$p(\tau) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{(p - p_{\infty}^+) + (p - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}(\tau-t)}}{-(p - p_{\infty}^+) + (p - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}(\tau-t)}}, \quad (3.5)$$

which originates at the point

$$\left(\frac{(p - p_{\infty}^+)p_{\infty}^- - (p - p_{\infty}^-)p_{\infty}^+ e^{2\sqrt{\Delta\rho L\lambda}t}}{(p - p_{\infty}^+) - (p - p_{\infty}^-)e^{2\sqrt{\Delta\rho L\lambda}t}}, 0 \right),$$

and goes to infinity as τ approaches $t^{**} = t + (1/2\sqrt{\Delta\rho L\lambda}) \ln(p - p_{\infty}^-/p - p_{\infty}^+)$ from the left.

CASE II. $\bar{p} < f_0/\alpha \leq \bar{p} + (\alpha/4\lambda)$.

(a) $p_0 \in [0, \bar{p}]$ gives, with

$$t^{***} = \frac{1}{\mu} \ln \frac{f_0 - \alpha p_0}{f_0 - \alpha \bar{p}},$$

$$p(t) = \begin{cases} \frac{f_0}{\alpha} (1 - e^{-\mu t}) + p_0 e^{-\mu t}, & t \leq t^{***}, \\ \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{\bar{p} - p_{\infty}^+ + (\bar{p} - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}(t-t^{***})}}{p_{\infty}^+ - \bar{p} + (\bar{p} - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}(t-t^{***})}}, & t > t^{***}, \end{cases} \quad t \rightarrow +\infty p_{\infty}^-.$$

(b) $p_0 \in (\bar{p}, p_{\infty}^+)$ gives

$$p(t) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{p_0 - p_{\infty}^+ + (p_0 - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}t}}{p_{\infty}^+ - p_0 + (p_0 - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}t}} \xrightarrow{t \rightarrow +\infty} p_{\infty}^-.$$

(c) $p_0 = p_{\infty}^+$ gives $p(t) \equiv p_{\infty}^+$.

(d) $p_0 \in (p_{\infty}^+, +\infty)$ gives

$$p(t) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{p_0 - p_{\infty}^+ + (p_0 - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}t}}{p_{\infty}^+ - p_0 + (p_0 - p_{\infty}^-)e^{-2\sqrt{\Delta\rho L\lambda}t}}, \quad t < t^{**},$$

and we see that $p(t) \xrightarrow{t \rightarrow t^{**}-} +\infty$, just as in Case I.

CASE III. $f_0/\alpha > \bar{p} + \alpha/4\lambda$.

(a) $p_0 \in [0, \bar{p}]$ gives

$$p(t) = \begin{cases} \frac{f_0}{\alpha} (1 - e^{-\mu t}) + p_0 e^{-\mu t}, & t \leq t^{***}, \\ \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{-\Delta} \tan \left(\sqrt{-\Delta} \rho L \lambda [t - t^{***}] - \tan^{-1} \frac{\alpha}{2\lambda \sqrt{-\Delta}} \right), & t^{***} < t < \tilde{t}, \end{cases}$$

where

$$\tilde{t} = t^{***} + \frac{1}{\sqrt{-\Delta} \rho L \lambda} \left(\frac{\pi}{2} + \tan^{-1} \frac{\alpha}{2\lambda \sqrt{-\Delta}} \right),$$

and we see that $p(t) \xrightarrow{t \rightarrow \tilde{t}^-} +\infty$.

(b) $p_0 \in (\bar{p}, +\infty)$ gives, with

$$\hat{t} = \frac{1}{\sqrt{-\Delta} \rho L \lambda} \left(\frac{\pi}{2} - \tan^{-1} \frac{p_0 - \bar{p} - \alpha/2\lambda}{\sqrt{-\Delta}} \right),$$

$$p(t) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{-\Delta} \tan \left(\sqrt{-\Delta} \rho L \lambda t + \tan^{-1} \frac{p_0 - \bar{p} - \alpha/2\lambda}{\sqrt{-\Delta}} \right), \quad t < \hat{t},$$

and we see that $p(t) \xrightarrow{t \rightarrow \hat{t}^-} +\infty$.

Note that for any combination of parameters, there are at most two possible steady states: p_{∞}^+ is always one, provided $\Delta > 0$; f_0/α is a steady state only when it lies below \bar{p} while p_{∞}^- is one only when it lies above \bar{p} . We see that the number of parasites grows without bound in all cases when $\Delta < 0$, in which case there are no steady states, and the same is true when $\Delta \geq 0$ if $p_0 > p_{\infty}^+$. Otherwise, p tends monotonically to the smaller steady state.

Observe that, for $p_0 \geq 0$ we have $p(t) \geq 0$, which is biologically necessary. It should also be noted that in all cases, $p(t)$ is either constant or, otherwise, a strictly monotone function. This guarantees that no two trajectories intersect.

As for the hosts, we can solve the first-order quasilinear equation (2.6) explicitly using standard techniques.

CASE I. $f_0/\alpha \leq \bar{p}$.

We consider four subregions of the first quadrant.

(a) $(f_0/\alpha)(1 - e^{-\mu t}) \leq p \leq (f_0/\alpha)(1 - e^{-\mu t}) + \bar{p}e^{-\mu t}$.

This corresponds to Case I(a) of the parasites dynamics, $0 \leq p_0 \leq \bar{p}$. In this case, we have

$$H(p, t) = H_0 \left(\frac{f_0}{\alpha} [1 - e^{\mu t}] + p e^{\mu t} \right) e^{\mu t - \int_0^t \mu_H((f_0/\alpha)[1 - e^{\mu\tau}] + p e^{\mu\tau}) d\tau}. \quad (3.6)$$

Note that (3.6) says that the density of hosts having p parasites at time t can be found by tracing back the trajectory $(t, p(t))$ to its "origin" $(0, p_0)$, then taking the density of hosts that had such parasite load initially and multiplying it by the reciprocal of the probability that parasites survive from time 0 to t (a density rescaling factor) and by the probability that hosts survive from time 0 to t with a parasite burden $p_0 = p^{-1}(t)$.

(b) $(f_0/\alpha)(1 - e^{-\mu t}) + \bar{p}e^{-\mu t} < p < \bar{p}$.

This corresponds to Case I(b) of the parasites dynamics, $\bar{p} < p_0 < p_{\infty}$. In this case, we have

$$H(p, t) = H_0(p_0) e^{\mu t - \mu_H(\bar{p})t_0 - (1/\mu) \int_{\bar{p}}^p (\mu_H(s)/s - (f_0/\alpha)) ds},$$

where

$$p_0 = \frac{(\bar{p} - p_{\infty}^+) p_{\infty}^- - (\bar{p} - p_{\infty}^-) p_{\infty}^+ e^{2\sqrt{\Delta} \rho L \lambda t_0}}{(\bar{p} - p_{\infty}^+) - (\bar{p} - p_{\infty}^-) e^{2\sqrt{\Delta} \rho L \lambda t_0}} \quad \text{and} \quad t_0 = t + \frac{1}{\mu} \ln \left(\frac{p - f_0/\alpha}{\bar{p} - f_0/\alpha} \right).$$

Note that, since $f_0/\alpha \leq \bar{p}$ together with $(f_0/\alpha)(1 - e^{-\mu t}) + \bar{p}e^{-\mu t} < p < \bar{p}$ imply that $f_0/\alpha < p < \bar{p}$, we then have $t_0 < t$.

(c) $\bar{p} < p$.

This corresponds to Cases I(b)–(d) of the parasites dynamics, $\bar{p} < p_0 < +\infty$. In this case, we have

$$H(p, t) = H_0(p_0) e^{(\mu+2\rho L\lambda\bar{p})t - \int_0^t [\mu_H(p(\tau)) + 2\rho L\lambda p(\tau)] d\tau}, \quad (3.7)$$

where

$$p_0 = \frac{(p - p_{\infty}^+) p_{\infty}^- - (p - p_{\infty}^-) p_{\infty}^+ e^{2\sqrt{\Delta}\rho L\lambda t}}{(p - p_{\infty}^+) - (p - p_{\infty}^-) e^{2\sqrt{\Delta}\rho L\lambda t}}, \quad (3.8)$$

and $p(\tau)$ is given by (3.3) with this p_0 when $\bar{p} < p_0 \leq p_{\infty}^+$, and it is given by (3.4) with this p_0 when $p > p_{\infty}^+$. In particular, we have

$$H(p_{\infty}^+, t) = H_0(p_{\infty}^+) e^{[\mu - \mu_H(p_{\infty}^+) + 2\rho L\lambda(\bar{p} - p_{\infty}^+)]t}.$$

(d) $0 \leq p < (f_0/\alpha)(1 - e^{-\mu t})$.

This corresponds to parasites dynamics originating from a negative p_0 or, alternatively, from 0 parasites at some positive time. Given that we do not have any hosts without parasites in this model, we necessarily have

$$H(p, t) \equiv 0.$$

Mathematically, this would result directly from (3.6) if we defined $\mu_H = +\infty$ for $p < 0$ (meaning that a host may not survive a “negative parasite burden”).

CASE II. $\bar{p} < f_0/\alpha \leq \bar{p} + (\alpha/4\lambda)$.

We consider again four subregions in the first quadrant.

(a)

$$\frac{f_0}{\alpha} (1 - e^{-\mu t}) < p < \bar{p}, \quad 0 \leq t \leq \bar{t} = \frac{1}{\mu} \ln \frac{f_0}{f_0 - \alpha\bar{p}}.$$

This corresponds to Case II(a) of the parasites dynamics, $0 < p_0 < \bar{p}$. In this case, we have the parasite density of the hosts given again by (3.6),

$$H(p, t) = H_0 \left(\frac{f_0}{\alpha} [1 - e^{-\mu t}] + p e^{\mu t} \right) e^{\mu t - \int_0^t \mu_H((f_0/\alpha)[1 - e^{-\mu\tau}] + p e^{\mu\tau}) d\tau}.$$

(b)

$$\begin{cases} \bar{p}, & 0 \leq t \leq \bar{t}, \\ \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{\bar{p} - p_{\infty}^- + (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda(t-\bar{t})}}{\bar{p} - p_{\infty}^- - (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda(t-\bar{t})}}, & t > \bar{t}, \end{cases}$$

$$\leq p < \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{\bar{p} - p_{\infty}^- + (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda t}}{\bar{p} - p_{\infty}^- - (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda t}}.$$

This also corresponds to Case II(a) of the parasites dynamics, $0 < p_0 < \bar{p}$. However, in this case we have

$$H(p, t) = H_0(p_0) e^{\mu t_0 - \int_0^{t_0} \mu_H((f_0/\alpha)[1 - e^{-\mu\tau}] + \bar{p} e^{\mu\tau}) d\tau} e^{(\mu+2\rho L\lambda\bar{p})(t-t_0) - \int_{t_0}^t [\mu_H(p(\tau)) + 2\rho L\lambda p(\tau)] d\tau},$$

where $p_0 = (f_0/\alpha)[1 - e^{\mu t_0}] + \bar{p} e^{\mu t_0}$,

$$t_0 = t - \frac{1}{2\sqrt{\Delta}\rho L\lambda} \ln \frac{(\bar{p} - p_{\infty}^-)(p - p_{\infty}^+)}{(\bar{p} - p_{\infty}^+)(p - p_{\infty}^-)},$$

and

$$p(\tau) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{\bar{p} - p_{\infty}^- + (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda(\tau-t_0)}}{\bar{p} - p_{\infty}^- - (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda(\tau-t_0)}}.$$

(c)

$$\bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{\bar{p} - p_{\infty}^- + (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda t}}{\bar{p} - p_{\infty}^- - (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda t}} < p.$$

This corresponds to Cases II(b)–(d) of the parasites dynamics, $\bar{p} < p_0 < +\infty$. In this case, we have

$$H(p, t) = H_0(p_0) e^{(\mu+2\rho L\lambda\bar{p})t - \int_0^t [\mu_H(p(\tau)) + 2\rho L\lambda p(\tau)] d\tau},$$

where p_0 is given by (3.8) and

$$p(\tau) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{p_0 - p_{\infty}^- + (p_0 - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda\tau}}{p_0 - p_{\infty}^- - (p_0 - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda\tau}}.$$

(d)

$$0 \leq p < \begin{cases} \frac{f_0}{\alpha}(1 - e^{-\mu t}), & 0 \leq t \leq \bar{t}, \\ \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{\Delta} \frac{\bar{p} - p_{\infty}^- + (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda(t-\bar{t})}}{\bar{p} - p_{\infty}^- - (\bar{p} - p_{\infty}^+) e^{2\sqrt{\Delta}\rho L\lambda(t-\bar{t})}}, & t > \bar{t}. \end{cases}$$

Just as in Case I(d) of the hosts dynamics, this case corresponds to parasites dynamics originating from a negative p_0 or from $p_0 = 0$ for some positive time t . Therefore, necessarily

$$H(p, t) \equiv 0$$

in this region.

CASE III. $f_0/\alpha > \bar{p} + (\alpha/4\lambda)$.

We consider again four subregions in the first quadrant.

(a) $0 \leq p < \bar{p}$,

$$0 \leq t \leq \frac{1}{\mu} \ln \frac{f_0}{f_0 - \alpha p}.$$

This corresponds to Case III(a) of the parasites dynamics, $0 \leq p_0 < \bar{p}$. In this case, we have once more the parasite density of the hosts given again by (3.6),

$$H(p, t) = H_0 \left(\frac{f_0}{\alpha} [1 - e^{\mu t}] + p e^{\mu t} \right) e^{\mu t - \int_0^t \mu_H((f_0/\alpha)[1 - e^{\mu\tau}] + p e^{\mu\tau}) d\tau}.$$

(b) $p \geq \bar{p}$

$$\frac{1}{\sqrt{-\Delta}\rho L\lambda} \left(\tan^{-1} \frac{p - \bar{p} - \alpha/2\lambda}{\sqrt{-\Delta}} + \tan^{-1} \frac{\alpha}{2\lambda\sqrt{-\Delta}} \right) < t \\ \leq \bar{t} + \frac{1}{\sqrt{-\Delta}\rho L\lambda} \left(\tan^{-1} \frac{p - \bar{p} - (\alpha/2\lambda)}{\sqrt{-\Delta}} + \tan^{-1} \frac{\alpha}{2\lambda\sqrt{-\Delta}} \right).$$

This corresponds again to Case III(a) of the parasites dynamics, $0 \leq p_0 < \bar{p}$. This time we have the parasite density of the hosts given, just as in Case II(b) of the hosts dynamics, by

$$H(p, t) = H_0(p_0) e^{\mu t_0 - \int_0^{t_0} \mu_H((f_0/\alpha)[1 - e^{\mu\tau}] + \bar{p} e^{\mu\tau}) d\tau} e^{(\mu+2\rho L\lambda\bar{p})(t-t_0) - \int_0^{t-t_0} [\mu_H(p(\tau)) + 2\rho L\lambda p(\tau)] d\tau},$$

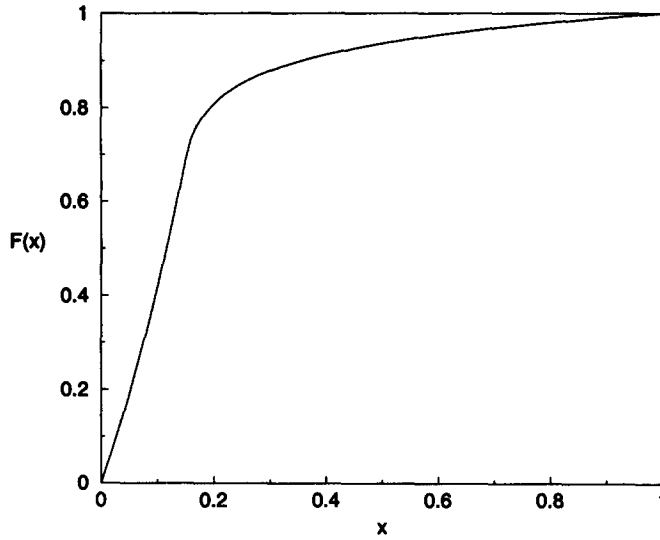


Figure 1.

where

$$t_0 = t - \frac{1}{\sqrt{-\Delta}\rho L\lambda} \left(\tan^{-1} \frac{p - \bar{p} - \alpha/2\lambda}{\sqrt{-\Delta}} + \tan^{-1} \frac{\alpha}{2\lambda\sqrt{-\Delta}} \right)$$

and

$$p(\tau) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{-\Delta} \tan \left(\sqrt{-\Delta}\rho L\lambda [\tau - t_0] - \tan^{-1} \frac{\alpha}{2\lambda\sqrt{-\Delta}} \right).$$

(c) $p \geq \bar{p}$,

$$0 \leq t \leq \frac{1}{\sqrt{-\Delta}\rho L\lambda} \left(\tan^{-1} \frac{p - \bar{p} - \alpha/2\lambda}{\sqrt{-\Delta}} + \tan^{-1} \frac{\alpha}{2\lambda\sqrt{-\Delta}} \right).$$

This corresponds again to Case III(b) of the parasites dynamics, $0 \leq p_0 < +\infty$. The parasite density of the hosts given again by (3.7)

$$H(p, t) = H_0(p_0) e^{(\mu + 2\rho L\lambda\bar{p})t - \int_0^t [\mu_H(p(\tau)) + 2\rho L\lambda p(\tau)] d\tau},$$

this time with

$$p_0 = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{-\Delta} \tan \left(\tan^{-1} \frac{p - \bar{p} - \alpha/2\lambda}{\sqrt{-\Delta}} - \sqrt{-\Delta}\rho L\lambda t \right), \quad \text{and}$$

$$p(\tau) = \bar{p} + \frac{\alpha}{2\lambda} + \sqrt{-\Delta} \tan \left(\sqrt{-\Delta}\rho L\lambda \tau - \tan^{-1} \frac{\alpha}{2\lambda\sqrt{-\Delta}} \right).$$

(d)

$$t > \begin{cases} \frac{1}{\mu} \ln \left(\frac{f_0}{f_0 - \alpha p} \right), & 0 \leq p < \bar{p}, \\ \bar{t} + \frac{1}{\sqrt{-\Delta}\rho L\lambda} \left(\tan^{-1} \frac{p - \bar{p} - \alpha/2\lambda}{\sqrt{-\Delta}} + \tan^{-1} \frac{\alpha}{2\lambda\sqrt{-\Delta}} \right), & p \geq \bar{p}. \end{cases}$$

Once more, just as in Cases I and II(d) of the hosts dynamics, this corresponds to parasites dynamics originating from a negative p_0 or from $p_0 = 0$ for some positive time t . Therefore, again, necessarily

$$H(p, t) \equiv 0$$

in this region.

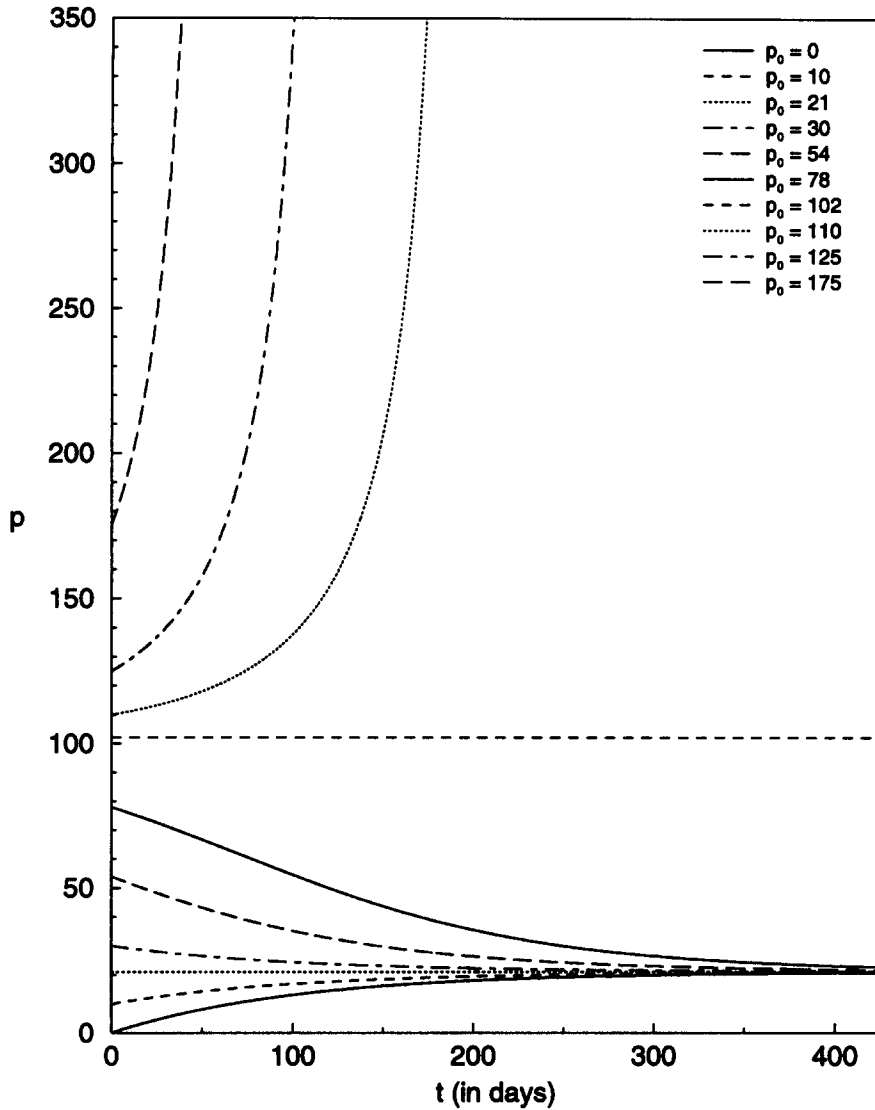


Figure 2.

The equation for the eggs and larvae (2.1) can be easily integrated along the characteristics. We obtain the formula

$$E(a, t) = \begin{cases} E_0(a - t) e^{-\int_{a-t}^a \mu_E(s) ds} + \int_0^t e^{-\int_{\tau+a-t}^a \mu_E(s) ds} \Lambda(\tau + a - t, \tau) d\tau, & a \geq t, \\ B(t - a) e^{-\int_0^a \mu_E(s) ds} + \int_0^a e^{-\int_\alpha^a \mu_E(s) ds} \Lambda(\alpha, \alpha + t - a) d\alpha, & t > a, \end{cases}$$

where B is given by (2.10) and (2.11).

Assume, for example, that $f_0/\alpha \leq \bar{p}$. If we now want to count the total number of adult parasites at a time $t > 20$, then we first divide the interval $(0, +\infty)$ into the following five subintervals:

$$I_1 = \left(0, \frac{f_0}{\alpha} (1 - e^{-\mu t}) \right), \quad I_2 = \left(\frac{f_0}{\alpha} (1 - e^{-\mu t}), \frac{f_0}{\alpha} (1 - e^{-\mu t}) + \bar{p} e^{-\mu t} \right), \\ I_3 = \left(\frac{f_0}{\alpha} (1 - e^{-\mu t}) + \bar{p} e^{-\mu t}, \bar{p} \right), \quad I_4 = (\bar{p}, p_\infty^+), \quad I_5 = (p_\infty^+, +\infty).$$

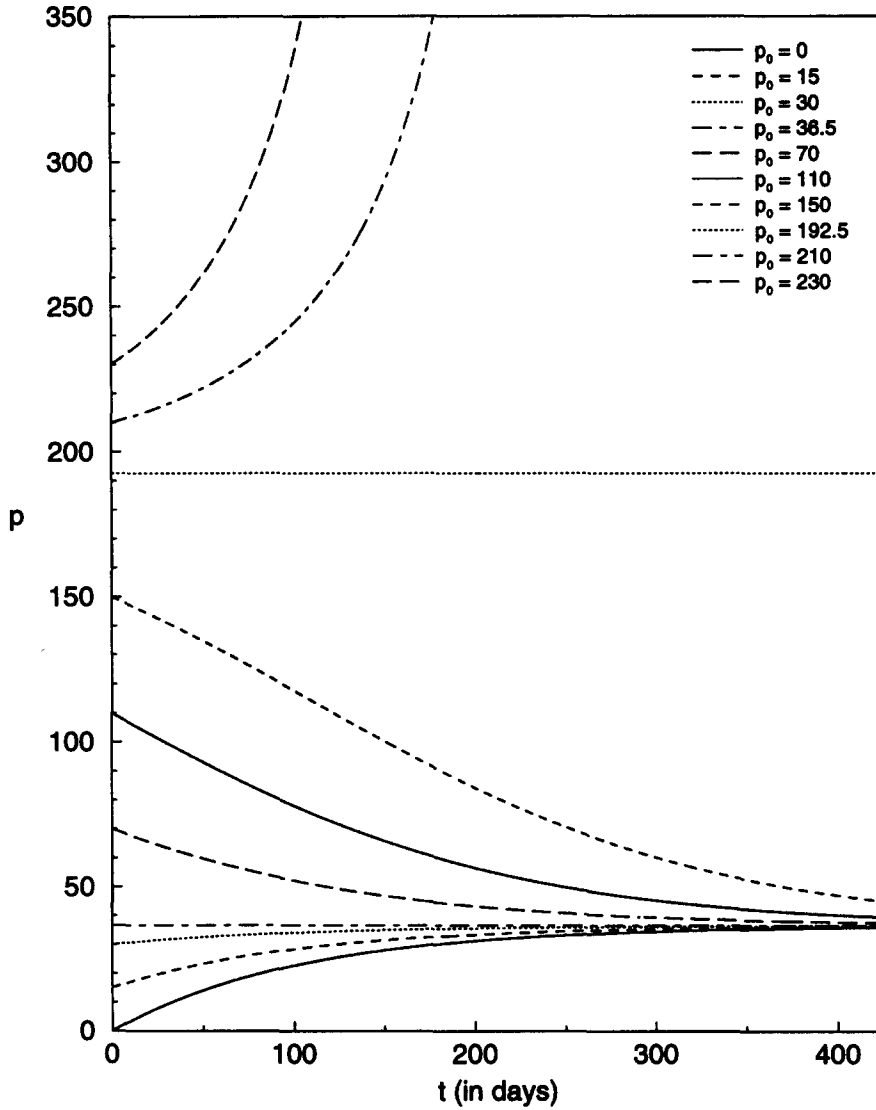


Figure 3.

Next, we compute the five integrals $S_i = \int_{I_i} H(p, t) p(t - 20) dp$, $1 \leq i \leq 5$, and we have

$$A(t) = e^{-20\mu} \sum_{i=1}^5 S_i.$$

For example, on I_1 the parasite density of the hosts vanishes identically. It follows that $S_1 = 0$. Similarly, on I_2 we have $p(\tau)$ and $H(p, t)$ given, respectively, by (3.2) and (3.6), and we readily see that

$$S_2 = \int_0^{\bar{p}} H_0(l) e^{-\int_0^l \mu_H (le^{-\mu\tau} + (f_0/\alpha)(1 - e^{-\mu\tau})) d\tau} \left[\frac{f_0}{\alpha} (1 - e^{\mu(t-20)}) + le^{\mu(t-20)} \right] dl.$$

4. NUMERICAL SIMULATIONS

We shall present now the results of some numerical simulations depicting the evolution of the parasite populations in Cases I–III, as well as the evolution of the host population in Case I. We use the following parameter values, similar to those found in [46]. For the parasite mortality, we

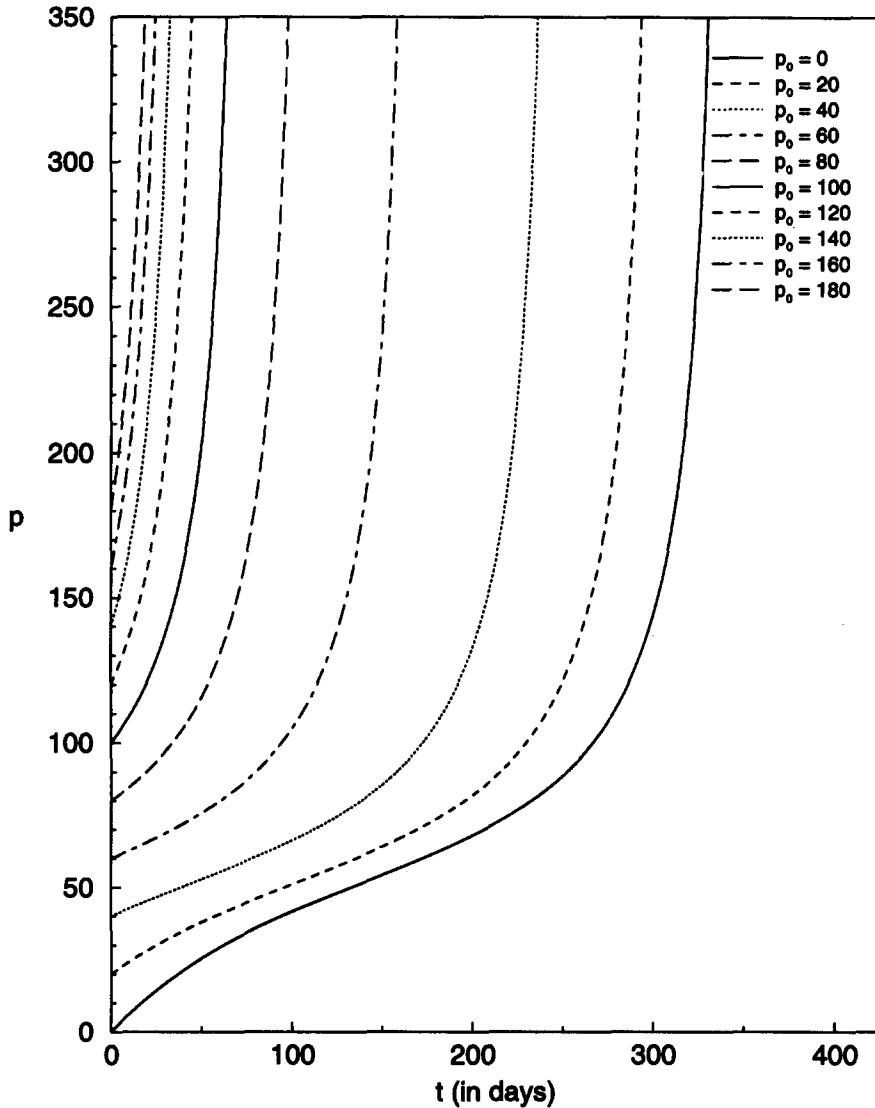


Figure 4.

use $\mu = 0.01$, giving an average life span of $1/\mu = 100$ days. For the threshold for accelerated recruitment, we use $\bar{p} = 30$. For the initial parasite density of the hosts, we chose a uniform distribution supported in the interval $[0, 50]$, $H_0(p) = 100 \chi_{[0,50]}$, which gives $\mathcal{H} = 5,000$. For the probability of attachment of a larva, $\rho(\mathcal{H}/\mathcal{H} + C)$, we use the value 0.5, obtained from $\rho = 0.6$, $\mathcal{H} = 5,000$, and $C = 1,000$. For the function F giving the proportion of recruited larvae attaching themselves to highly parasited hosts, we use

$$F(x) = \begin{cases} e^{3.5x} - 1, & x \leq 0.15, \\ 0.69 + 0.07285 \ln(81.215x - 11.182), & x > 0.15, \end{cases}$$

where the coefficients have been chosen so that $F(0) = 0$, $F(1) = 1$, F is increasing and continuously differentiable with an inflection point at 0.15 and having exponential growth until that point and logarithmic growth from then on. The graph of F is presented in Figure 1.

First, we chose f_0 , λ , and L in order to make $f_0/\alpha = f_0\rho L\mu$ fall into the ranges of Cases I-III of the parasite dynamics and have a good separation of the roots p_∞^+ and p_∞^- from f_0/α . For Case I, we chose $f_0 = 0.05866$, $\lambda = 0.00004365$, and $L = 7$, giving $f_0/\alpha = 21$ and $p_\infty^+ = 102$. We present in Figure 2 several trajectories originating from various initial values p_0 .

Host Dynamics

Case I

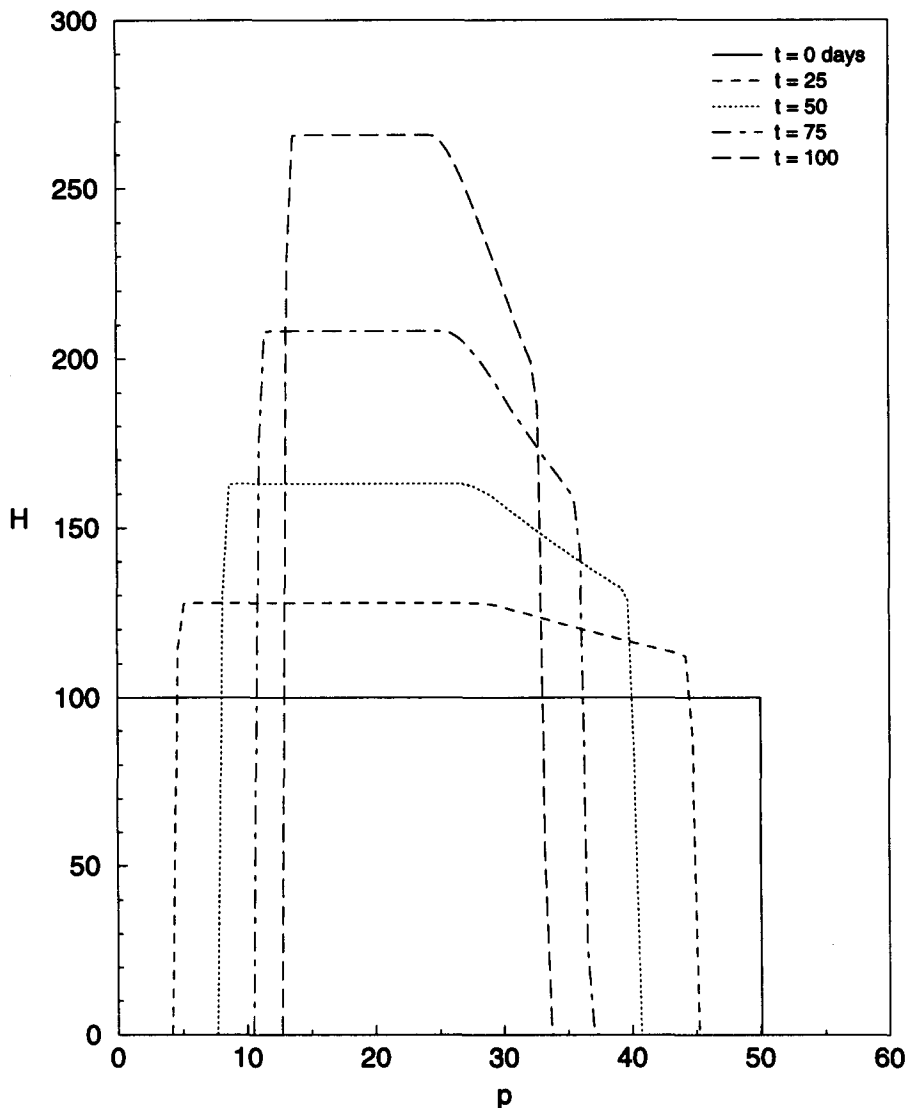


Figure 5.

We clearly see the predicted behavior that trajectories emanating from values of p_0 smaller than p_{∞}^+ asymptotically tend to f_0/α , while those emanating from values of p_0 larger than p_{∞}^+ blow up in a finite time.

For Case II, we chose $f_0 = 18.125$, $\lambda = 0.002959$, and $L = 0.03911$, giving $p_{\infty}^- = 36.5$ and $p_{\infty}^+ = 192.5$. We present in Figure 3 several trajectories for this case.

For Case III, we chose $f_0 = 33$, $\lambda = 0.01183$, and $L = 0.03911$. We present in Figure 4 several trajectories originating from various initial values p_0 .

In each case, we see that the graphs clearly depict the behavior predicted theoretically.

Finally, we present in Figures 5 and 6 the curves of parasite density of the hosts at various times. The former corresponds to an initial distribution which is constant and the latter to a normal one.

In both cases, we see that the parasite density of the hosts slowly tends to a unimodal distribution, with all hosts eventually having $f_0/\alpha = 21$ parasites.

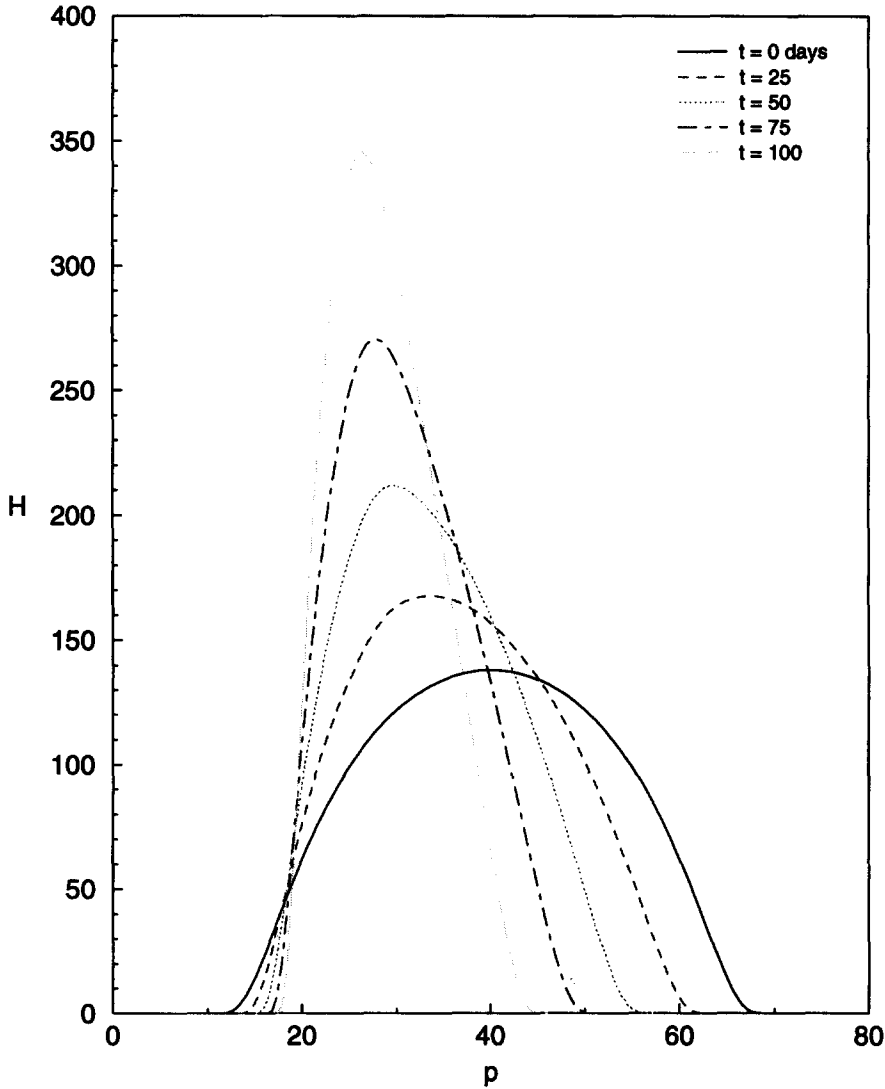


Figure 6.

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