

CONTINUOUS HOST-MACROPARASITE MODELS WITH APPLICATION TO AQUACULTURE

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ABSTRACT. We study a continuous deterministic host-macroparasite system which involves populations of hosts, parasites, and larvae. This system leads to a countable number of partial differential equations that under certain hypotheses, is reduced to finitely many equations. Also we assume hypotheses to close the system and to define the global dynamics for the hosts. Then, we analyze the spatially homogeneous model without demography (aquaculture hypothesis), and show some preliminary results for the spatially structured model.

1. INTRODUCTION

The aim of this paper is to study the dynamics of epidemic models for a host-macroparasite system. A spatially discrete model concerning a marine host-parasite system was first modelled in [13, 20]. The host is a fish, the sea bass *Dicentrarchus labrax*, and the parasite is a flat worm, *Diplectanum aequans* (Plathelminth, Monogenea), which parasitizes the gills of this host. After a cross-fertilization on fish gills [18], adult parasites lay eggs from which larvae hatch. The larvae try actively to find a host. If they succeed, the larvae settle on the host's scales and then move to its gills. At that time, the larvae undergo a maturing process leading to an adult stage that is capable of laying eggs.

A more complete age-structured formulation of the parasite population dynamics has been proposed in [7, 8]. This model, which is also a discrete model, concerns a fish-farmed population of sea bass, so the parasite population dynamics are described for a cohort of fish having the same age and initially without parasites. We have incorporated in this model a couple new features. First, we have integrated the existence of different cohorts into the parasite population. Second, as some demographical parameters (development of eggs, death rate or fertility rate of parasites) are under the influence of temperature linked to the season, we have added some temperature effects to this model.

The discrete model involves numerous parameters which cause two main problems. First, the complexity of the model makes the mathematical analysis of it extremely difficult. Second, this complexity results in long computation times when

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attempting to study the behavior of the model by performing numerical simulations. These difficulties lead to the consideration of a new approach. In the first part of this paper we introduce a continuous spatially structured model. The model will follow the idea first used by Anderson where one breaks the host population into a countable number of “populations” –hosts with $0, 1, 2, \dots$ parasites.

In [14, 15] we can find another approach. The authors introduced modelling host-parasite dynamics through a convection then a convection-diffusion partial differential equation which uses the parasites density as a continuous structure variable. Here, one conserves the Anderson’s well accepted hypothesis:

- (H1) These “populations” could increase by the death of one parasite within the next higher increment of infection or by immigration of one parasite into a host belonging to the “population” of hosts with the next lower increment of infection[1].

This gives a countable number of equations –one for each class of host having k parasites, where k is a nonnegative integer. As with the discrete model, one assumes a particular parasite distribution on the hosts. This assumption allows to reduce the model to a system of equations involving three population classes: hosts, parasites, and larvae. We will show that hosts and parasites have the same spatial structure. Also, if one supposes there is no spatial structure, one obtains some known models [1, 2, 3, 4, 5, 6].

In the second part of this paper, we analyze the ordinary differential equation model and give some results for the partial differential equation model. Describing the model, one includes births and intrinsic mortality, mortality not due to the presence of parasites, with the host population, but in the analysis one ignores it, because one is thinking of situations where it is not important, for example, in some aquaculture situations.

2. DESCRIPTION OF A CONTINUOUS SPATIALLY STRUCTURED MODEL

2.1. The structured populations. Let $h^k = h^k(x, t)$ denote the spatial density of hosts having k parasites, $k \in \mathbb{N}$, at a point x and time t . So $\int_{\Omega} h^k(x, t) dx$ is the total number of hosts in the region Ω with a load of k parasites. Let $H = H(x, t)$ be the spatial density of the total number of hosts. It is given by

$$H = \sum_{k=0}^{+\infty} h^k. \quad (2.1)$$

One defines the following parameters related to hosts.

- $b((h^l)_l, x, t)$ is the natural fertility rate of hosts at a point x and time t , where $(h^l)_l = (h^0, h^1, h^2, \dots)$.
- $\gamma(k)$ is the factor reducing the fertility of hosts having k parasites; $0 \leq \gamma(k) \leq 1$.
- $m_h((h^l)_l, x, t)$ is the intrinsic mortality of hosts at a point x and time t .
- $\alpha(k)$ is the induced mortality of hosts due to the burden of having k parasites. So, in each class of hosts with k parasites, the host mortality is given by $m_h((h^l)_l, x, t) + k\alpha(k)$
- $d_h \nabla h^k$ is the flux of the host population.

Let $P = P(x, t)$ denote the spatial density of parasites at a point x and time t . It can be obtained by

$$P = \sum_{k=0}^{+\infty} kh^k. \quad (2.2)$$

Parasites are subject to three mortalities:

- A natural mortality for parasites with a rate $\mu(k)$
- A mortality due to the intrinsic host mortality
- A mortality due to the induced mortality of hosts caused by a burden of k parasites linked to $\alpha(k)$.

The last two mortalities are due to the fact that if a host dies, its parasites must die.

The spatial density of larvae at a point x and time t is given by $L = L(x, t)$. One defines the following parameters related to larvae.

- $\nu(L, x, t)$ is the natural death rate of larvae at a point x and time t ;
- $\hat{\lambda}(k)$ is the laying rate per host in the class h^k of parasites at time t ;
- $R^k((h^l)_l, L, x, t)$ is the fixation rate of larvae on hosts of class h^k ;
- $d_L \nabla L$ is the flux of the larvae population.

2.2. The population dynamics. First we consider hosts having no parasites. The following assumption is made

- (H2) Hosts are born free from parasites. That is, at birth they belong to the class h^0 .

Aside from spatial migration, the rate of change of the size of the class h^0 consists of the following four terms.

- $m_h((h^l)_l, x, t)h^0 = m_h h^0$, $l \geq 0$, is the spatial density of hosts having 0 parasite which die from natural mortality at a point x and time t .
- $R^0((h^l)_l, x, t)h^0$, $l \geq 0$ is the spatial density of hosts having 0 parasite at a point x and time t that recruit larvae with rate R^0 .
- $\mu(1)h^1$ is the spatial density of hosts which come into the class h^0 from class h^1 because of natural mortality of their parasites (H1).
- The fertility of hosts having k parasites is $\gamma(k)b((h^l)_l, x, t)$, and the total birth rate of hosts is

$$\sum_{k=0}^{\infty} \gamma(k)b((h^l)_l, x, t)h^k.$$

Then the equation for hosts having 0 parasite is

$$\frac{\partial h^0}{\partial t} - d_h \Delta h^0 = \sum_{k=0}^{+\infty} b((h^l)_l, x, t)\gamma(k)h^k - m_h h^0 - R^0 h^0 + \mu(1)h^1. \quad (2.3)$$

Second, we consider hosts having parasites. The equation for the class h^k , $k \geq 1$, is similar to (2.3). Because of (H2), the birth term is not present. These hosts possess parasites, so there is an added mortality term, $k\alpha(k)h^k$, due to parasitism. There is also an additional positive term on the right side of the equation, $R^{k-1}h^{k-1}$, that takes into account hosts from class h^{k-1} that recruit a parasite and enter class h^k . Finally, there is an additional negative term, $k\mu(k)h^k$, that takes into account hosts from class h^k that have a parasite that dies moving these hosts to class h^{k-1} .

The other terms are analogous to the ones in (2.3). So the equation describing the dynamics of hosts with k parasites is

$$\begin{aligned} \frac{\partial h^k}{\partial t} - d_h \Delta h^k \\ = (k+1)\mu(k+1)h^{k+1} - [m_h + k\alpha(k) + R^k + k\mu(k)]h^k + R^{k-1}h^{k-1} \\ = F^k. \end{aligned} \quad (2.4)$$

One adds some hypotheses to close the system and to define the global dynamics for hosts, $H = \sum_{k=0}^{+\infty} h^k$. First one assumes

$$(H3) \quad R^k = R^k((h^l)_l, L, x, t) = R(H, L).$$

One considers two different functions for R :

$$R(H, L) = \beta L \quad (2.5)$$

where β is a positive constant, and

$$R(H, L) = \frac{\rho L}{\hat{C}_0 + H}. \quad (2.6)$$

where ρ and \hat{C}_0 are positive constants. The function (2.5) was proposed by Anderson [4]. With it one supposes the recruitment function is proportional to the number of larvae. For the second function (2.6), one takes inspiration from what was proposed by Langlais *et al.* [13] and Bouloux *et al.* [8] in the discrete model. One also includes the following hypotheses in order to describe the global dynamics of hosts.

(H4) The fertility rate is spatially and temporally homogeneous, and density dependent: $b((h^l)_l, x, t) = b(H)$.

(H5) The intrinsic death rate of hosts is spatially and temporally homogeneous, and density dependent: $m_h = m_h((h^l)_l, x, t) = m_h(H)$.

(H6) $d_h \geq 0$.

(H7) The natural death rate of larvae is spatially and temporally homogeneous, and density dependent: $\nu(L, x, t) = \nu(L)$.

The global dynamics of hosts can be described as follows. One assumes that X is a random variable that represents the number of parasites. The probability for a host to have k parasites is $P(X = k) = \frac{h^k}{H}$; see [9, 10, 11]. Summing (2.3) and (2.4) over all classes, we obtain

$$\frac{\partial H}{\partial t} - d_h \Delta H = [b(H)E(\gamma(X)) - m_h(H) - E(X\alpha(X))]H. \quad (2.7)$$

To obtain the global dynamics for parasites, we multiply (2.4) by k , then sum over all k , and recall (2.2). Using (H6), this gives

$$\frac{\partial P}{\partial t} = d_h \sum_{k=1}^{+\infty} k \Delta h^k + \sum_{k=1}^{+\infty} k F^k, \quad (2.8)$$

where F^k is defined by (2.4). After some calculations using hypothesis (H3) and the fact that $h^k = P(X = k)H$, one can express the dynamics of parasites by

$$\frac{\partial P}{\partial t} - d_h \Delta P = [R(H, L) - m_h(H)E(X) - E(X\mu(X)) - E(X^2\alpha(X))]H. \quad (2.9)$$

The larvae dynamics involves three phenomena:

- There is one gain term which corresponds to the number of larvae that parasites lay. $\hat{\lambda}(k)h^k$ is the number of eggs laid by parasites on hosts having k parasites, so $\sum_{k=0}^{+\infty} \hat{\lambda}(k)h^k$ is the total number of laid eggs by parasites on all hosts.
- There are two loss terms:
 - One is the recruitment of larvae by hosts at a point x and time t . $R(H, L)H$ is the rate at which larvae manage to attach themselves on hosts.
 - The other is the number of larvae which die from natural death at a point x and time t , $\nu(L)L$.

Following (H3) and (H7), one models the larvae dynamics as

$$\frac{\partial L}{\partial t} - d_L \Delta L = E(\hat{\lambda}(X))H - R(H, L)H - \nu(L)L. \quad (2.10)$$

Putting equations (2.7), (2.9), and (2.10) together, the dynamics for the host-parasite system is described by

$$\begin{aligned} \frac{\partial H}{\partial t} - d_h \Delta H &= b(H)E(\gamma(X))H - [m_h(H) + E(X\alpha(X))]H, \\ \frac{\partial P}{\partial t} - d_h \Delta P &= H[R(H, L) - m_h(H)E(X)] - [E(X\mu(X)) + E(X^2\alpha(X))]H, \\ \frac{\partial L}{\partial t} - d_L \Delta L &= E(\hat{\lambda}(X))H - R(H, L)H - \nu(L)L. \end{aligned} \quad (2.11)$$

For biological reasons, all parameters are nonnegative. So one has

- (H8) $m_h(H) \geq 0$, $b(H) \geq 0$, $\hat{\lambda}(k) \geq 0$, $\nu(L) \geq 0$, $\alpha(k) \geq 0$, $\mu(k) \geq 0$, $R(H, L) \geq 0$.
- (H9) $\mu(k) = \mu k^{l-1}$ and $\alpha(k) = \alpha k^{l-1}$ for $l = 1, 2$, $\gamma(k) = \gamma^k$, $0 < \gamma \leq 1$, $\hat{\lambda}(k) = \hat{\lambda}k$,

where $l = 2$ means that natural parasite death rates or induced mortality of hosts are dependent on the number of parasites, whereas $l = 1$ means that those rates do not depend on how many parasites are present on hosts.

To have a generic model in terms of H , P and L , one makes assumptions on the distribution of parasites in hosts. One assumes that parasites are distributed on the host population according to a Poisson law with mean $z = \frac{P}{H}$ or a negative binomial with the same mean and a clumping parameter Ψ [4, 5]. The second distribution is characterized by the fact that a few hosts carry a high parasite burden, while the majority of hosts have few parasites [1, 2, 3, 4, 5, 7, 8, 13]. This type of distribution is said to be *overdispersed*.

One obtains four types of models, denoted I to IV, in which one supposes the induced mortality of hosts is intensity dependent or independent, and the natural death rate of parasites is density dependent or not.

- In model I the induced mortality of hosts is intensity independent, and the natural death rate of parasites is density independent. This can be expressed by $\alpha(k) = \alpha$ and $\mu(k) = \mu$.
- In model II the induced mortality of hosts is intensity dependent, and the natural death rate of parasites is density independent. This can be expressed by $\alpha(k) = \alpha k$ and $\mu(k) = \mu$.

- In model III the induced mortality of hosts is intensity independent, and the natural death rate of parasites is density dependent. This can be expressed by $\alpha(k) = \alpha$ and $\mu(k) = \mu k$.
- In model IV the induced mortality of hosts is intensity dependent, and the natural death rate of parasites is density dependent. This can be expressed by $\alpha(k) = \alpha k$ and $\mu(k) = \mu k$.

For each model, using the Poisson or binomial distribution, one can calculate the different moments in the model (2.11), and whatever the distribution used, one has the generic model

$$\begin{aligned} \frac{\partial H}{\partial t} - d_h \Delta H &= H[h(H, P) - m_h(H) - M(H, P)], \\ \frac{\partial P}{\partial t} - d_h \Delta P &= R(H, L)H - P[(m_h(H) + \mu + \alpha) + Q(H, P)], \\ \frac{\partial L}{\partial t} - d_L \Delta L &= \hat{\lambda}P - R(H, L)H - \nu(L)L, \end{aligned} \quad (2.12)$$

where $M(H, P) = E(\alpha(X))$, $Q(H, P)$ satisfies

$$P[\mu + \alpha + Q(H, P)] = H[E(X\mu(X)) + E(X^2\alpha(X))]$$

and $h(H, P) = b(H)E(\gamma(X))$ (see the second equations of (2.11) and (2.12)). Whatever the model one chooses, one always finds the terms $\mu + \alpha$ in the second equation of (2.12). Finally, using the Poisson or negative binomial distributions, one obtains the forms for $h(H, P)$, $M(H, P)$ and $Q(H, P)$ [7] listed in Tables 1 and 2 in the Appendix. In the rest of the paper, it will be assumed that $M(H, P)$ and $Q(H, P)$ are given by one of those forms.

3. ANALYSIS OF ODE MODELS WITHOUT DEMOGRAPHY

As for the discrete model in , we assume that

$$b(H) = m_h(H) = 0.$$

When there is no spatial structure, in order to work with the total parasite population, one uses the mean number of parasites on hosts, $z = \frac{P}{H}$. This gives the spatially homogeneous model without demography

$$\begin{aligned} \frac{dH}{dt} &= -\tilde{M}(z)H, \\ \frac{dz}{dt} &= R(H, L) - z[\mu + \alpha + \tilde{Q}(z)], \\ \frac{dL}{dt} &= \hat{\lambda}zH - R(H, L)H - \nu L, \end{aligned} \quad (3.1)$$

with initial conditions

$$H(0) = H_0 > 0, \quad z(0) = z_0 > 0, \quad L(0) = L_0 > 0, \quad (3.2)$$

and under the hypotheses

- (B0) $\mu \geq 0, \alpha \geq 0, \alpha + \mu > 0, \nu > 0$,
- (B1) $\tilde{M}(z) = a_1 z + a_2 z^2, a_1 > 0, a_2 \geq 0$ (defined in the appendix),
- (B2) $\tilde{Q}(z) = b_1 z + b_2 z^2, b_1, b_2 \geq 0$ (defined in the appendix)
- (B3) $R(H, L)$ defined by (2.5) or (2.6).

Note that $R(H, 0) = 0$, $R(H, L) > 0$ for $H \geq 0$, $L > 0$ and $R_L = \frac{\partial R}{\partial L}(H, L) > 0$ for $H \geq 0$ and $L > 0$. See the Appendix for explicit values for a_j and b_j , for $j = 1, 2$. These values do not affect the analysis.

Proposition 3.1. $\mathbb{B} = \{(H, z, L) : H \geq 0, z \geq 0, L \geq 0\}$ is an invariant region for (3.1)-(3.2). In addition, under hypothesis (B0), (B1), (B2), and (B3), the system (3.1)-(3.2) has one and only one nonnegative solution defined on $[0, +\infty)$.

Proof. The persistence of nonnegativity is a consequence of the fact that the vector field $F(\cdot, \cdot, \cdot)$ defined by

$$F(H, z, L) = \{F_i(H, z, L)\}_{i=1,2,3} = \begin{pmatrix} -\tilde{M}(z)H \\ R(H, L) - z[\mu + \alpha + \tilde{Q}(z)] \\ \hat{\lambda}zH - R(H, L)H - \nu L \end{pmatrix}$$

does not point out of the positive octant \mathbb{R}_+^3 , and hence \mathbb{R}_+^3 is an invariant region for solutions. From hypothesis (B1), (B2), and (B3), $F(\cdot, \cdot, \cdot)$ is locally Lipschitz continuous, so from the Cauchy-Lipschitz theorem, there exists a unique local maximal solution defined on a maximal interval $[0, T_{max})$, $T_{max} > 0$. If $T_{max} < +\infty$, then

$$\lim_{t \rightarrow T_{max}} (|H(t)| + |z(t)| + |L(t)|) = +\infty.$$

From the equation for H in (3.1), one sees that $H(t)$ is non-increasing by the nonnegativity of \tilde{M} (B1) and H , so $\lim_{t \rightarrow +\infty} H(t) = H_\infty \geq 0$. Also we have

$$\frac{dz}{dt} + \frac{dL}{dt} \leq R(H_\infty, L) + \hat{\lambda}zH_0.$$

One can write R as $R(H_\infty, L) = cL$. Then by (B3),

$$\frac{dz}{dt} + \frac{dL}{dt} \leq \max(c, \hat{\lambda}H_0)(z + L).$$

One concludes that $T_{max} = +\infty$. □

Theorem 3.2. One has $\lim_{t \rightarrow +\infty} H(t) = H_\infty > 0$. In addition, trajectories of (3.1) are bounded and $z(t) \rightarrow 0$, $P(t) \rightarrow 0$ and $L(t) \rightarrow 0$ when $t \rightarrow +\infty$.

Proof. First, we show that $\lim_{t \rightarrow +\infty} L(t) = 0$. If one considers the expression $AH'(t) + L'(t)$ where $A > 0$, one has

$$\begin{aligned} AH'(t) + L'(t) &= -A\tilde{M}(z)H + \hat{\lambda}zH - R(H(t), L(t))H - \nu L \\ &= -A(a_1z + a_2z^2)H + \hat{\lambda}zH - R(H(t), L(t))H - \nu L \\ &\leq (\hat{\lambda} - Aa_1)zH - \nu L \end{aligned}$$

Choosing $A > \hat{\lambda}/a_1$, $AH' + \nu L' < 0$. One integrates over $[0, t]$, and obtains

$$0 \leq AH(t) + L(t) + \nu \int_0^t L(\tau) d\tau \leq AH(0) + L(0) = C$$

So, $L \in L^1 \cap L^\infty$ and thanks to the nonnegativity of L , $\liminf_{t \rightarrow +\infty} L(t) = 0$. Besides,

$$\frac{dL}{dt} \leq \hat{\lambda}zH$$

But, from the equation for H ,

$$\frac{dH}{dt} = (-a_1z - a_2z^2)H \leq -a_1zH$$

Integrating over $[0, t]$,

$$\int_0^t (zH)(\tau) d\tau \leq -\frac{1}{a_1} (H(t) - H(0)) \leq \frac{1}{a_1} H(0)$$

Therefore, $zH \in L^1$. L can be written as the function $L(t) = \int_0^t L'(\tau) d\tau + L(0)$. From the fact that $L' \in L^1$, and $\liminf_{t \rightarrow +\infty} L(t) = 0$, one has $\lim_{t \rightarrow +\infty} L(t) = 0$.

Next we show that $\lim_{t \rightarrow +\infty} z(t) = 0$. Note that from the expression of R (see (B3)), $R(H, L) \in L^1 \cap L^\infty$. Consider the equation for z :

$$\begin{aligned} z'(t) &\leq R(H, L) - (\mu + \alpha)z \\ \Leftrightarrow e^{(\mu+\alpha)s} z'(s) + (\mu + \alpha)e^{(\mu+\alpha)s} z(s) &\leq R(H, L)e^{(\mu+\alpha)s} \\ \Leftrightarrow \frac{d}{ds} \left[e^{(\mu+\alpha)s} z(s) \right] &\leq R(H, L)e^{(\mu+\alpha)s} \\ \Leftrightarrow e^{(\mu+\alpha)t} z(t) - z(0) &\leq \int_0^t R(H, L)e^{(\mu+\alpha)s} ds \\ \Leftrightarrow z(t) &\leq e^{-(\mu+\alpha)t} z(0) + \int_0^t R(H, L)e^{-(\mu+\alpha)(t-s)} ds \end{aligned}$$

The right-hand side is in $L^1 \cap L^\infty$; therefore, (1) $z \in L^1 \cap L^\infty$. Since $\frac{dz}{dt} \leq R(H, L)$, one can immediately conclude that (2) $\frac{dz}{dt} \in L^1 \cap L^\infty$. From (1) and (2), z is uniformly continuous. Indeed,

$$z(t) = z(t_0) + \int_{t_0}^t z'(s) ds$$

Thanks to (2), there exists $B > 0$ such that $\|z'\| < B$, so

$$|z(t) - z(t_0)| \leq \int_{t_0}^t |z'(s)| ds \leq |t - t_0| B \leq B\eta.$$

Choosing $\eta = \frac{\epsilon}{B}$, one obtains the desired result. The uniform continuity and the fact that $z \in L^1$, implies that $\lim_{t \rightarrow \infty} z(t) = 0$.

Next we show that $\lim_{t \rightarrow \infty} H(t) = H_\infty > 0$. One has $\tilde{M}(z) = a_1 z + a_2 z^2$, so integrating over $[0, t]$, one obtains

$$\begin{aligned} \int_0^t |\tilde{M}(z(\tau))| d\tau &\leq \int_0^t a_1 |z(\tau)| d\tau + \int_0^t a_2 |z^2(\tau)| d\tau \\ &\leq a_1 \|z\|_{L^1} + a_2 \|z\|_{L^\infty} \|z\|_{L^1} \end{aligned}$$

So $\tilde{M}(z) \in L^1$. From the H equation in (3.1),

$$H(t) = H(0) \exp \left(- \int_0^t \tilde{M}(z(\tau)) d\tau \right) \quad (3.3)$$

where $H(0) > 0$. Suppose that $\lim_{t \rightarrow \infty} H(t) = H_\infty = 0$. This implies

$$\lim_{t \rightarrow \infty} \int_0^t \tilde{M}(z(\tau)) d\tau = \int_0^{+\infty} \tilde{M}(z(\tau)) d\tau = +\infty.$$

But this is inconsistent with the fact that $\tilde{M}(z) \in L^1$. So $\lim_{t \rightarrow \infty} H(t) = H_\infty > 0$.

We may conclude that without demography on the host population, trajectories are bounded and the origin is globally asymptotically stable—there is no regulation of parasite and larva populations. And the theorem is proven. \square

Besides, from (3.3),

$$\begin{aligned} H(t+s) &= H(0) \exp\left(-\int_0^{t+s} \tilde{M}(z(\tau)) d\tau\right) \\ &= H(0) \exp\left(-\int_0^t \tilde{M}(z(\tau)) d\tau\right) \exp\left(-\int_t^{t+s} \tilde{M}(z(\tau)) d\tau\right) \\ &= H(t) \exp\left(-\int_t^{t+s} \tilde{M}(z(\tau)) d\tau\right) \end{aligned}$$

When $s \rightarrow +\infty$, one obtains

$$H_\infty = H(t) \exp\left(-\int_t^{+\infty} \tilde{M}(z(\tau)) d\tau\right)$$

We remark that the set $\{(z, L) = (0, 0)\}$ is an invariant manifold for the system (3.1), so each point $(H, z, L) = (H, 0, 0)$ is a stationary solution for (3.1).

4. SOME RESULTS FOR THE PDE MODEL

Once again one has the assumption that

$$b(H) = m_h(H) = 0.$$

One must define some notation. Suppose Ω is a bounded domain in \mathbb{R}^n , $n = 1$ or 2 , with a smooth boundary, $\partial\Omega$. Let $Q(0, t) = \Omega \times (0, t)$. If $u \in L^p(\Omega)$, one takes the L^p -norm of u , $\|u\|_{p,\Omega}$, to be

$$\|u(\cdot)\|_{p,\Omega} = \begin{cases} (\int_\Omega |u(x)|^p dx)^{1/p} & \text{if } 1 \leq p < +\infty, \\ \text{ess sup}_{x \in \Omega} |u(x)| & \text{if } p = +\infty. \end{cases}$$

The $L^p(Q(0, t))$ -norm is

$$\|u(\cdot, \cdot)\|_{p,Q(0,t)} = \begin{cases} (\int_0^t \|u(\cdot, \tau)\|_{p,\Omega}^p d\tau)^{1/p} & \text{if } 1 \leq p < +\infty, \\ \text{ess sup}_{\tau \in (0,t)} \|u(\cdot, \tau)\|_{\infty,\Omega} & \text{if } p = +\infty. \end{cases}$$

For $(x, t) \in \Omega \times (0, +\infty)$, one recalls the spatially structured model

$$\begin{aligned} \frac{\partial H}{\partial t} - d_H \Delta H &= -HM(H, P), \\ \frac{\partial P}{\partial t} - d_H \Delta P &= R(H, L)H - P[(\mu + \alpha) + Q(H, P)], \\ \frac{\partial L}{\partial t} - d_L \Delta L &= \hat{\lambda}P - R(H, L)H - \nu L, \end{aligned} \quad (4.1)$$

with the initial conditions on $\Omega \times \{0\}$

$$H(x, 0) = H_0(x) > 0, \quad P(x, 0) = P_0(x) > 0, \quad L(x, 0) = L_0(x) > 0, \quad (4.2)$$

and for $(x, t) \in \partial\Omega \times [0, +\infty)$ one chooses homogeneous Neumann conditions

$$\frac{\partial H(x, t)}{\partial \eta} = \frac{\partial P(x, t)}{\partial \eta} = \frac{\partial L(x, t)}{\partial \eta} = 0. \quad (4.3)$$

Here hypotheses (B0) and (B3) apply, and $M(H, P)$ and $Q(H, P)$ are defined in the appendix. Problem (4.1)-(4.3) is a singular problem because $M(H, P) = M(\frac{P}{H})$ and $Q(H, P) = Q(\frac{P}{H})$ (see the appendix). So, one approximates this problem by a regular problem containing a small coefficient ϵ , where $0 < \epsilon \leq 1$. One replaces H

in the functions M and Q by $H_\epsilon + \epsilon$. This gives the following approximate problem

$$\begin{aligned} \frac{\partial H_\epsilon}{\partial t} - d_H \Delta H_\epsilon &= -H_\epsilon M(H_\epsilon + \epsilon, P_\epsilon), \\ \frac{\partial P_\epsilon}{\partial t} - d_H \Delta P_\epsilon &= R(H_\epsilon, L_\epsilon)H_\epsilon - P_\epsilon[(\mu + \alpha) + Q(H_\epsilon + \epsilon, P_\epsilon)], \\ \frac{\partial L_\epsilon}{\partial t} - d_L \Delta L_\epsilon &= \hat{\lambda}P_\epsilon - R(H_\epsilon, L_\epsilon)H_\epsilon - \nu L_\epsilon, \end{aligned} \quad (4.4)$$

with initial conditions, on $\Omega \times \{0\}$,

$$H_\epsilon(x, 0) = H_0(x) > 0, \quad P_\epsilon(x, 0) = P_0(x) > 0, \quad L_\epsilon(x, 0) = L_0(x) > 0, \quad (4.5)$$

and the boundary conditions on $\Omega \times (0, +\infty)$

$$\frac{\partial H_\epsilon(x, t)}{\partial \eta} = \frac{\partial P_\epsilon(x, t)}{\partial \eta} = \frac{\partial L_\epsilon(x, t)}{\partial \eta} = 0. \quad (4.6)$$

One now shows that (4.4)-(4.6) possesses a unique, nonnegative solution.

Theorem 4.1. *For any initial condition $(H_0, P_0, L_0) \in C(\bar{\Omega})^3$, there exists a unique nonnegative continuous classical solution, $(H_\epsilon, P_\epsilon, L_\epsilon)$ defined on $Q(0, \infty) = \Omega \times (0, +\infty)$ to (4.4)-(4.6). In addition, if $\hat{\lambda} \leq \mu + \alpha$, $\int_\Omega (P_\epsilon(x, t) + L_\epsilon(x, t)) dx$ is a partial Lyapunov function and the solution is globally bounded in $L^\infty(Q(0, \infty))$.*

Proof. As in the previous section, one may check that $(H_\epsilon, P_\epsilon, L_\epsilon)$ for the system (4.4)-(4.6) is nonnegative [21]. In addition, the regularity of the vector field $F(\cdot, \cdot, \cdot) = \{F_i(H, P, L)\}_{i=1,2,3}$ implies local existence of a unique classical solution $(H_\epsilon, P_\epsilon, L_\epsilon) \geq (0, 0, 0)$, defined on $Q(0, T_{max})$. Also, by the positivity of H_ϵ and $M(H_\epsilon + \epsilon, P_\epsilon)$, looking at the first equation in (4.4) one can see that

$$\frac{\partial H_\epsilon}{\partial t} - d_H \Delta H_\epsilon \leq 0. \quad (4.7)$$

Then, by the maximum principle, H_ϵ is globally bounded in $L^\infty(\Omega \times (0, +\infty))$, because

$$\|H_\epsilon(\cdot, t)\|_{\infty, \Omega} \leq \|H_0(\cdot)\|_{\infty, \Omega}, \quad (4.8)$$

for $t \geq 0$, and so

$$\sup_{t \geq 0} \|H_\epsilon(\cdot, t)\|_{\infty, \Omega} \leq \|H_0(\cdot)\|_{\infty, \Omega}. \quad (4.9)$$

One now considers P_ϵ and L_ϵ . If one sums the last two equations in (4.4) and integrates over Ω , one has, after throwing out some negative terms on the right hand side,

$$\frac{d}{dt} \|P_\epsilon(\cdot, t) + L_\epsilon(\cdot, t)\|_{1, \Omega} \leq (\hat{\lambda} - \mu - \alpha) \|P_\epsilon\|_{1, \Omega}. \quad (4.10)$$

There are two cases to be considered.

Case 1: $\hat{\lambda} \leq \mu + \alpha$. One has

$$\frac{d}{dt} \|P_\epsilon(\cdot, t) + L_\epsilon(\cdot, t)\|_{1, \Omega} \leq 0,$$

so $\|P_\epsilon(\cdot, t) + L_\epsilon(\cdot, t)\|_{1, \Omega}$ is a Lyapunov function. In addition, one has the following two inequalities. First,

$$\frac{\partial P_\epsilon}{\partial t} - d_H \Delta P_\epsilon \leq CL_\epsilon, \quad (4.11)$$

where C is a constant depending on choice for $R(H_\epsilon, P_\epsilon)$, and second,

$$\frac{\partial L_\epsilon}{\partial t} - d_L \Delta L_\epsilon \leq \hat{\lambda} P_\epsilon. \quad (4.12)$$

Thus, the condition of partial sums referred to as the intermediate sums conditions of Morgan in [16, 17] are satisfied. One may directly apply global existence and boundedness results contained therein to guarantee a global solution $(H_\epsilon, P_\epsilon, L_\epsilon)$, globally bounded in $L^\infty(Q(0, \infty))$.

Case 2: $\hat{\lambda} > \mu + \alpha$. According to (4.10),

$$\frac{d}{dt} \|P_\epsilon(\cdot, t) + L_\epsilon(\cdot, t)\|_{1, \Omega} \leq (\hat{\lambda} - \mu - \alpha) \|P_\epsilon(\cdot, t) + L_\epsilon(\cdot, t)\|_{1, \Omega}. \quad (4.13)$$

The L^1 norm does not blow up, so there is global existence in $(0, +\infty)$ with $(H_\epsilon, P_\epsilon, L_\epsilon)$ bounded in $L^\infty(Q(0, T))$, for each $T > 0$, by Morgan [16, 17]. So one has shown the existence of a global, unique, classical, nonnegative solution $(H_\epsilon, P_\epsilon, L_\epsilon)$ defined on $Q(0, \infty)$, with $0 < \epsilon \leq 1$, for (4.4)-(4.6), and the theorem is proven. \square

The final step is to take solutions to the approximate problems, let ϵ shrink to 0, and obtain a solution to the desired problem. Before one argues that this is possible, one needs a couple a priori estimates.

Proposition 4.2. *There exists $\alpha_1 > 0$ such that for each initial condition $H_0 \in C^{\alpha_1}(\bar{\Omega})$, and for each $T > 0$, $(H_\epsilon)_{\epsilon \geq 0}$ is bounded in $C^{\alpha_1}(\bar{\Omega} \times [0, T])$ independently of ϵ , for $0 < \epsilon \leq 1$.*

Proof. We have shown that H_ϵ is nonnegative and bounded in $L^\infty(\Omega \times [0, +\infty))$ independently of ϵ . Using the inequality (4.7), we conclude the result thanks to [12, theorem 10.1 chapter III]. \square

Proposition 4.3. *For each initial condition $(P_0, L_0) \in C^{\alpha_1}(\bar{\Omega})^2$, and for each $T > 0$, P_ϵ and L_ϵ are bounded in $C^{\alpha_1}(\bar{\Omega} \times [0, T])^2$ independently of ϵ , for $0 < \epsilon \leq 1$.*

Proof. We will outline the two steps required. First, note that one has coupled equations, thanks to the inequalities (4.11) and (4.12). Then one uses [12, theorem 2.2 chapter VII], to ensure that P_ϵ and L_ϵ are bounded in $L^\infty(\Omega \times [0, T])$ independently of ϵ . Second, one uses [12, theorem 3.1 chapter VII] to conclude that P_ϵ and L_ϵ belong to a bounded set of $C^{\alpha_1}(\bar{\Omega} \times [0, T])^2$. \square

One is now ready to pass to the limit.

Proposition 4.4. *There exists three subsequences $(H_{\epsilon_n})_{n \in \mathbb{N}}$, $(P_{\epsilon_n})_{n \in \mathbb{N}}$, $(L_{\epsilon_n})_{n \in \mathbb{N}}$ which converge strongly to (H, P, L) in $C^0(\bar{\Omega} \times [0, \infty])^3$. In addition, for each (x_0, t_0) such that $H(x_0, t_0) > 0$, there exists a neighborhood $v(x_0, t_0)$ in which (H, P, L) is a solution of the partial differential equations (4.1) in $\mathbb{D}'(v(x_0, t_0))$.*

Proof. One knows the family $(H_\epsilon, P_\epsilon, L_\epsilon)_\epsilon$ is bounded in $C^{\alpha_1}(\bar{\Omega} \times [0, T])^3$, so one can extract three subsequences (H_{ϵ_N}) , (P_{ϵ_N}) , (L_{ϵ_N}) which converge strongly to (H, P, L) in $C^0(\bar{\Omega} \times [0, \infty])^3$. But, because of singularities, one defines the following set

$$\theta = \{(x, t) : H(x, t) > 0\}.$$

If $(x, t) \notin \theta$, then $H(x, t) = 0$. If $(x_0, t_0) \in \theta$, there exists a neighborhood $v(x_0, t_0) \subset \theta$. In $v(x_0, t_0)$, the problem (4.1) has no singularities. So one can pass to the limit in

the sense of distribution to obtain that (H, P, L) is a solution in $\mathbb{D}'(v(x_0, t_0))$. Some questions are not answered here and will be addressed elsewhere. For example, is there uniqueness and can H be null in $\bar{\Omega} \times (0, +\infty)$? One remarks that if one adds a diffusion term to the infinite system, there are no problems with existence, uniqueness and positivity. But that would create a different mathematical model. \square

Proposition 4.5. *The nonnegative steady states are $(H^* \geq 0, 0, 0)$*

Proof. For these models, $M(H, P) = C_1 \frac{P}{H} + C_2 \frac{P^2}{H^2}$, with $C_1 > 0$ and $C_2 \geq 0$ (see Appendix). The equation for H in system (4.1) is

$$\frac{\partial H}{\partial t} - d_H \Delta H = -M(H, P)H, \quad (4.14)$$

and the steady states satisfy

$$\frac{\partial H}{\partial t} = \frac{\partial P}{\partial t} = \frac{\partial L}{\partial t} = 0.$$

So the PDE system associated at equilibrium satisfies

$$-d_H \Delta H^* = -M(H^*, P^*)H^*, \quad (4.15)$$

$$-d_H \Delta P^* = R(H^*, L^*) - P^*[\mu + \alpha + Q(H^*, P^*)], \quad (4.16)$$

$$-d_L \Delta L^* = \hat{\lambda}P^* - R(H^*, L^*)H^* - \nu L^*. \quad (4.17)$$

One multiplies (4.15) by H^* , and one integrates over Ω . One thus obtains

$$d_H \int_{\Omega} |\nabla H^*|^2 dx = -C_1 \int_{\Omega} H^* P^* dx - C_2 \int_{\Omega} P^{*2} dx \leq 0,$$

because H^* and P^* are nonnegative. In order to have the equality instead of less than or equal to, H^* and P^* must satisfy

$$\nabla H^* = 0, \quad H^* P^* = 0, \quad P^{*2} = 0, \quad \text{in } \Omega.$$

So, $H^* = C \geq 0$, a constant, and $P^* = 0$. Then equation (4.17) becomes

$$-d_L \Delta L^* = -R(H^*, L^*)H^* - \nu L^*. \quad (4.18)$$

But R , which is defined by (2.5) or (2.6), can be expressed in the general form

$$R(H^*, L^*) = C_3 L^*.$$

So, (4.18) can be expressed as

$$-d_L \Delta L^* = -C_4 L^*. \quad (4.19)$$

Now multiply (4.19) by L^* , and integrate over Ω , to obtain that $L^* = 0$. Consequently, the nonnegative steady states are $(H^* \geq 0, 0, 0)$. \square

Conclusions. We introduced a continuous spatially structured model for host-macroparasite systems. To obtain a finite system of equations, one assumed that parasites are distributed on the host population according to a Poisson or a negative binomial distribution. The choice of distribution along with the choices one has for the factor reducing the fertility of host due to parasitism and for the mortality rate of parasites, (H10), result in eight different possibilities for right hand sides of generic model (2.12) (see the appendix for the different forms the functions h , M , and Q can take). One then eliminated demography in the host population in order to apply the model to a system where the birth and intrinsic death rates of

the host population were not important. In this situation, with the hypotheses one made, one did not prove that the long term behavior of the solution of the continuous spatially structured model does not depend on the spatial variable. Some analysis of the system showing existence of a solution was performed. Such issues as uniqueness, positivity and the asymptotic behavior of the solution of the partial differential equation system will be discussed elsewhere. Possible continuations of this work would be to apply this model to a host-parasite system where demography in the host population needs to be considered or to a system where birth and death rates may not be spatially homogeneous.

5. APPENDIX

Let

$$h(H, P) = \begin{cases} be^{\frac{P}{H}(\gamma-1)} & \text{for a Poisson distribution} \\ b(\frac{\Psi H}{\Psi H + (1-\gamma)P})^\Psi & \text{for a negative binomial distribution.} \end{cases}$$

Then we have

TABLE 1. Functions M, \tilde{M}, Q and \tilde{Q} for a Poisson distribution

	Model Ia	Model IIa	Model IIIa	Model IVa
$M(H, P)$	$\alpha \frac{P}{H}$	$\alpha \frac{P}{H} (1 + \frac{P}{H})$	$\alpha \frac{P}{H}$	$\alpha \frac{P}{H} (1 + \frac{P}{H})$
$Q(H, P)$	$\alpha \frac{P}{H}$	$\alpha \frac{P}{H} (3 + \frac{P}{H})$	$(\mu + \alpha) \frac{P}{H}$	$\frac{P}{H} (\mu + 3\alpha + \alpha \frac{P}{H})$
$\tilde{M}(z)$	αz	$\alpha z (1 + z)$	αz	$\alpha z (1 + z)$
$\tilde{Q}(z)$	0	$2\alpha z$	μz	$(\mu + 2\alpha)z$

TABLE 2. Functions M, \tilde{M}, Q and \tilde{Q} for a negative binomial distribution

	Model Ib	Model IIb
$M(H, P)$	$\alpha \frac{P}{H}$	$\alpha \frac{P}{H} (1 + (\frac{\Psi+1}{\Psi}) \frac{P}{H})$
$Q(H, P)$	$\alpha (\frac{\Psi+1}{\Psi}) \frac{P}{H}$	$\alpha (\frac{\Psi+1}{\Psi}) \frac{P}{H} [3 + (\frac{\Psi+2}{\Psi}) \frac{P}{H}]$
$\tilde{M}(z)$	αz	$\alpha z (1 + (\frac{\Psi+1}{\Psi}) z)$
$\tilde{Q}(z)$	$\frac{\alpha}{\Psi} z$	$\alpha z [(\frac{2\Psi+3}{\Psi}) + 2(\frac{\Psi+1}{\Psi^2}) z]$
	Model IIIb	Model IVb
$M(H, P)$	$\alpha \frac{P}{H}$	$\alpha \frac{P}{H} [1 + (\frac{\Psi+1}{\Psi}) \frac{P}{H}]$
$Q(H, P)$	$(\mu + \alpha) \frac{P}{H} (\frac{\Psi+1}{\Psi})$	$(\frac{\Psi+1}{\Psi}) \frac{P}{H} [\mu + 3\alpha + \alpha (\frac{\Psi+2}{\Psi}) \frac{P}{H}]$
$\tilde{M}(z)$	αz	$\alpha z [1 + (\frac{\Psi+1}{\Psi}) z]$
$\tilde{Q}(z)$	$z [\frac{\alpha}{\Psi} + (\frac{\Psi+1}{\Psi}) \mu]$	$[\mu (\frac{\Psi+1}{\Psi}) + (\frac{2\Psi+3}{\Psi}) \alpha + 2\alpha (\frac{\Psi+1}{\Psi^2}) z] z$

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