A diffusion model for host–parasite interaction

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Abstract

A variety of host–parasite models are found in the literature. They usually consist of a small number of ordinary differential equations, which describe the dynamics of the total number of hosts and the total number of parasites.

The authors introduced earlier a new approach to such models using a partial differential equation which uses the parasite density as a continuous structure variable. So far the new model contained only convective terms with respect to this variable, and the qualitative properties of solutions were not in agreement with observed parasite distributions.

In the present work, the authors introduce diffusive terms to the previous model. Results of simulations for a specific host–parasite system appearing in fish farms are presented. These show a much better qualitative fit with real data than results from simulations with any other models.

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1. Introduction

A variety of host–parasite models are found in the literature. They usually consist of a small number of ordinary differential equations, which describe the dynamics of the total number of hosts and the total number of parasites [1]. When hosts can have large parasite loads, this approach may give reasonable values for the mean parasite load and its variance but it may not be suitable for understanding the distribution of parasites among the hosts.

In order to model this distribution directly, one has to either consider an infinite countable (or a very large finite) number of ordinary differential equations—one for each allowable number of
parasites, or replace the discrete variable counting the parasite load by a continuous one and replace the ordinary differential equations that describe the host dynamics by one partial differential equation which has this new variable as a structure variable.

In this paper, we derive a continuous mathematical model for host–parasite systems, using the parasite density as a continuous structure variable. This idea has already been used by the authors but it led to models that include only convective terms [4,5]. In the present work we shall also introduce diffusive terms. Only once had the idea been suggested before [9].

The lack of diffusive terms [4,5] results in the undesirable property that after any amount of time (large or small) all hosts are parasitized. That is in visible disagreement with some host–parasite systems in which a few hosts may have several thousand parasites while the vast majority of hosts have none.

We shall first focus our attention on describing the dynamics of a generic host–parasite system. Later, we shall show the results of numerical simulations for a specific host–parasite system drawn from real life, and compare the resulting numerical distribution of parasites with those resulting from other models.

In Section 2, we start by constructing a discrete mathematical model describing the host–parasite dynamics. Then we take a “diffusion limit” along the lines of Aronson [2] to obtain a continuous model of the dynamics. This involves making some assumptions on the behavior of some functions as we let some parameters go to zero. The diffusion term we obtain will not represent spatial diffusion, but rather a redistribution of parasites within a cohort of hosts with a given mean recruitment and mortality of parasites. There are two main goals here. First, we hope that the discrete mathematical model gives a good description of the biological model. Second, we hope that taking the diffusion limit results in a good approximation of the discrete model.

We build the underlying discrete model by considering a one-dimensional random walk—a host with \(i\) parasites can become a host with \(j\) parasites during a time step of length \(\tau\) by gaining or losing \(|i - j|\) parasites, where \(\eta\) is a fixed positive real number and \(i\) and \(j\) are any nonnegative integers. We define transition probabilities to go from one class of hosts to another, and then give the appropriate recurrence relation to give us the discrete model. This recurrence relation resembles the equations for the discrete model for the host–parasite system *Dicentrarchus–Diplectanum* described by Langlais and Silan [3], which was also modeled earlier by the authors [4,5].

In Section 3, we describe the numerical methods and the parameters we use for the numerical simulations. We also present results from simulations using the discrete model and the continuous ones with and without diffusion. The simulations done with our new model show a much better qualitative fit with real-life systems such as the one mentioned earlier. In particular, the new model will lead to parasite distributions which can be heavily concentrated near zero, as actually happens in nature.

### 2. A diffusion model

Some of the earliest diffusion models in population biology are due to Skellam [8]. About a decade later, Aronson described a (spatial) diffusion model for population dynamics where he allows the organism to make a jump of more than one spatial step during a time step [2] in contrast with the “random walk” approach to diffusion of Okubo [7] where only a jump of a single spatial step
is allowed during one time step. Aronson also allows the transition probabilities to depend on the population density but says the same ideas can be applied much more generally. A similar approach is found in the work of Nisbet and Gurney [6] around the same time.

We now derive a diffusion model that uses a structure variable $p$, which represents the parasite density of the hosts, in the spirit of Aronson [2]. We will first describe a discrete process in which hosts gain or lose parasites and then take a “diffusion limit” that we hope gives a good approximation of the discrete process.

For now we ignore host mortality (and as we have all along, we do not allow the hosts to reproduce). A host can have $p$ parasites, $p \geq 0$. Let us discretize this so that hosts must have $i/\tau$ parasites with $i \in \{0, 1, 2, \ldots\}$ and $\eta > 0$. We also discretize time, $t \geq 0$, into time steps of size $\tau$.

Let

$$H_i^n = \text{host population density at } i/\tau \text{ and time } n/\tau.$$ 

So the total host and parasite populations at time $n\tau$ are given by, respectively,

$$\mathcal{H}(n) = \sum_{i=0}^{\infty} H_i^n \quad \text{and} \quad \mathcal{P}(n) = \sum_{i=0}^{\infty} iH_i^n.$$

During a time step a host’s parasite burden can either increase, decrease, or remain the same. We specify transition probabilities for the different cases. As mentioned earlier, Aronson [2] assumed the transition probabilities to depend on the population density. Here we will take them dependent on time, $t = n/\tau$, a host’s current parasite load, $p = i/\eta$, and the total host population at time $n/\tau$, $\mathcal{H}(n)$.

Then, for transition probabilities let

the probability that a host with $i/\eta$ parasites at time $n\tau$ will lose (if $j < 0$) or gain (if $j > 0$) $j/\tau$ parasites during the next time interval of length $\tau$ given that at time $n\tau$ there are $\mathcal{H}(n)$ hosts, $j \in \mathbb{Z}$, $j \geq -i$.

We assume that $k^n_{i,j} = 0$ if $|j|$ is sufficiently large, which is biologically necessary. We also require for all $\mathcal{H}(n) > 0$ and $i, n \in \mathbb{N}_0$, that

$$\sum_{j=-i}^{\infty} k^n_{i,j} = 1,$$

which is just a statement of determinism: if a host having $i$ parasites at a given time does not have $i$ parasites at a later time, then it must have either gained or lost parasites (or both) in the intervening time. Then $H_i^n$ must satisfy the recurrence relation

$$H_i^{n+1} = \sum_{j=-i}^{\infty} H_i^n k^n_{i+j,-j}.$$
for all $i, n \in \mathbb{N}_0$. This equation constitutes the discrete model for our host–parasite system. To make the model complete, we need to indicate what the transition probabilities are. One possible way of choosing them was described by Langlais and Silan [3]. These authors used truncated Poisson distributions with a prescribed mean. That mean is given, in the case $j < 0$, by $m^n_i = (i\eta)\mu$—the expected number of parasites that die in a time interval of length $\tau$ from a group of $i\eta$ parasites [3]. For the case $j > 0$, the mean is given by $m^n_i = f(i\eta, n\tau)L_r(n\tau)$, where $L_r(n\tau)$ is the number of larvae that are recruited at time $n\tau$ (this is an explicit fraction of the total number of larvae available), and $f(p, t)$ is a phenomenologically defined function expressing the proportion of all recruited larvae that are recruited by hosts having already $p$ parasites at time $t$. Then, we define the truncation factor

$$K = \frac{1}{\sum_{j=1}^i (m^n_i)^j/j! + \sum_{j=0}^{p^*} (m^n_i)^j/j!}$$  \hfill (3)

and let, for $-i \leq j < 0$,

$$k^n_{i,j} = K \frac{(m^n_i)^{-j}}{(-j)!},$$  \hfill (4)

while, for $0 < j \leq p^*(n\tau)$,

$$k^n_{i,j} = K \frac{(m^n_i)^j}{j!}.$$  \hfill (5)

Finally, the probability of neither gaining nor loosing any parasites is given by the sum of the corresponding values of (4) and (5) for $j = 0$:

$$k^n_{i,0} = 2K.$$  \hfill (6)

The factor $K$ given by (3) is defined precisely so that the transition probabilities (4)–(6) satisfy (1) exactly. We refer to the work of Langlais and Silan [3] for more details about $f(p, t)$ and $L_r(t)$.

Next, we would like to derive a continuous approximation to model (2). To obtain this, we assume that $H^n_i = H(i\eta, n\tau)$ $\rightarrow H(p, t))$

and

$$k^n_{i,j}(\mathcal{H}(n)) = k(i\eta, j\eta, \mathcal{H}(n\tau), n\tau) \rightarrow k(p, q, x, t))$$

are sufficiently smooth. Then we take Taylor expansions of terms from (2). Finally we will let $\tau, \eta \rightarrow 0$ and $i, n \rightarrow \infty$ in a special way to obtain an equation involving diffusion.
Expanding (2) about \((i\eta, n\tau)\) we get

\[
H(i\eta, n\tau) + \tau \frac{\partial}{\partial t} H(i\eta, n\tau) + O(\tau^2)
\]

\[=
H(i\eta, n\tau) \sum_{j=-i}^{\infty} k(i\eta, -j\eta, \mathcal{H}(n\tau), n\tau) + \eta \sum_{j=-i}^{\infty} j \frac{\partial}{\partial p} \left[ H(i\eta, n\tau)k(i\eta, -j\eta, \mathcal{H}(n\tau), n\tau) \right]
\]

\[+ \frac{\eta^2}{2} \sum_{j=-i}^{\infty} j^2 \frac{\partial^2}{\partial p^2} \left[ H(i\eta, n\tau)k(i\eta, -j\eta, \mathcal{H}(n\tau), n\tau) \right] + O(\eta^2).
\]

Using (1) and performing some algebraic simplifications we obtain

\[
\frac{\partial}{\partial t} H(i\eta, n\tau) = \frac{\eta^2}{\tau} \frac{\partial}{\partial p} \left[ H(i\eta, n\tau) \sum_{j=-i}^{\infty} \frac{j}{\eta} k(i\eta, -j\eta, \mathcal{H}(n\tau), n\tau) \right]
\]

\[+ \frac{\eta^2}{2\tau} \frac{\partial^2}{\partial p^2} \left[ H(i\eta, n\tau) \sum_{j=-i}^{\infty} j^2 k(i\eta, -j\eta, \mathcal{H}(n\tau), n\tau) \right]
\]

\[+ O \left( \frac{\eta^3}{\tau} + \tau \right).
\]

Now we take our “diffusion limit.” We let \(\tau, \eta \to 0\) and \(i, n \to \infty\) so that \(i\eta \to p, n\tau \to t\), and \(\eta^2/(2\tau) \to D_0\). We also make the following assumptions:

\[
\sum_{j=-i}^{\infty} \frac{j}{\eta} k(i\eta, -j\eta, \mathcal{H}(n\tau), n\tau) \to -\psi(p, \mathcal{H}(t), t), \quad (7)
\]

\[
\sum_{j=-i}^{\infty} j^2 k(i\eta, -j\eta, \mathcal{H}(n\tau), n\tau) \to \phi(p, \mathcal{H}(t), t). \quad (8)
\]

This gives us the equation

\[
\frac{\partial}{\partial t} H(p, t) = -2D_0 \frac{\partial}{\partial p} [H(p, t)\psi(p, \mathcal{H}(t), t)]
\]

\[+ D_0 \frac{\partial^2}{\partial p^2} 2[H(p, t)\phi(p, \mathcal{H}(t), t)].
\]

If we define

\[
D(p, \mathcal{H}(t), t) = D_0 \phi(p, \mathcal{H}(t), t)
\]

and

\[
v(p, \mathcal{H}(t), t) = 2D_0 \psi(p, \mathcal{H}(t), t) - D(p, \mathcal{H}(t), t),
\]
we can write this equation in the standard convection–diffusion form

$$\frac{\partial}{\partial t} H(p, t) = -\frac{\partial}{\partial p} [v(p, t) H(p, t)] + \frac{\partial}{\partial p} \left[ D(p, t) \frac{\partial}{\partial p} H(p, t) \right].$$

Finally, if we add a term for host mortality, include a homogeneous Neumann boundary condition at $p=0$ in order to avoid negative parasite loads, and include initial conditions for the host population, we obtain the following new model for the host–parasite dynamics:

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

$$v(0, t) H(0, t) - D(0, t) \frac{\partial}{\partial p} H(0, t) = 0,$$

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

We assumed above that the transition probabilities depend on $t = \lim_{n/FS} t$, $p = \lim_{i/DC1} p$, and $H(n/FS)$. Note that the derivation of our model was not affected by the $H(n/FS)$ dependence. So, if we modified the transition probabilities to depend on other parameters such as $P(n/FS)$, we could follow the same derivation to get a similar continuous model.

Note that for the transition probabilities of Langlais and Silan we can almost identify the resulting diffusion coefficient (up to the constant $D_0$): assume we do not truncate the Poisson distributions for recruitment and mortality; then,

$$m^n_i \rightarrow p \mu(t), \quad \tilde{m}^n_i \rightarrow \phi(p, t) L_r(t), \quad K \rightarrow \frac{1}{e^{p \mu(t)} + e^{f(p, t) L_r(t)}}$$

and the function $\phi$ in (8) is the limit of the following sum:

$$\sum_{j=-\infty}^{\infty} j^2 K(i \eta, -j \eta, H(n \tau), n \tau)$$

$$= \sum_{j=-\infty}^{0} j^2 K \left[ \mu(n \tau)(i \eta) \right]^{-j} (-j)! + \sum_{j=0}^{\infty} j^2 K \left[ f(i \eta, n \tau) L_r(n \tau) \right]^{-j} j!$$

$$= \frac{m^n_i (m^n_i + 1) + \tilde{m}^n_i (\tilde{m}^n_i + 1)}{e^{m^n_i} + e^{\tilde{m}^n_i}}.$$

that is,

$$\phi(p, t) = \frac{p \mu(t) [p \mu(t) + 1] + f(p, t) L_r(t) [f(p, t) L_r(t) + 1]}{e^{p \mu(t)} + e^{f(p, t) L_r(t)}}.$$

The derivation of an explicit formula for the function $\psi$ given by (7) is impossible in this case.
In the next section we offer some choices for what to take for the functions \( v(p,t) \) and \( D(p,t) \) and present some results from simulations. With those numerical simulations, we try to put this continuous model with diffusion into the context of the host–parasite pair *Dicentrarchus–Diplectanum* described by Langlais and Silan [3].

3. Comparison of numerical simulations from several models

In this section, we first present the results from numerical simulations performed using the discrete model of Langlais and Silan [3] for the system *Dicentrarchus–Diplectanum* that appears in some fish farms [3], as well as the continuous one described and analyzed by the authors in earlier work [4,5], and using the model presented in the previous section.

To see the details of the first two models model we refer the reader, respectively, to the papers of Langlais and Silan [3], and by these authors [4,5].

Next we state specific parameter values and describe functions we used for all of the models including the discrete one. As much as possible, these are the ones chosen by Langlais and Silan [3]. We show graphs of \( H(p,t) \) as a function of \( p \) for fixed values of \( t \). We notice that by taking the parameter \( \rho \) small, for all models there is little parasite recruitment, and the total number of hosts remains constant. By taking \( \rho \) a little larger, all models show a great deal of parasite recruitment taking place resulting in the death of many hosts. We also observe that the model with diffusion allows for hosts to have no parasites at all times addressing a complaint we have with the continuous model without diffusion and with the discrete model when there is a great deal of parasite recruitment.

3.1. Numerical approximations of the continuous model without diffusion

The equations describing the host population dynamics are

\[
\frac{\partial H}{\partial t} + \frac{\partial}{\partial p} (vH) = -\mu_H(p)H, \\
H(p,0) = H_0(p), \\
H(0,t) = 0.
\]  

(10)

To perform numerical simulations we discretize time into steps of size \( \Delta t \), and we discretize \( p \) into steps of size \( \Delta p \). We use the following notation with the assumption \( t = n\Delta t \) and \( p = i\Delta p \) where \( n \) and \( i \) are nonnegative integers:

\[
f(p,t) = f^n_i, \\
g(t) = g^n, \\
h(p) = h^*_i.
\]

Let \( i_{\text{max}} = p^*/\Delta p \).
Then the approximation we use for (10) is based on the finite-difference method of characteristics: for $n = 0$,

$$H_0^0 = H_0, \quad i = 0, 1, 2, \ldots, i_{\text{max}}$$

and for $n = 1, 2, 3, \ldots$

$$H_0^n = 0,$$

$$\frac{H_i^n - H_i^{n-1}}{\Delta t} + \frac{v_i^n H_{i+1}^n - v_i^{n-1} H_i^{n-1}}{2 \Delta p} = -\mu_H H_i^n, \quad i = 1, 2, 3, \ldots, i_{\text{max}} - 1,$$

$$H_{i_{\text{max}}}^n = 0.$$ 

Due to the fact that

$$\lim_{p \to p^*} \mu_H(p) = +\infty,$$

we have $H_{i_{\text{max}}}^n = 0$. If at time $n\Delta t$ we know $v_i^n$ for $i = 0, 1, 2, \ldots, i_{\text{max}}$, then to obtain $H_i^n$ we must solve a tridiagonal linear system of equations. But recall that

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

where $\mu(t)$, $H(t)$, and $L(t)$ depend on $H(p, t)$ [5]. To avoid trying to solve a system of nonlinear equations for $H_i^n$ at each time step, we linearly extrapolate any quantities in $v_i^n$ that we have not yet computed. For example, for $\mu^n$ we use $2\mu^n_{n-1} - \mu^n_{n-2}$. So at each time step we only solve a tridiagonal linear system of equations to get $H_i^n$.

Once $H_i^n$, $i = 0, 1, 2, \ldots, i_{\text{max}}$, is computed, we can approximate the total number of hosts and parasites,

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

respectively. First we determine the “support” of $H_i^n$ to some extent. We set

$$i_{\text{low}}^n = \min\{i \in \{0, 1, 2, \ldots, i_{\text{max}}\}: H_i^n > \varepsilon\},$$

and

$$i_{\text{up}}^n = \max\{i \in \{0, 1, 2, \ldots, i_{\text{max}}\}: H_i^n > \varepsilon\},$$

where $\varepsilon$ is some positive lower bound. Then we approximate the two integrals by changing their limits of integration to from $p = i_{\text{low}}^n \Delta p$ to $p = i_{\text{up}}^n \Delta p$ and using Simpson’s rule.

If $n\Delta t > 20$ days, we next need to compute the number of adult parasites, $\mathcal{A}(t)$, present so that we can determine how many eggs will be laid. Recall that the total number of adult parasites is
given by the definite integral

\[ A(t) = e^{-\int_{t-20}^{t} \mu(\sigma) \, d\sigma} \int_{0}^{p^*} G(t-20; p, t) H(p, t) \, dp, \]

where \( p = G(t; t_0, p_0) \) is the solution to the initial value problem

\[
\begin{align*}
\frac{dp}{dt} &= v(p, t), \\
p(t_0) &= p_0.
\end{align*}
\] (11)

So in order to compute \( A^n \), we need to save \( \mu_m \) for \( m = n, n-1, n-2, \ldots, n-20/\Delta t \). We must do this for other terms in \( v(p, t) \) as well.

We use the trapezoidal rule to approximate the integral in

\[ S(t) = e^{-\int_{t-20}^{t} \mu(\sigma) \, d\sigma}. \]

We do not actually compute this integral each time step. Instead we use the fact that

\[ S(t) = e^{\int_{t-20}^{t} \mu(\sigma) \, d\sigma} S(t - \Delta t) e^{-\int_{t-\Delta t}^{t} \mu(\sigma) \, d\sigma}. \]

Before attempting to approximate \( \int_{0}^{p^*} G(t-20; p, t) H(p, t) \, dp \), we need to approximate \( G(t-20; i \Delta p, t) \) for \( i = l_{\text{low}}, l_{\text{low}} + 1, l_{\text{low}} + 2, \ldots, l_{\text{up}} \). This involves approximating the solution to (11) at time \( t - 20 \) days for the initial condition \( p(t) = i \Delta p, i = l_{\text{low}}, l_{\text{low}} + 1, l_{\text{low}} + 2, \ldots, l_{\text{up}} \). We use the fourth-order Runge–Kutta method with a step size of \( k \Delta t \), where \( k \) is a positive integer, to approximate \( G(t-20; i \Delta p, t) \). We choose \( k \Delta t \) instead of \( \Delta t \) because this Runge–Kutta method has more accuracy than we need, so we lengthen the time step to save some computation time.

When running simulations, it sometimes happens that we compute \( G(t-20; i \Delta p, t) \) to be negative. This is saying that some of the parasites on hosts at time \( t \) came from hosts who had a negative number of parasites 20 days ago. Clearly this is absurd. So when this occurs, we set \( G(t-20; i \Delta p, t) = 0 \) and accept the fact that we are most likely underestimating the number of adult parasites at that time step. This error could come from solving (11) too crudely or from not determining \( H^n \) accurately enough so that we end up underestimating \( i_{\text{low}}^{\text{up}} \).

Once \( G(t-20; i \Delta p, t) \) is determined, we approximate

\[
\int_{l_{\text{low}} \Delta p}^{l_{\text{up}} \Delta p} G(t-20; p, t) H(p, t) \, dp
\]

by using Simpson’s rule. Multiplying this result by \( S(t) \) gives us our estimation of \( A(t) \). We can now determine \( \mu(t) \) with

\[
\mu(t) = \frac{\mu_s A(t) + \mu_a A(t)}{A(t)}.
\]

This brings us to the egg and larva dynamics.
Recall [5] that the equations the egg and larva populations satisfy are
\[
\frac{\partial E}{\partial t} + \frac{\partial E}{\partial a} = -\mu_E(a)E + \Lambda(a,t),
\]
\[E(0,t) = \beta \mathcal{A}(t),\]
\[E(a,0) = E_0(a), \quad 0 \leq a \leq 6. \quad (12)\]

We use the following notation with the assumption \( t = n\Delta t \) and \( a = m\Delta t \) where \( n \) and \( m \) are nonnegative integers:

\[f(a,t) = f_{m,n},\]
\[g(t) = g^n,\]
\[h(a) = h_m.\]

Let \( m_{\text{max}} = 6/\Delta t. \)

Then the finite-difference approximation we use for (12) is for \( n = 0 \)

\[E^0_m = E_{0,n}, \quad m = 0, 1, 2, \ldots, m_{\text{max}} \]

and for \( n = 1, 2, 3, \ldots \)

\[\frac{E^n_m - E^{n-1}_{m-1}}{\Delta t} = -\mu_E E_m^n + A_m^n, \quad m = 1, 2, 3, \ldots, m_{\text{max}},\]
\[E^0_m = \beta \mathcal{A}^n.\]

So at each time step, one loop back from \( m = m_{\text{max}} \) down to \( m = 0 \) updates \( E^n_m \) for the current time step.

The total number of larvae at the current time step can now be computed. Recall that

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

To approximate \( L^n \) we use Simpson’s rule.

3.2. Numerical approximations of the continuous model with diffusion

We now describe how we approximate the solution to the model presented in Section 2, where there is a diffusion term in the equation describing the host dynamics. We use the same numerical techniques here as those that we used in the last section.

The addition of the diffusion term takes away our ability to compute the number of adult parasites as we did with the no diffusion model. To circumvent this problem, we make the simplifying assumption that all parasites present act as adult parasites. From a computational point of view, this is a nice simplification. From a modeling point of view, it is not clear how satisfactory or unsatisfactory it is.
We begin again by looking at the host dynamics, given by (9). Using the same notation that we used in the previous section, for our finite-difference approximation we take for $n = 0$

$$H_i^0 = (H_0), \quad i = 0, 1, 2, \ldots, i_{\text{max}}$$

and for $n = 1, 2, 3, \ldots$

$$v_0^n H_0^n - D_0^n H_i^n - D_0^n H_i^{n-1} = 0,$$

$$\frac{H_i^n - H_i^{n-1}}{\Delta t} + \frac{v_{i+1}^n H_{i+1}^n - v_{i-1}^n H_{i-1}^n}{2\Delta p} - \frac{D_{i+1/2}^n(H_{i+1}^n - H_i^n) - D_{i-1/2}^n(H_i^n - H_{i-1}^n)}{(\Delta p)^2} = - \mu H_i^n, \quad i = 1, 2, 3, \ldots, i_{\text{max}} - 1,$$

$$H_{i_{\text{max}}}^n = 0.$$  

Again, since

$$\lim_{p \to p^*} - \mu_H(p) = +\infty,$$

we have $H_{i_{\text{max}}}^n = 0$. So to solve for $H_i^n$ at $n = 1, 2, 3, \ldots$, we use linear extrapolation to make $v_i^n$ and $D_i^n$ known (if necessary) and then solve a tridiagonal linear system of equations.

Once we compute $H_i^n$, we proceed just as we did for the model without diffusion with the following exceptions. We do not compute $H_i^n$. We do not need to compute $\mu_H$. Here for all $t$, $\mu_H = \mu_g$.

Moreover, the boundary condition, $E(0, t) = \beta \mathcal{A}(t)$, in system (12) describing egg and larva dynamics is changed to $E(0, t) = \beta \mathcal{A}(t)$.  

3.3. Parameter values and prescribed functions

The following is a list of parameter values used. Unless otherwise indicated, the value listed is used for all models that use that particular parameter.

Death rates are

$$\mu_e = 1/10,$$

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

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

$$\mu_a = 1/70.$$  

Egg laying rate is

$$\beta = 7.$$  

Special $p$ values used are

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

$$p_{\text{crit}} = 300.$$
Parameters affecting larvae recruitment include

\[ \rho \in [0, 1] \] (various values used),
\[ C = 1000. \]

Next we prescribe some functions that we used when performing the numerical simulations whose results we present in the next section. We begin with the exterior supply of eggs and larvae. For the continuous models we use

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

The reasoning behind this choice is as follows. During the warmer months of the year, it is more likely that water being piped into the fish farm basins from the sea to refresh the basin water will contain eggs and larvae. This is because during the warmer months, sea bass in the wild are more likely to be closer to the coast (where the particular fish farm is) than they are during the colder months of the year. It is from the wild fish where the exterior supply of eggs and larvae ultimately comes. We are starting our simulations at the beginning of the warm month period and taking the length of a year to be 360 days. For the discrete model we use

\[ A_e^m(t) = 0, \quad m = 1, 2, \]
\[ A_l(t) = \begin{cases} 50 & \text{if } 0 \leq \text{mod}(t, 360) \leq 180, \\ 0 & \text{otherwise}. \end{cases} \]

For the functions \( f(p, t) \) (continuous no diffusion model) [5] and \( f(i, t) \) (discrete model) [3], 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 [3]. The goal is to model the fact that hosts with less than \( p_{\text{thresh}} \) parasites act the same as far as recruiting new parasites goes, but for hosts with more parasites, parasite recruitment increases.

We describe how one determines \( f_0(t) \) and \( \lambda(t) \) for the continuous model. With the discrete model, they are determined in the same manner except integrations are replaced by sums.
As mentioned earlier, one condition $f$ must satisfy is
\[ \int_0^{p^*} f(p,t)H(p,t)\,dp = 1. \] (13)

To determine $f_0(t)$ and $\dot{\lambda}(t)$ we need a second condition. The second equation comes from field observations, giving the proportion of larvae that attach to highly parasitized hosts as a function $F$ of the proportion of the highly parasitized hosts among all hosts:
\[ \int_0^{p_{\text{thresh}}} f(p,t)H(p,t)\,dp = F\left( \frac{\int_0^{p_{\text{thresh}}} H(p,t)\,dp}{\mathcal{H}(t)} \right). \] (14)

We want $F(x) \geq x$, $F(0) = 0$, and $F(1) = 1$. For the simulations we took
\[ F(x) = \begin{cases} e^{3.5x} - 1 & \text{if } x \leq 0.15, \\ 0.69 + 0.07285 \ln(81.215x - 11.182) & \text{if } x > 0.15. \end{cases} \]

Substituting $f(p,t) = f_0(t) + \dot{\lambda}(t)[(p - p_{\text{thresh}})^+]^2$ into (13) and (14) and performing some algebra, we obtain for $f_0(t)$
\[ f_0(t) = \frac{1 - F(\int_0^{p_{\text{thresh}}} H(p,t)\,dp/\mathcal{H}(t))}{\int_0^{p_{\text{thresh}}} H(p,t)\,dp} \] (15)

if $\int_0^{p_{\text{thresh}}} H(p,t)\,dp \neq 0$. If this condition is not satisfied, then (13) and (14) reduce to the same equation. So to determine $f_0(t)$ in this situation, we take the limit of (15) as $\int_0^{p_{\text{thresh}}} H(p,t)\,dp$ goes to zero. This gives us
\[ f_0(t) = \frac{F'(1)}{\mathcal{H}(t)}. \]

Then for $\dot{\lambda}(t)$ we have
\[ \dot{\lambda}(t) = \begin{cases} \frac{1 - f_0(t)\mathcal{H}(t)}{\int_0^{p_{\text{thresh}}} (p - p_{\text{thresh}})^2 H(p,t)\,dp} & \text{if } \int_0^{p_{\text{thresh}}} (p - p_{\text{thresh}})^2 H(p,t)\,dp \neq 0, \\ 0 & \text{otherwise}. \end{cases} \]

It is not clear how good of a choice this $f$ is for any of the models. There is the problem that $\dot{\lambda}(t)$ may not remain bounded at all times. For the existence proof [5] it was required that it remained bounded. It is also unclear that this function does a good job of modeling parasite recruitment. We used this $f$ with the continuous model without diffusion. As long as $i_{\text{up}}^a \Delta p$ remained less than $p_{\text{thresh}}$, there were no problems as is to be expected. But if $i_{\text{up}}^a \Delta p$ crept above $p_{\text{thresh}}$, it would not take long before $i_{\text{up}}^a$ would shoot up to $i_{\text{max}}$ (a couple days of simulated time while it might take over 100 days for $i_{\text{up}}^a \Delta p$ to reach $p_{\text{thresh}}$). When one looks at graphs of $H(p,t)$ versus $p$ for fixed values of $t$ after $i_{\text{up}}^a \Delta p$ passes $p_{\text{thresh}}$, one notices oscillations appearing. At first they are just at the edges of the support of $H$, but eventually they completely take over. Below we suggest a reason why the oscillations may be appearing and suggest a way to eliminate them while still using this form of $f$. 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 $f(p,t) = m(t)p$. Putting this in (13), we see that $m(t) = 1/\mathcal{P}(t)$. 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.
Fig. 3. Snapshots of $N(i,t)$ for $140 \leq t \leq 200$ using the $f$ of Langlais and Silan; $\rho = 0.6$.

Fig. 4. Snapshots of $N(i,t)$ for $320 \leq t \leq 370$ using the $f$ of Langlais and Silan; $\rho = 0.6$.

The mortality rate of hosts, $\mu_H(i)$, is defined as follows: we choose a survival curve of standard shape based on a Gompertz function,

$$S(p) = 1.0001 - 10^{-4e^{-\lambda(p-p_{\text{min}})}}$$
Fig. 5. Snapshots of $H(p,t)$ for $0 \leq t \leq 240$ using the $f$; $\rho = 0.005$; $\mu_H$ with $n = 1$.

Fig. 6. Snapshots of $H(p,t)$ for $270 \leq t \leq 480$ using the linear $f$; $\rho = 0.005$; $\mu_H$ with $n = 1$.

with $a$ chosen so that $S(p_{\text{leth}}) = 0.02$. Finally, to take care of values of $i$ between $p_{\text{leth}}$ and $p^*$, we consider the associated mortality function $\mu_H(p) = -S'(p)/S(p)$. We want $\mu_H(p)$ to be such that it is increasing and that

$$S(p^*) = e^{-\int_{p_{\text{leth}}}^{p^*} \mu_H(s)ds} = 0.$$
To accomplish this, we choose for $p_{\text{leth}} < p < p^*$

$$\mu_H(p) = -\frac{S'(p_{\text{leth}})}{S(p_{\text{leth}})} + C \frac{(p - p_{\text{leth}})^2}{p^* - p},$$
where $C$ is some positive constant. There is one situation where we modify $\mu_H(p)$ slightly; this is when there is heavy parasite recruitment. That is, when $\rho$ is larger. In an attempt to eliminate the oscillations that appear in our graphs of $H(p,t)$, for the continuous model without diffusion but with heavy parasite recruitment, we tried modifying $\mu_H(p)$ for values of $p$ in the interval ($p_{\text{left}}, p^*$).
Fig. 11. Snapshots of $H(p,t)$ for $0 \leq t \leq 180$ using the linear $f$; $\rho = 0.5$; $\mu_H$ with $n = 1$.

Fig. 12. Snapshots of $H(p,t)$ for $210 \leq t \leq 390$ using the linear $f$; $\rho = 0.5$; $\mu_H$ with $n = 1$.

We took for these values of $p$

$$
\mu_H(p) = -\frac{S'(p_{\text{leth}})}{S(p_{\text{leth}})} + C \frac{(p - p_{\text{leth}})^2}{(p^* - p)^n},
$$
where $n \geq 1$. From a modeling viewpoint, we are not sure if $n = 1$ or 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 $f(p,t) \approx C p^2$, where $C$ depends on the parasite recruitment, the off-diagonal terms in the tridiagonal system we must solve to find $H_n$ 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
Fig. 15. Snapshots of $H(p,t)$ for $210 \leq t \leq 390$ using the $f$ of Langlais and Silan; $\rho = 0.5$; $\mu_H$ with $n = 1$.

Fig. 16. Snapshots of $H(p,t)$ for $420 \leq t \leq 600$ using the $f$ of Langlais and Silan; $\rho = 0.5$; $\mu_H$ with $n = 1$.

the linear system easier to solve. Numerical simulations indicate that this choice of $\mu_H(p)$ indeed helped.

Finally, we must say what we prescribed for $v(p,t)$ and $D(p,t)$ for the continuous model with diffusion. For $v(p,t)$ we used the homonymous function from the continuous model without diffusion, where for $f$ we took the linear $f$. For $D(p,t)$ we tried two choices: one an increasing function of
Fig. 17. Snapshots of $H(p,t)$ for $0 \leq t \leq 240$ using the $f$ of Langlais and Silan; $\rho = 0.5$; $\mu_H$ with $n = 4$.

Fig. 18. Snapshots of $H(p,t)$ for $270 \leq t \leq 420$ using the $f$ of Langlais and Silan; $\rho = 0.5$; $\mu_H$ with $n = 4$.

$p$ and the other a decreasing function of $p$. For the increasing function we took

$$D(p,t) = \mu_a p + \frac{1}{2} \rho \frac{H(t)}{H(t) + C} \frac{L(t)}{P(t)} \sigma$$
Fig. 19. Snapshots of $H(p,t)$ for $450 \leq t \leq 690$ using the $f$ of Langlais and Silan; $\rho = 0.5$; $\mu_H$ with $n = 4$.

Fig. 20. Snapshots of $H(p,t)$ for $0 \leq t \leq 240$ using decreasing $D$; $\rho = 0.005$.

and for the decreasing function we took

$$D(p,t) = \frac{1}{2} e^{-\left(\frac{1}{1000}\right)p}.$$
3.4. Numerical results and conclusions

We now present graphs of $H(p,t)$ as a function of $p$ for fixed values of $t$. Figs. 1–4 are graphs generated from the discrete model [3]; Figs. 5–19 are graphs generated from the continuous model.
without diffusion [5]; Figs. 20–31 are graphs generated from the continuous model with diffusion presented in this paper.

For the discrete model we have simulations of 600 days with $\rho = 0.36$—representing low larva recruitment (Fig. 1), and of 370 days of the model with $\rho = 0.6$—representing high larva recruitment (Figs. 2–4). All runs are with $n = 1$ in $\mu_L(p)$ and use the $f$ of Langlais and Silan. With the smaller
value of $\rho$, almost no recruitment of new larvae takes place, as is to be expected. With the larger value of $\rho$, a good deal of larva recruitment takes place. Soon after 200 days, there are no hosts that are free of parasites. Biologically, this does not seem reasonable, and it contradicts field observations.

For the continuous model without diffusion we have simulations of 720 days of the model with the linear $f$ and $\rho = 0.005$ (Figs. 5–7), with the $f$ of Langlais and Silan and $\rho = 0.005$ (Figs. 8–10),
Fig. 27. Snapshots of $H(p,t)$ for $120 \leq t \leq 270$ using increasing $D_1 \mu_H(p)$:

Fig. 28. Snapshots of $H(p,t)$ for $300 \leq t \leq 510$ using decreasing $D_1 \mu_H(p)$:

with the linear $f$ and $\rho = 0.5$ (Figs. 11–13), with the $f$ of Langlais and Silan and $\rho = 0.5$ (Figs. 14–16), and with the $f$ of Langlais and Silan, $n = 4$ in $\mu_H(p)$, and $\rho = 0.5$ (Figs. 17–19). Except for Figs. 17–19, we had $n = 1$ in $\mu_H(p)$. For the smaller value of $\rho$ we see again that little recruitment takes place. For the larger value of $\rho$, we see that much parasite recruitment takes place and that the host population dies out as a consequence. For the run with the $f$ of Langlais and Silan and $\rho = 0.5$
(Figs. 15 and 16), we notice the oscillations in the graphs when $i_{\text{max}} \Delta p > 30 = p_{\text{leth}}$. Negative values of $H$ even appear, which is definitely undesirable. But when we increase $n$ to 4 (Figs. 18 and 19), those problems disappear. 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 have used so far force that to be the case.

Fig. 29. Snapshots of $H(p,t)$ for $0 \leq t \leq 90$ using increasing $D; \rho = 0.5$.

Fig. 30. Snapshots of $H(p,t)$ for $120 \leq t \leq 270$ using increasing $D; \rho = 0.5$. 
For the continuous model with diffusion we have runs of 720 days for the model with $D$ decreasing and $\rho = 0.005$ (Figs. 20–22), with $D$ increasing and $\rho = 0.005$ (Figs. 23–25), with $D$ decreasing and $\rho = 0.5$ (Figs. 26–28), and with $D$ increasing and $\rho = 0.5$ (Figs. 29–31). For the smaller value of $\rho$ we see once more that little recruitment takes place, as is to be expected. For the larger value of $\rho$, we see that much parasite recruitment takes place and that the host population dies out as a result. However, we notice that with this new model with diffusion, we can have many hosts free of parasites, a situation which is well matched with the observed prevalence of parasites, and qualitatively new by comparison with all previous models.

The discrete model is computationally much more complex and expensive. It shows, together with the continuous model without diffusion, at least one major qualitative flaw in that all hosts become parasitized after a few months, which contradicts the field observations of parasite distributions. For the discrete model, this seems to be a consequence of the recruitment function chosen, $f$, which in fact forces all hosts to recruit parasites because it is positive and bounded away from zero.

The continuous model without diffusion is much simpler and faster to run, and it produces qualitatively and quantitatively similar results to those of the discrete model. However, it includes several simplifications that cannot be avoided, due to the lack of an age-structure for the parasite population. Another major flaw in it is the fact that it does not mix cohorts: if, for example, at some time there is a cohort of 200 fish having seven parasites each and at a later time one of those fish has nine parasites, then ALL the remaining ones necessarily have nine parasites each. This is a direct consequence of the convection term in the model, which transports cohorts along the parasite-time characteristic without redistributing parasites.

The continuous model with diffusion fixes this major flaw from the one without diffusion. Moreover, this redistribution of parasites (or mixing of cohorts) allows now for many hosts to remain free of parasites, matching observed field data.

Fig. 31. Snapshots of $H(\rho, t)$ for $300 \leq t \leq 510$ using increasing $D$; $\rho = 0.5$. 
References


