

**A STRUCTURED MODEL FOR THE SPREAD OF  
*MYCOBACTERIUM MARINUM*: FOUNDATIONS FOR A  
NUMERICAL APPROXIMATION SCHEME**

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**ABSTRACT.** We develop a finite difference scheme to approximate the solution of a novel size-structured mathematical model of the transmission dynamics of *Mycobacterium marinum* (Mm) in an aquatic environment. The model consists of a system of nonlinear hyperbolic partial differential equations coupled with three nonlinear ordinary differential equations. Existence and uniqueness results are established and convergence of the finite difference approximation to the unique bounded variation weak solution of the model is obtained. Numerical simulations demonstrating the accuracy of the method are presented. We also conducted preliminary studies on the key features of this model, such as various forms of growth rates (indicative of possible theories of development), and conditions for competitive exclusion or coexistence as determined by reproductive fitness and genetic spread in the population.

**1. Introduction.** Despite extensive public health efforts, *Mycobacterium tuberculosis* (Mtb), the etiological agent of tuberculosis (TB) in humans, continues to pose a major global public health problem, afflicting more than two billion people, or about one-third of humanity [37]. Activation of TB occurs relatively infrequently ( $\sim 0.1\%$ ), and yet, because of the large size of the TB-infected population, acute TB remains the leading cause of mortality by a single infectious agent, killing approximately 2 million annually [16, 19, 37]. A fish pathogen, *Mycobacterium marinum* (Mm), is one of the most closely related species to the Mtb complex, sharing many of the same bacterial virulence genes required by Mtb to infect, grow, spread and cause disease in humans [17, 30, 41, 44].

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The impact of *Mm* infections provides substantial motivation for their study independent of the additional benefit of providing insight into the persistence of an important human pathogen. *Mm* is known to infect at least 200 fish species in marine and fresh water environments [17, 19, 28]. Annually, fish mycobacteriosis costs billions of dollars in combined losses to wild-caught fisheries, to aquaculture-raised fish, to the aquarium trade and to research colonies [22, 24, 28]. The study of these pathogens in animal models provides an attractive alternative to working with TB directly. Since *Mm* grows much faster than *Mtb*, represents less risk to researchers, and similarly infects host macrophages (both human and fish), *Mm* has recently become a tractable surrogate pathogen to study TB-like infections [17, 18, 30, 36, 42, 44]. Transmission studies have indicated that *Mm* retrieved from infected tissues is considerably more infectious, likely because these bacteria reside in host macrophages of the target organs [17, 20, 21, 31, 36], and are in an ‘activated’ state. The work of [17, 18, 33] has made significant progress toward establishing a model of *Mm* infections in medaka, a Japanese ricefish, which have been shown to be efficiently infected from ingestion of mosquito larvae carrying a number of *Mm*. This mechanism is thought to be relevant to a natural situation. Mosquito larvae, which are plentiful in aquatic environments, feed readily on *Mm* in the laboratory setting. Further, it is commonly known that mosquito larvae are a food source for ricefish and other small fish. Therefore, the spread of these infections within a food network must be considered for this pathogen. Since this inherently involves nonlinear processes between dynamically changing quantities, a mathematical model has been developed in [9] as a tool to understand and make use of this biological model.

The structure of the model developed in [9] to address *Mm* transmission dynamics in aquatic animals, necessitated the development of a novel scheme with which to compute its solutions, similar to the one we discuss in this paper. Key to the model’s structure is a food network, since many modes by which *Mm* is transmitted are a result of the consumption of infected tissues. Therefore, the metabolic activity of the fish is important, and so is any process that may accelerate or hinder that activity. To account for commonly observed variability in feeding behavior (even within genetically inbred fish stocks) as well as variability in other processes represented in the model (susceptibility, growth, death, etc.), the authors considered  $m$  ‘physiological groups’. Within these, all individuals were characterized as equivalent and the processes therefore occurred at the same rates. These rates depend on the size of the fish or possibly also the severity of its infection. A model structured by size allows for the study of various metabolic effects on transmission dynamics through the network, whereas a bacterial load-structured model allows one to consider the effect of differences in infection severity; namely, the effect of progressing from a chronic to an acute state. A general model would include the dependence on both fish size and intra-animal bacterial load. However, for tractability, a model structured by bacterial load only is presented in [9], and here, we consider a size-structured version. In [9], theoretical foundations for the numerical scheme were not developed; the aim of the paper was mainly on the development and preliminary studies of the model. However, since the differences between the model we present here and that in [9] are not major from a mathematical point of view (they are from the biology point of view as each model is well suited to answer different biological questions), the theoretical results we establish here - existence and uniqueness of solutions and convergence for the computational scheme - apply to the model [9].

Structured models have been studied numerically using various approaches including finite element methods [13, 14, 32], monotone approximations [5], finite difference schemes [4, 6, 7, 38, 43], integration along characteristics [1, 3, 11, 12, 25, 26, 29, 35], and ideas from semigroup theory [15]. Several different methods for numerically solving structured population models are reviewed and compared in [2]. Here, we develop an implicit first order finite difference method for solving a novel structured model and establish the convergence of this method to a bounded variation weak solution of the model using an approach in the spirit of those used in [4, 6, 7, 8, 10, 43]. As will be clear in the next section, the model we develop here is complex and consists of a large system of partial differential equations coupled to a system of ordinary differential equations. Thus, we choose a finite difference approach due to its simplicity of implementation even when the vital rates are nonlinear and time dependent (see [2]). Other popular approaches like integration along characteristics require solving two coupled problems simultaneously: 1) the characteristic curves have to be numerically solved to obtain the grid points and 2) the PDEs have to be numerically solved along characteristics [2]. Often in these methods the number of grid points increase in every time step and hence a grid selection method has to be used to control the grid size [2, 12].

In addition to the fact that the model we present here is new, there are mathematical differences in the structure of this model and those studied in [4, 6, 7, 8, 10, 43]. One key difference is that here, as mentioned above, we explicitly model genetic or phenotypic heterogeneity between individuals in a size-structured framework for susceptible and infected fish. This results in  $2m$  partial differential equations coupled to three ordinary differential equations with quadratic nonlinearities to model the transmission of the disease. These nonlinearities, in turn, require a clever choice of mixed explicit and implicit approximations to preserve positivity, which is important for the biological integrity of model solutions. Also, our choice of mixed explicit and implicit approximations resulted in stability of the method without the need of a CFL condition. Thus, to obtain a priori estimates needed for proving convergence, substantial modifications of existing techniques are necessary to adapt them to the new model.

We succinctly present the size-structured model of Mm transmission dynamics between aquatic animals in Section 2, highlighting the key differences between this and the model structured by bacterial load in [9]. The weak solution for the model is given in Section 3. The finite difference approximation is given in 4, and its convergence is established in Section 5. We then numerically demonstrate the convergence as the time and mesh sizes decrease, as well as examples of the model's behavior under investigations of differences in growth functions, and long-term effects of different reproductive patterns on the genetic heterogeneity of the population in Section 6.

**2. Mathematical model structured by fish size.** We present here a model of Mm transmission dynamics in an aquatic environment, in which the fish dynamics are structured by size. This is complementary to the model developed recently in [9], where each mechanism was derived carefully, citing either biological evidence or rationale for each assumption. These models have several similarities and a few key differences. Those differences will be highlighted here. For further explanation on mechanisms that appear in both models, we point the interested reader to the more detailed derivation in [9]. This model is well suited to explore questions of

metabolic effects and reproductive fitness on the overall infection dynamics, which is particularly relevant to study the establishment and maintenance of a chronically infected population. The large chronically infected population is likely a key aspect of the persistence of this pathogen, and therefore, of great interest.

We consider  $m$  distinct physiological groups of fish with identical characteristics amongst fish of the same group. The density (per size) of susceptible and infected fish is represented by  $S^i(t, x)$  and  $I^i(t, x)$ , respectively, of physiological group  $i$  for  $i = 1, \dots, m$ . Other model variables are the number of carrier mosquito larvae  $M(t)$ , activated bacteria  $B_a(t)$ , and unactivated bacteria  $B_u(t)$ . To account for the effect of fish size on model processes (growth, death, susceptibility, etc.), we model the dynamics of these fish populations as they change in time  $t$  using the following system of partial differential equations:

$$\begin{aligned} \frac{\partial S^i}{\partial t} + \frac{\partial(g^i S^i)}{\partial x} + \mu^i S^i + (\nu_1 \delta_1 B_u + \nu_2 \delta_2 B_a + \nu_3 \zeta c_2^i M + \nu_4 c_1^i B_u) S^i &= 0, \\ \frac{\partial I^i}{\partial t} + \frac{\partial(\tilde{g}^i I^i)}{\partial x} + \tilde{\mu}^i I^i - (\nu_1 \delta_1 B_u + \nu_2 \delta_2 B_a + \nu_3 \zeta c_2^i M + \nu_4 c_1^i B_u) S^i &= 0, \end{aligned}$$

with initial conditions

$$S^i(0, x) = S^{i,0}(x), \quad I^i(0, x) = I^{i,0}(x),$$

for  $0 \leq t \leq T$ ,  $x \in [x_{\min}, x_{\max}]$ , and  $i = 1, \dots, m$ . Here  $x_{\min}$  is the assumed smallest fish size (the average birth size of the fish population considered),  $x_{\max}$  is the assumed largest fish size, and  $T$  is some arbitrary finite time.

Susceptible and infected fish of type  $i$  grow at rates  $g^i(P, x)$  and  $\tilde{g}^i(P, x)$ , and die at rates  $\mu^i(P, x)$  and  $\tilde{\mu}^i(P, x)$  respectively. Both the growth and death rates are dependent on the total size of the population  $P(t)$  of susceptible fish and infected fish at the current time  $t$  and the size  $x$  of the fish. The dependency on population size, given by  $P(t) = \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} (S^i(t, x) + I^i(t, x)) dx$ , allows for the possibility of reduced growth and increased death at high population levels, and the dependence on the size of the fish allows for varying growth rates depending on the individual's current stage of development. For instance, it may be reasonable to consider much faster growth rates for smaller (juvenile) fish than larger (adult) fish. We also note that  $g^i(P, x_{\max}) = \tilde{g}^i(P, x_{\max}) = 0$  to implement the assumption that growth will stop when a fish reaches its maximum size.

The remaining terms are new infection rates by distinct transmission modes, and therefore are loss rates from the susceptible population and corresponding gains in the infected population. Fish can be infected (per capita) through consumption of various contaminated food sources (feces of other fish, etc.) containing planktonic inactivated ( $\nu_1 \delta_1 B_u$ ) or activated ( $\nu_2 \delta_2 B_a$ ) bacteria. They can also become infected by consuming mosquito larvae that are carrying an effective load of bacteria ( $\nu_3 \zeta c_2^i M$ ), and by consuming biofilms, which potentially contain Mm ( $\nu_4 c_1^i B_u$ ). It is a reasonable assumption that these Mm are not activated, but this assumption will be explored in the future, and the model can easily be modified. The rates  $\nu_1, \nu_2, \nu_3, \nu_4$  are effective transmission rates and  $c_1^i(x), c_2^i(x)$  are fish consumption rates that may depend on the size of the animal.

The boundary condition for the susceptible fish of type  $i$  is given by

$$g^i(P, x_{\min}) S^i(t, x_{\min}) = \sum_{\ell=1}^m p^{i\ell} \int_{x_{\min}}^{x_{\max}} \left[ \beta^\ell(P, x) S^\ell(t, x) + \tilde{\beta}^\ell(P, x) I^\ell(t, x) \right] dx,$$

and for the infected fish is given by

$$I^i(t, x_{\min}) = 0.$$

The conditions reflect the assumption that all individuals are born susceptible, as this disease is not transmitted vertically [17, 18]. Here,  $p^{i\ell}$  is the probability of the progeny of fish of type  $\ell$  being of type  $i$ , and is the  $(i, \ell)$ -th entry of the selection-mutation matrix  $p$ . The construction of this matrix is such that the entries are ordered according to similarity. We observe that  $\sum_{i=1}^m p^{i\ell} = 1$  since the fractions of all type- $i$  hatchlings from an individual of type  $\ell$  must add up to one. The fecundity kernel of a fish of type  $\ell$  is dependent on  $P(t)$  to account for the possible impact of crowding on the ability of a fish of type  $\ell$  to reproduce where this factor decreases at high population levels. In the special case of progeny being genetically identical to their parents (where individuals of type  $i$  produce individuals of type  $i$  only), the only nonzero entries are  $p^{ii} = 1$  for  $i = 1, \dots, m$ . To mathematically represent the case in which fish beget fish of similar genetic make-up in addition to identical types, there are other nonzero entries, for example,  $p^{i\ell}$  where  $\ell = \{i - 1, i, i + 1\}$ . The extent of genetic spread (mutation) can be represented by choosing different probabilities in this manner.

The dynamics of the unactivated bacteria  $B_u(t)$  (which may be planktonic or residing in biofilms) and planktonic activated bacteria  $B_a(t)$  in the environment are given by

$$\begin{aligned} \frac{dB_u}{dt} &= H + \lambda B_a - c_M M^* B_u - \delta_1 B_u P - \mathcal{S}(t; c_1) B_u - \mathcal{I}(t; \tilde{c}_1) B_u, \\ \frac{dB_a}{dt} &= \mathcal{I}(t; \rho) - \delta_2 B_a P - \lambda B_a, \end{aligned}$$

where we have used the notation

$$\begin{aligned} \mathcal{S}(t; c_1) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} c_1^i(x) S^i(t, x) dx, \\ \mathcal{I}(t; \tilde{c}_1) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} \tilde{c}_1^i(x) I^i(t, x) dx, \\ \mathcal{I}(t; \rho) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} \rho^i(x) I^i(t, x) dx, \text{ where } \rho^i(x) = \bar{\rho}^i \frac{x - x_{\min}}{x_{\max} - x_{\min}}. \end{aligned}$$

The (indirect) actions of humans  $H(t)$  (for example, agricultural run-off, industrial waste, etc.) can provide a source of unactivated mycobacterial populations. Unactivated bacteria in biofilms are lost through consumption by susceptible and infected fish at rates  $\mathcal{S}(t; c_1)$  and  $\mathcal{I}(t; \tilde{c}_1)$ , respectively. All unactivated bacteria may be consumed by mosquito larvae at rate  $c_M M^* B_u$ , where  $c_M$  is the consumption rate of bacteria per capita mosquito larva and  $M^*$  denotes the (constant by assumption) total larval population. Planktonic unactivated and activated bacteria are taken up by fish along with other planktonic sources of nutrients, which are contaminated by these bacterial populations. The planktonic unactivated and activated bacteria are taken up at rates  $\delta_1 B_u P$  and  $\delta_2 B_a P$ , respectively. Activated bacteria are released into the environment primarily through shedding by infected fish at rate  $\mathcal{I}(t; \rho)$  (where  $\rho^i(x)$  is the per capita shedding rate of fish of type  $i$  and size  $x$ ), and go into an unactivated state if they remain planktonic for a period of time  $1/\lambda$ .

TABLE 1. Description of Model Parameters

|                                      |   |
|--------------------------------------|---|
| $\nu_1$                              | effective number of planktonic unactivated bacteria required to result in infection   |
| $\nu_2$                              | effective number of planktonic activated bacteria required to result in infection   |
| $\nu_3$                              | effective number of ingested carrier mosquito larvae required to result in infection  |
| $\nu_4$                              | effective number of unactivated bacteria found in biofilms required to result in infection  |
| $c_1^i(x), \tilde{c}^i(x)$           | consumption rate of unactivated bacteria in biofilms by susceptible and infected fish, respectively, of size $x$ in physiological class $i$ |
| $\tilde{c}_2^i(x), \tilde{c}_2^i(x)$ | consumption rate of mosquito larvae by susceptible and infected fish, respectively, of size $x$ in physiological class $i$                  |
| $\zeta$                              | bacterial dose within a “typical” mosquito larvae   |
| $\delta_1$                           | encounter rate of planktonic unactivated bacteria with fish per unit of time  |
| $\delta_2$                           | encounter rate of planktonic activated bacteria with fish per unit of time  |
| $p^{i\ell}$                          | $(i, \ell)$ -th entry of the selection mutation matrix: probability of the progeny of fish of type $\ell$ being of type $i$                 |
| $\lambda$                            | inactivation rate of activated bacteria   |
| $c_M$                                | mosquito larvae consumption rate of bacteria  |
| $\epsilon$                           | effective number of bacteria necessary to consider a mosquito larvae a carrier of Mm  |
| $\rho^i(x)$                          | per capita shedding rate of fish of type $i$ and size $x$   |
| $\mu_M$                              | mortality rate of carrier mosquito larvae   |
| $M^*$                                | total mosquito larvae population  |
| $H(t)$                               | number of unactivated bacteria in the environment due to human action   |

The dynamics governing the size of the mosquito larvae population carrying Mm are given by

$$\frac{dM}{dt} = \epsilon c_M (M^* - M) B_u - \mu_M M - \mathcal{S}(t; c_2) M - \mathcal{I}(t; \tilde{c}_2) M,$$

and we note that it is not necessary to explicitly consider the non-carrier larvae since we have assumed the total larvae population is always in excess, and therefore, constant. Mosquito larvae become carriers upon consuming an *effective* number of unactivated bacteria at rate  $\epsilon c_M (M^* - M) B_u$ . That is, the larvae feed on bacteria (presumably unactivated Mm aggregated in biofilms) at rate  $c_M$ , the factor  $\epsilon$  scales for the effective number of bacteria necessary to consider a mosquito larvae a carrier of Mm, and  $M^* - M$  are larvae that are not carriers. These carrier larvae are lost through consumption by the susceptible and infected fish at (per capita fish) rates  $\tilde{c}_2^i(x)$  and  $\tilde{c}_2^i(x)$ , respectively, and are the feeding rates of susceptible and infected fish of type  $i$  on mosquito larvae. The terms  $\mathcal{S}(t; c_2) M$  and  $\mathcal{I}(t; \tilde{c}_2) M$  are analogous to the consumption rate of unactivated bacteria by fish, as specified above.

The model, in summary, is then

$$\begin{aligned} \frac{\partial S^i}{\partial t} + \frac{\partial(g^i S^i)}{\partial x} + \mu^i S^i + (\nu_1 \delta_1 B_u + \nu_2 \delta_2 B_a + \nu_3 \zeta c_2^i M + \nu_4 c_1^i B_u) S^i &= 0 \\ \frac{\partial I^i}{\partial t} + \frac{\partial(\tilde{g}^i I^i)}{\partial x} + \tilde{\mu}^i I^i - (\nu_1 \delta_1 B_u + \nu_2 \delta_2 B_a + \nu_3 \zeta c_2^i M + \nu_4 c_1^i B_u) S^i &= 0 \\ \frac{dB_a}{dt} &= \mathcal{I}(t; \rho) - \delta_2 B_a P - \lambda B_a \\ \frac{dB_u}{dt} &= H + \lambda B_a - c_M M^* B_u - \delta_1 B_u P - \mathcal{S}(t; c_1) B_u - \mathcal{I}(t; \tilde{c}_1) B_u \\ \frac{dM}{dt} &= \epsilon c_M (M^* - M) B_u - \mu_M M - \mathcal{S}(t; c_2) M - \mathcal{I}(t; \tilde{c}_2) M, \end{aligned} \tag{1}$$

with the boundary conditions (for the susceptible and infected fish equations only) given by

$$\begin{aligned} g^i(P, x_{\min}) S^i(t, x_{\min}) &= \sum_{\ell=1}^m p^{i\ell} \int_{x_{\min}}^{x_{\max}} [\beta^\ell(P, x) S^\ell(t, x) + \tilde{\beta}^\ell(P, x) I^\ell(t, x)] dx, \\ I^i(t, x_{\min}) &= 0 \end{aligned} \tag{2}$$

and initial conditions

$$\begin{aligned} S^i(0, x) &= S^{i,0}(x), \\ I^i(0, x) &= I^{i,0}(x), \\ B_a(0) &= B_a^0, \\ B_u(0) &= B_u^0, \\ M(0) &= M^0, \end{aligned} \tag{3}$$

for  $0 \leq t \leq T$ ,  $x \in [x_{\min}, x_{\max}]$ , and for  $i = 1, \dots, m$ . We note that for simplicity of notation, we let the function

$$Z^i(t) = \sum_{\ell=1}^m p^{i\ell} \int_{x_{\min}}^{x_{\max}} [\beta^\ell(P, x) S^\ell(t, x) + \tilde{\beta}^\ell(P, x) I^\ell(t, x)] dx \tag{4}$$

throughout the paper.

**3. Weak solution.** Throughout the discussion we let  $c > 1$  be a sufficiently large positive constant. We assume that the parameters in (1)–(3) satisfy the following assumptions for  $i = 1, \dots, m$ :

- (A1) The functions  $g^i(P, x)$  and  $\tilde{g}^i(P, x)$  are twice continuously differentiable with respect to  $x$  and  $P$ . Also,  $0 < g^i(P, x) \leq c$ ,  $0 < \tilde{g}^i(P, x) \leq c$  for  $(P, x) \in [0, \infty) \times [x_{\min}, x_{\max}]$  and  $g^i(P, x_{\max}) = \tilde{g}^i(P, x_{\max}) = 0$  for  $P \in [0, \infty)$ .
- (A2) The functions  $\mu^i(P, x)$  and  $\tilde{\mu}^i(P, x)$  are continuously differentiable with respect to  $x$  and  $P$ . Also,  $0 \leq \mu^i(P, x) \leq c$ ,  $0 \leq \tilde{\mu}^i(P, x) \leq c$  for  $(P, x) \in [0, \infty) \times [x_{\min}, x_{\max}]$ .
- (A3) The functions  $\beta^i(P, x)$  and  $\tilde{\beta}^i(P, x)$  are continuously differentiable with respect to  $x$  and  $P$ . Also,  $0 \leq \beta^i(P, x) \leq c$ ,  $0 \leq \tilde{\beta}^i(P, x) \leq c$  for  $(P, x) \in [0, \infty) \times [x_{\min}, x_{\max}]$ .
- (A4) The functions  $c_1^i(x)$ ,  $c_2^i(x)$ ,  $\tilde{c}_1^i(x)$ ,  $\tilde{c}_2^i(x)$ , are continuously differentiable and  $0 \leq c_1^i(x) \leq c$ ,  $0 \leq c_2^i(x) \leq c$ ,  $0 \leq \tilde{c}_1^i(x) \leq c$ ,  $0 \leq \tilde{c}_2^i(x) \leq c$  for  $x \in [x_{\min}, x_{\max}]$ .

- (A5) The functions  $S^{i,0}(x)$  and  $I^{i,0}(x)$  are nonnegative functions having total variation bounded by  $c$ , and  $B_a(0), B_u(0), M(0)$  are nonnegative constants less than  $c$ .
- (A6) The function  $H(t)$  is a nonnegative function bounded above by  $c$  for  $0 \leq t \leq T$ .
- (A7) The parameters  $\nu_1, \nu_2, \nu_3, \nu_4, \delta_1, \delta_2, \zeta, c_M, \lambda, \bar{\rho}^i, \epsilon, M^*$ , and  $\mu_M$  are nonnegative constants less than  $c$ .

We point out that the characteristic curve for the equation for  $S^i, i = 1, \dots, m$ , in (1) passing through the point  $(t_0, x_0)$  is given by

$$\frac{dx^i(t; t_0, x_0)}{dt} = g^i(P(t), x^i(t; t_0, x_0)), \quad x^i(t_0; t_0, x_0) = x_0,$$

and that for equation  $I^i, i = 1, \dots, m$ , in (1) passing through the point  $(t_0, x_0)$  is given by

$$\frac{dx^i(t; t_0, x_0)}{dt} = \tilde{g}^i(P(t), x^i(t; t_0, x_0)), \quad x^i(t_0; t_0, x_0) = x_0.$$

These characteristic curves are nonlinear and their solutions are coupled to the solution of the model (1) due to the dependency of  $g$  and  $\tilde{g}$  on the total population  $P$  of susceptible and infected fish. Furthermore, from assumption (A1) it follows that the characteristic curves are monotone and asymptotically approach  $x = x_{\max}$  as  $t \rightarrow \infty$ .

We now proceed to define a weak solution for the model (1). To this end, for notational convenience, we let

$$L^i(B_a, B_u, M, x) = \nu_1 \delta_1 B_u + \nu_2 \delta_2 B_a + \nu_3 \zeta c_2^i(x) M + \nu_4 c_1^i(x) B_u, \tag{5}$$

for the remainder of the paper. We let the vectors  $\vec{S} = (S^1, \dots, S^m)^T$  and  $\vec{I} = (I^1, \dots, I^m)^T$  denote the susceptible and infected fish densities for all  $m$  physiological groups. Multiplying the first and second equations of (1) by  $\phi(t, x)$  and  $\psi(t, x)$ , respectively, and formally integrating by parts, we define a weak solution of our system (1)–(3) as a tuple  $(\vec{S}, \vec{I}, B_a, B_u, M) \in \prod_{i=1}^m BV([0, T] \times [x_{\min}, x_{\max}]) \times \prod_{i=1}^m BV([0, T] \times [x_{\min}, x_{\max}]) \times C[0, T] \times C[0, T] \times C[0, T]$  satisfying (6)–(7) below

$$\begin{aligned} & \int_{x_{\min}}^{x_{\max}} S^i(t, x) \phi(t, x) dx - \int_{x_{\min}}^{x_{\max}} S^{i,0}(x) \phi(0, x) dx \\ = & \int_0^t \left( \sum_{\ell=1}^m p^{i\ell} \int_{x_{\min}}^{x_{\max}} \left[ \beta^\ell(P(\tau), x) S^\ell(\tau, x) + \tilde{\beta}^\ell(P(\tau), x) I^\ell(\tau, x) \right] dx \right) \phi(\tau, x_{\min}) d\tau \\ & + \int_0^t \int_{x_{\min}}^{x_{\max}} S^i(\tau, x) \left( \phi_\tau(\tau, x) + g^i(P(\tau), x) \phi_x(\tau, x) - \mu^i(P(\tau), x) \phi(\tau, x) \right) dx d\tau \\ & - \int_0^t \int_{x_{\min}}^{x_{\max}} S^i(\tau, x) L^i(B_a(\tau), B_u(\tau), M(\tau), x) \phi(\tau, x) dx d\tau, \\ & \int_{x_{\min}}^{x_{\max}} I^i(t, x) \psi(t, x) dx - \int_{x_{\min}}^{x_{\max}} I^{i,0}(x) \psi(0, x) dx \\ = & \int_0^t \int_{x_{\min}}^{x_{\max}} I^i(\tau, x) \left( \psi_\tau(\tau, x) + \tilde{g}^i(P(\tau), x) \psi_x(\tau, x) - \tilde{\mu}^i(P(\tau), x) \psi(\tau, x) \right) dx d\tau \\ & + \int_0^t \int_{x_{\min}}^{x_{\max}} \psi(x, \tau) S^i(\tau, x) L^i(B_a(\tau), B_u(\tau), M(\tau), x) dx d\tau, \end{aligned} \tag{6}$$



$$\begin{aligned}
 B_a(t) &= B_a(0) + \int_0^t \left[ \mathcal{I}(s; \rho) - \delta_2 B_a(s) P(s) - \lambda B_a(s) \right] ds, \\
 B_u(t) &= B_u(0) + \int_0^t \left[ H(s) + \lambda B_a(s) - c_M M^* B_u(s) - \delta_1 B_u(s) P(s) \right. \\
 &\quad \left. - \mathcal{S}(s; c_1) B_u(s) - \mathcal{I}(s; \tilde{c}_1) B_u(s) \right] ds, \\
 M(t) &= M(0) + \int_0^t \left[ \epsilon c_M (M^* - M(s)) B_u(s) - \mu_M M(s) \right. \\
 &\quad \left. - \mathcal{S}(s; c_2) M(s) - \mathcal{I}(s; \tilde{c}_2) M(s) \right] ds,
 \end{aligned} \tag{7}$$

for each  $t \in (0, T)$ ,  $i = 1, \dots, m$ , every  $\phi \in C^1([0, T] \times [x_{\min}, x_{\max}])$  and every  $\psi \in C^1([0, T] \times [x_{\min}, x_{\max}])$ .

**4. Numerical scheme.** As described in Section 2, we assume that there is a smallest size  $x_{\min}$  and a largest size  $x_{\max}$  (we may assume that  $x_{\max} \leq c$ ) for the fish population(s) considered. We divide this interval into  $N$  subintervals of equal length so the size of the mesh length is given by  $\Delta x = (x_{\max} - x_{\min})/N$  and the mesh points are given by  $x_j = x_{\min} + j\Delta x$ , with  $j = 0, 1, \dots, N$  (thus,  $x_0 = x_{\min}$  and  $x_N = x_{\max}$ ). However, the scheme readily applies to a nonuniform mesh also, as was done in [9]. We denote by  $K$  the number of time steps taken over the finite interval  $[0, T]$  so the time points are  $t_k = k\Delta t$ , for  $k = 0, 1, \dots, K$  and  $\Delta t = T/K$ .

We denote by  $S_j^{i,k}$  the numerical approximation of  $S^i(t_k, x_j)$  and we use  $I_j^{i,k}$  to represent the approximation of  $I^i(t_k, x_j)$ . We use  $M^k$ ,  $B_a^k$ , and  $B_u^k$  to denote the approximations of  $M(t_k)$ ,  $B_a(t_k)$ , and  $B_u(t_k)$ . We let  $B_a^0, B_u^0, M^0, S_j^{i,0}$  and  $I_j^{i,0}$  represent the initial conditions for the variables  $B_a, B_u, M, S^i, I^i$ , for  $i = 1, \dots, m$ , respectively. We denote by  $g_j^{i,k}, \tilde{g}_j^{i,k}, \mu_j^{i,k}, \tilde{\mu}_j^{i,k}, \beta_j^{i,k}, \tilde{\beta}_j^{i,k}, c_{1,j}^i, \tilde{c}_{1,j}^i, c_{2,j}^i, \tilde{c}_{2,j}^i$ , and  $\rho_j^i$ , the values  $g^i(P^k, x_j), \tilde{g}^i(P^k, x_j), \mu^i(P^k, x_j), \tilde{\mu}^i(P^k, x_j), \beta^i(P^k, x_j), \tilde{\beta}^i(P^k, x_j), c_1^i(x_j), \tilde{c}_1^i(x_j), c_2^i(x_j), \tilde{c}_2^i(x_j)$  and  $\rho^i(x_j)$ , respectively.

We now discretize the model (1)–(3), using the approximation of (5) which is given by

$$L_j^{i,k} = \nu_1 \delta_1 B_u^k + \nu_2 \delta_2 B_a^k + \nu_3 \zeta c_{2,j}^i M^k + \nu_4 c_{1,j}^i B_u^k, \tag{8}$$

and we have

$$\frac{S_j^{i,k+1} - S_j^{i,k}}{\Delta t} + \frac{g_j^{i,k} S_j^{i,k+1} - \tilde{g}_{j-1}^{i,k} S_{j-1}^{i,k+1}}{\Delta x} + \mu_j^{i,k} S_j^{i,k+1} + L_j^{i,k} S_j^{i,k+1} = 0, \tag{9}$$

$$\frac{I_j^{i,k+1} - I_j^{i,k}}{\Delta t} + \frac{\tilde{g}_j^{i,k} I_j^{i,k+1} - \tilde{g}_{j-1}^{i,k} I_{j-1}^{i,k+1}}{\Delta x} + \tilde{\mu}_j^{i,k} I_j^{i,k+1} - L_j^{i,k} S_j^{i,k+1} = 0, \tag{10}$$

$$\frac{B_a^{k+1} - B_a^k}{\Delta t} = \sum_{i=1}^m \left[ \sum_{j=1}^N \rho_j^i I_j^{i,k+1} \Delta x \right] - \delta_2 B_a^{k+1} P^{k+1} - \lambda B_a^{k+1}, \tag{11}$$

$$\begin{aligned}
 \frac{B_u^{k+1} - B_u^k}{\Delta t} &= H^k + \lambda B_a^{k+1} - c_M M^* B_u^{k+1} - \delta_1 B_u^{k+1} P^{k+1} \\
 &\quad - B_u^{k+1} \sum_{i=1}^m \sum_{j=1}^N \left[ c_{1,j}^i S_j^{i,k+1} + \tilde{c}_{1,j}^i I_j^{i,k+1} \right] \Delta x,
 \end{aligned} \tag{12}$$

$$\begin{aligned} \frac{M^{k+1} - M^k}{\Delta t} &= \epsilon c_M (M^* - M^{k+1}) B_u^{k+1} - \mu_M M^{k+1} \\ &\quad - M^{k+1} \sum_{i=1}^m \sum_{j=1}^N \left[ c_{2,j}^i S_j^{i,k+1} + \tilde{c}_{2,j}^i I_j^{i,k+1} \right] \Delta x, \end{aligned} \tag{13}$$

where  $0 \leq k \leq K - 1$  and  $1 \leq j \leq N$ , for  $i = 1, \dots, m$ .

The boundary conditions for the susceptible and infected fish are approximated by

$$g_0^{i,k} S_0^{i,k+1} = \sum_{\ell=1}^m p^{i\ell} \sum_{j=1}^N \left[ \beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k} \right] \Delta x \quad \text{and} \quad I_0^{i,k} = 0. \tag{14}$$

We note that from (4) we have  $g_0^{i,k} S_0^{i,k+1} = Z^{i,k}$ . Then one can compute the approximate solution explicitly in the order specified below. First from (14) compute

$$S_0^{i,k+1} = \frac{1}{g_0^{i,k}} \sum_{\ell=1}^m p^{i\ell} \sum_{j=1}^N \left[ \beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k} \right] \Delta x \quad \text{and} \quad I_0^{i,k} = 0. \tag{15}$$

Then for  $j = 1, \dots, N$ , compute the following quantities:

$$S_j^{i,k+1} = \frac{S_j^{i,k} + \frac{\Delta t}{\Delta x} g_{j-1}^{i,k} S_{j-1}^{i,k+1}}{1 + \Delta t \left( \frac{1}{\Delta x} g_j^{i,k} + \mu_j^{i,k} + L_j^{i,k} \right)}, \tag{16}$$

$$I_j^{i,k+1} = \frac{I_j^{i,k} + \frac{\Delta t}{\Delta x} \tilde{g}_{j-1}^{i,k} I_{j-1}^{i,k+1} + \Delta t L_j^{i,k} S_j^{i,k+1}}{1 + \Delta t \left( \frac{1}{\Delta x} \tilde{g}_j^{i,k} + \tilde{\mu}_j^{i,k} \right)}, \tag{17}$$

$$B_a^{k+1} = \frac{B_a^k + \Delta t \sum_{i=1}^m \sum_{j=1}^N \rho_j^i I_j^{i,k+1} \Delta x}{1 + \Delta t (\delta_2 P^{k+1} + \lambda)}, \tag{18}$$

$$B_u^{k+1} = \frac{B_u^k + \Delta t (H^k + \lambda B_a^{k+1})}{1 + \Delta t \left[ c_M M^* + \delta_1 P^{k+1} + \sum_{i=1}^m \sum_{j=1}^N (c_{1,j}^i S_j^{i,k+1} + \tilde{c}_{1,j}^i I_j^{i,k+1}) \Delta x \right]}, \tag{19}$$

$$M^{k+1} = \frac{M^k + \Delta t \epsilon c_M M^* B_u^{k+1}}{1 + \Delta t \left[ \epsilon c_M B_u^{k+1} + \mu_M + \sum_{i=1}^m \sum_{j=1}^N (c_{2,j}^i S_j^{i,k+1} + \tilde{c}_{2,j}^i I_j^{i,k+1}) \Delta x \right]}, \tag{20}$$

for  $i = 1, \dots, m$ .

The novelty of the approximation above lies in the preservation of positivity and unconditional stability (no CFL condition) using an implicit form without having to pay the computational price of matrix inversion (which is common with implicit schemes). Namely, using a clever mixture of implicit and explicit approximations for the nonlinear terms in equations (9)–(10) where the coefficients (which may depend on the total population) are evaluated at the current ( $k$ ) time step while the unknown functions,  $S$  and  $I$ , are evaluated at the next ( $k + 1$ ) time step, allows one to solve this implicit scheme in an explicit fashion, resulting in the aforementioned

benefits. Furthermore, using such an implicit-explicit approximation mixture in the mortality terms allows for one to incorporate large mortality rates (which are very common for infected individuals) without affecting the stability of the scheme. We remark that an explicit-implicit mixture approach has been used for the approximation of other models (e.g., [6, 7]).

**5. Convergence of finite difference approximation.** We begin this section by defining the difference operator

$$D_{\Delta x}^-(u_j^{i,k}) = \frac{u_j^{i,k} - u_{j-1}^{i,k}}{\Delta x}, \quad 1 \leq j \leq N,$$

and we let the  $\ell^1$  and  $\ell^\infty$  norms be given by

$$\|u^{i,k}\|_1 = \sum_{j=1}^N |u_j^{i,k}| \Delta x, \quad \text{and} \quad \|u^{i,k}\|_\infty = \max_{0 \leq j \leq N} |u_j^{i,k}|.$$

We establish several results to prove that the above finite difference approximation converges to the weak solution of the model (1). For convenience, we include the proofs of these results in *Appendix A*. We begin by establishing the fact that our system has a unique nonnegative solution.

**Lemma 5.1.** *The system (9)–(14) has a unique nonnegative solution.*

Next, we establish a bound on the  $\ell_1$  norm of the approximations  $S_j^{i,k}$  and  $I_j^{i,k}$ .

**Lemma 5.2.** *There exists a positive constant  $C_1$  such that*

$$\sum_{i=1}^m (\|S^{i,k}\|_1 + \|I^{i,k}\|_1) \leq C_1.$$

As a consequence of Lemma 5.2, we now have that  $0 \leq P^k \leq C_1$  for  $k = 0, 1, \dots, K$ . For the remainder of the paper we will define  $\mathbb{D} = [0, C_1] \times [x_{\min}, x_{\max}]$ . We now establish the boundedness of  $B_a$ ,  $B_u$ , and  $M$ .

**Lemma 5.3.** *There exists a positive constant  $C_2$  such that*

$$|B_a^k| + |B_u^k| + |M^k| \leq C_2.$$

In the next two lemmas we establish the boundedness of  $L_j^{i,k}$ ,  $D_{\Delta x}^-(L_j^{i,k})$ , and the boundedness of the approximations of the susceptible and infected fish in each physiological group  $i \in \{1, \dots, m\}$ , and at any time  $t_k$ ,  $k \in \{0, 1, \dots, K\}$  in the infinity norm.

**Lemma 5.4.** *There exist positive constants  $C_3$  and  $C_4$  such that for  $i = 1, \dots, m$ ,*

$$0 \leq L_j^{i,k} \leq C_3 \quad \text{and} \quad |D_{\Delta x}^-(L_j^{i,k})| \leq C_4.$$

**Lemma 5.5.** *There exists a positive constant  $C_5$  such that for  $i = 1, \dots, m$ ,*

$$\|S^{i,k}\|_\infty + \|I^{i,k}\|_\infty \leq C_5.$$

The next two lemmas are necessary to show that the approximations for  $S^i$  and  $I^i$  have bounded total variation.

**Lemma 5.6.** *There is a positive constant  $C_6$  such that for  $k = 0, 1, \dots, K - 1$ ,*

$$\left| \frac{P^{k+1} - P^k}{\Delta t} \right| < C_6.$$

**Lemma 5.7.** *There is a positive constant  $C_7$  such that for  $k = 0, 1, \dots, K - 1$ ,*

$$\left| \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} \right| \leq C_7.$$

In Lemma 5.8, we show that the approximations  $S_j^{i,k}$  and  $I_j^{i,k}$  have bounded total variation.

**Lemma 5.8.** *There exists a positive constant  $C_8$  such that for  $i = 1, \dots, m$ ,*

$$\|D_{\Delta x}^-(S_j^{i,k})\|_1 + \|D_{\Delta x}^-(I_j^{i,k})\|_1 \leq C_8.$$

The next result shows that the difference approximations satisfy a Lipschitz-type condition in time  $t$ .

**Lemma 5.9.** *There are positive constants  $C_9, C_{10}, C_{11}, C_{12}$  and  $C_{13}$  such that for any  $r > q$  the following hold.*

$$\sum_{j=1}^N \left| \frac{S_j^{i,r} - S_j^{i,q}}{\Delta t} \right| \Delta x \leq C_9(r - q), \quad \sum_{j=1}^N \left| \frac{I_j^{i,r} - I_j^{i,q}}{\Delta t} \right| \Delta x \leq C_{10}(r - q),$$

$$\left| \frac{B_u^r - B_u^q}{\Delta t} \right| \leq C_{11}(r - q), \quad \left| \frac{B_a^r - B_a^q}{\Delta t} \right| \leq C_{12}(r - q), \quad \left| \frac{M^r - M^q}{\Delta t} \right| \leq C_{13}(r - q).$$

Following [40], we define a family of functions  $\{\mathbb{S}_{\Delta t, \Delta x}^i\}, \{\mathbb{I}_{\Delta t, \Delta x}^i\}, \{\mathbb{B}_{a_{\Delta t}}\}, \{\mathbb{B}_{u_{\Delta t}}\}$ , and  $\{\mathbb{M}_{\Delta t}\}$  by

$$\mathbb{S}_{\Delta t, \Delta x}^i(t, x) = S_j^{i,k}, \quad \mathbb{I}_{\Delta t, \Delta x}^i(t, x) = I_j^{i,k},$$

$$\mathbb{B}_{a_{\Delta t}}(t) = B_a^k + \frac{B_a^{k+1} - B_a^k}{\Delta t}(t - t_k), \quad \mathbb{B}_{u_{\Delta t}}(t) = B_u^k + \frac{B_u^{k+1} - B_u^k}{\Delta t}(t - t_k),$$

$$\mathbb{M}_{\Delta t}(t) = M^k + \frac{M^{k+1} - M^k}{\Delta t}(t - t_k),$$

for  $x \in [x_j, x_{j+1}), t \in [t_k, t_{k+1})$ , where  $j = 0, \dots, N - 1$  and  $k = 0, \dots, K - 1$ . Then the sets of functions  $\{\mathbb{S}_{\Delta t, \Delta x}^i\}$ , and  $\{\mathbb{I}_{\Delta t, \Delta x}^i\}$  are compact in the topology of  $L^1((0, T) \times (x_{\min}, x_{\max}))$  for each  $i = 1, \dots, m$  and  $\{\mathbb{B}_{a_{\Delta t}}\}, \{\mathbb{B}_{u_{\Delta t}}\}$ , and  $\{\mathbb{M}_{\Delta t}\}$  are compact in the topology of  $C(0, T)$ . We now have the following result.

**Theorem 5.10.** *There exist sequences  $\{\mathbb{S}_{\Delta t_l, \Delta x_l}^i\} \subset \{\mathbb{S}_{\Delta t, \Delta x}^i\}$  and  $\{\mathbb{I}_{\Delta t_l, \Delta x_l}^i\} \subset \{\mathbb{I}_{\Delta t, \Delta x}^i\}$  which converge to BV  $([0, T] \times [x_{\min}, x_{\max}])$  functions  $S^i(t, x)$  and  $I^i(t, x)$  for each  $i = 1, \dots, m$ . There are also sequences  $\{\mathbb{B}_{a_{\Delta t_l}}\} \subset \{\mathbb{B}_{a_{\Delta t}}\}, \{\mathbb{B}_{u_{\Delta t_l}}\} \subset$*

$\{\mathbb{B}_{u_{\Delta t_l}}\}$ , and  $\{\mathbb{M}_{\Delta t_l}\} \subset \{\mathbb{M}_{\Delta t}\}$  that converge to functions  $B_a(t)$ ,  $B_u(t)$ ,  $M(t) \in C[0, T]$ . This happens in the sense that for all  $t > 0$ ,

$$\begin{aligned} \int_{x_{\min}}^{x_{\max}} \left| \mathbb{S}_{\Delta t_l, \Delta x_l}^i(t, x) - S^i(t, x) \right| dx &\rightarrow 0, \\ \int_{x_{\min}}^{x_{\max}} \left| \mathbb{I}_{\Delta t_l, \Delta x_l}^i(t, x) - I^i(t, x) \right| dx &\rightarrow 0, \\ \int_0^T \int_{x_{\min}}^{x_{\max}} \left| \mathbb{S}_{\Delta t_l, \Delta x_l}^i(t, x) - S^i(t, x) \right| dx dt &\rightarrow 0, \\ \int_0^T \int_{x_{\min}}^{x_{\max}} \left| \mathbb{I}_{\Delta t_l, \Delta x_l}^i(t, x) - I^i(t, x) \right| dx dt &\rightarrow 0, \end{aligned}$$

and

$$\begin{aligned} \max_{t \in [0, T]} \left| \mathbb{B}_{a_{\Delta t_l}}(t) - B_a(t) \right| &\rightarrow 0, \quad \max_{t \in [0, T]} \left| \mathbb{B}_{u_{\Delta t_l}}(t) - B_u(t) \right| \rightarrow 0, \\ \max_{t \in [0, T]} \left| \mathbb{M}_{\Delta t_l}(t) - M(t) \right| &\rightarrow 0, \end{aligned}$$

for each  $i$  and as  $l \rightarrow \infty$ . Furthermore, there exists a positive constant  $C_{14}$  such that the limit functions satisfy

$$\begin{aligned} \|S\|_{BV([0, T] \times [x_{\min}, x_{\max}])} + \|I\|_{BV([0, T] \times [x_{\min}, x_{\max}])} \\ + \|B_a\|_{C[0, T]} + \|B_u\|_{C[0, T]} + \|M\|_{C[0, T]} \leq C_{14}. \end{aligned}$$

The next theorem shows that the set of limit functions  $S^i(t, x)$ ,  $I^i(t, x)$ ,  $B_a(t)$ ,  $B_u(t)$ , and  $M(t)$  constructed using our difference scheme is a weak solution of (1)–(3).

**Theorem 5.11.** *The set of limit functions  $S^i(t, x)$ ,  $I^i(t, x)$ ,  $B_a(t)$ ,  $B_u(t)$ , and  $M(t)$  defined in Theorem 5.10 is a weak solution of (1)–(3) and satisfies*

$$\|S^i(t, \cdot)\|_1 + \|I^i(t, \cdot)\|_1 + |B_a(t)| + |B_u(t)| + |M(t)| \leq C_{15},$$

and

$$\begin{aligned} \|S^i\|_{L^\infty((0, T) \times (x_{\min}, x_{\max}))} + \|I^i\|_{L^\infty((0, T) \times (x_{\min}, x_{\max}))} \\ + \|B_a\|_{C[0, T]} + \|B_u\|_{C[0, T]} + \|M\|_{C[0, T]} \leq C_{16}, \end{aligned}$$

for some positive constants  $C_{15}$  and  $C_{16}$ .

The following theorem shows the continuous dependency of the solution set  $\{S_j^{i,k}, I_j^{i,k}, B_a^k, B_u^k, M^k\}$  to (9)–(13) with respect to the initial conditions  $\{S_j^{i,0}, I_j^{i,0}, B_a^0, B_u^0, M^0\}$ .

**Theorem 5.12.** *Let  $\{S_j^{i,k}, I_j^{i,k}, B_a^k, B_u^k, M^k\}$  and  $\{\hat{S}_j^{i,k}, \hat{I}_j^{i,k}, \hat{B}_a^k, \hat{B}_u^k, \hat{M}^k\}$  be the solutions to (9)–(13) corresponding to the initial conditions  $\{S_j^{i,0}, I_j^{i,0}, B_a^0, B_u^0, M^0\}$  and  $\{\hat{S}_j^{i,0}, \hat{I}_j^{i,0}, \hat{B}_a^0, \hat{B}_u^0, \hat{M}^0\}$ , respectively. Then there exist constants  $h_1$  and  $h_2$  such that*

$$(1 - h_1 \Delta t) \hat{E}^{k+1} \leq (1 + h_2 \Delta t) \hat{E}^k,$$

where

$$\hat{E}^{i,k} = \|S^{i,k} - \hat{S}^{i,k}\|_1 + \|I^{i,k} - \hat{I}^{i,k}\|_1 + |B_a^k - \hat{B}_a^k| + |B_u^k - \hat{B}_u^k| + |M^k - \hat{M}^k|.$$

We now give an argument for uniqueness of the weak BV solution of (1). Suppose for  $i = 1, \dots, m$ ,  $P(t), Z^i(t), \mathcal{I}(t; \rho), \mathcal{S}(t; c_1), \mathcal{S}(t; c_2), \mathcal{I}(t; \tilde{c}_1)$ , and  $\mathcal{I}(t; \tilde{c}_2)$  are given Lipschitz continuous functions, where we are not imposing the conditions  $P(t) = \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} (S^i(t, x) + I^i(t, x)) dx, Z^i(t)$  as in (4), or the previous integral definitions of  $\mathcal{S}(t; c_1), \mathcal{S}(t; c_2), \mathcal{I}(t; \tilde{c}_1)$ , and  $\mathcal{I}(t; \tilde{c}_2)$ . Then the initial value problems

$$\frac{dB_a(t)}{dt} = \mathcal{I}(t; \rho) - \delta_2 B_a(t) P(t) - \lambda B_a(t), \quad B_a(0) = B_a^0, \tag{21}$$

$$\begin{aligned} \frac{dB_u(t)}{dt} &= H(t) + \lambda B_a(t) - c_M M^* B_u(t) - \delta_1 B_u(t) P(t) \\ &\quad - \mathcal{S}(t; c_1) B_u(t) - \mathcal{I}(t; \tilde{c}_1) B_u(t), \quad B_u(0) = B_u^0, \end{aligned} \tag{22}$$

$$\begin{aligned} \frac{dM(t)}{dt} &= \epsilon c_M (M^* - M(t)) B_u(t) - \mu_M M(t) \\ &\quad - \mathcal{S}(t; c_2) M(t) - \mathcal{I}(t; \tilde{c}_2) M(t), \quad M(0) = M^0, \end{aligned} \tag{23}$$

where  $0 \leq t \leq T$ , have unique solutions when calculated in the given order. Now, consider the initial-boundary value problem with the unique solutions  $B_a(t), B_u(t)$  and  $M(t)$ ,

$$\begin{aligned} \frac{\partial S^i(t, x)}{\partial t} + \frac{\partial (g^i(P, x) S^i(t, x))}{\partial x} + \mu^i(P, x) S^i(t, x) + L^i(B_a, B_u, M, x) S^i(t, x) &= 0, \\ 0 < t < T, \quad x_{\min} < x < x_{\max}, \\ g^i(P, x_{\min}) S^i(t, x_{\min}) = Z^i(t), \quad 0 < t < T, \\ S^i(0, x) = S^{i,0}(x), \quad x_{\min} \leq x \leq x_{\max}, \end{aligned} \tag{24}$$

where  $L^i(B_a, B_u, M, x)$  is defined in (5). Then one can easily show that (24) has a unique solution  $S^i(t, x)$  (note that this is a nonlinear equation with a local boundary condition). In fact, a weak solution can be defined as a limit of the difference approximation (9)–(14) with the given numbers  $B_a^k = B_a(t_k), B_u^k = B_u(t_k), M^k = M(t_k)$ , and uniqueness can be established using a similar technique as in [40] (p.282). With the unique solution  $S^i(t, x)$  of (24) now known, we can argue in a similar manner that the problem

$$\begin{aligned} \frac{\partial I^i(t, x)}{\partial t} + \frac{\partial (\tilde{g}^i(P, x) I^i(t, x))}{\partial x} + \tilde{\mu}^i(P, x) I^i(t, x) - L^i(B_a, B_u, M, x) S^i(t, x) &= 0, \\ 0 < t < T, \quad x_{\min} < x < x_{\max}, \\ I^i(t, x_{\min}) = 0, \quad 0 < t < T, \\ I^i(0, x) = 0, \quad x_{\min} \leq x \leq x_{\max}, \end{aligned} \tag{25}$$

has a unique solution. Let  $(S_j^{i,k}, I_j^{i,k}, B_a^k, B_u^k, M^k)$  and  $(\hat{S}_j^{i,k}, \hat{I}_j^{i,k}, \hat{B}_a^k, \hat{B}_u^k, \hat{M}^k)$  be solutions to (9)–(14) corresponding to the given functions  $(P^k, Z^{i,k}, \mathcal{I}^k(\rho), \mathcal{S}^k(c_1), \mathcal{I}^k(\tilde{c}_1), \mathcal{S}^k(c_2), \mathcal{I}^k(\tilde{c}_2))$  and  $(\hat{P}^k, \hat{Z}^{i,k}, \hat{\mathcal{I}}^k(\rho), \hat{\mathcal{S}}^k(c_1), \hat{\mathcal{I}}^k(\tilde{c}_1), \hat{\mathcal{S}}^k(c_2), \hat{\mathcal{I}}^k(\tilde{c}_2))$  respectively, where we denote by  $\mathcal{I}^k(\rho), \mathcal{S}^k(c_1), \mathcal{S}^k(c_2), \mathcal{I}^k(\tilde{c}_1)$ , and  $\mathcal{I}^k(\tilde{c}_2)$  the values of  $\mathcal{I}(t_k; \rho), \mathcal{S}(t_k; c_1), \mathcal{S}(t_k; c_2), \mathcal{I}(t_k; \tilde{c}_1)$  and  $\mathcal{I}(t_k; \tilde{c}_2)$ . Also, let  $u_j^{i,k} = S_j^{i,k} - \hat{S}_j^{i,k}, v_j^{i,k} = I_j^{i,k} - \hat{I}_j^{i,k}, w^k = B_a^k - \hat{B}_a^k, y^k = B_u^k - \hat{B}_u^k$ , and  $z^k = M^k - \hat{M}^k$ . Then from the proof

of Theorem 5.12, we refer to (43),(47),(49), (50), and (51) to obtain

$$\begin{aligned} \frac{\|u^{i,k+1}\|_1 - \|u^{i,k}\|_1}{\Delta t} &\leq \omega_6 \|u^{i,k+1}\|_1 + \omega_7(|w^k| + |y^k| + |z^k|) + \omega_8|P^k - \hat{P}^k| \\ &\quad + |Z^{i,k} - \hat{Z}^{i,k}| \\ \frac{\|v^{i,k+1}\|_1 - \|v^{i,k}\|_1}{\Delta t} &\leq \omega_{11} \|u^{i,k+1}\|_1 + \omega_{12} \|v^{i,k+1}\|_1 \\ &\quad + \omega_7(|w^k| + |y^k| + |z^k|) + \omega_{10}|P^k - \hat{P}^k| \\ \frac{|w^{k+1}| - |w^k|}{\Delta t} &\leq |\mathcal{I}^{k+1}(\rho) - \hat{\mathcal{I}}^{k+1}(\rho)| + \omega_{24}|P^{k+1} - \hat{P}^{k+1}| + \omega_{15}|w^{k+1}|, \\ \frac{|y^{k+1}| - |y^k|}{\Delta t} &\leq \omega_{18}|w^{k+1}| + \omega_{19}|y^{k+1}| + \omega_{25}|P^{k+1} - \hat{P}^{k+1}| \\ &\quad + \omega_{26}|\mathcal{S}^{k+1}(c_1) - \hat{\mathcal{S}}^{k+1}(c_1)| + \omega_{26}|\mathcal{I}^{k+1}(\tilde{c}_1) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_1)|, \\ \frac{|z^{k+1}| - |z^k|}{\Delta t} &\leq \omega_{22}|y^{k+1}| + \omega_{23}|z^{k+1}| \\ &\quad + \omega_{26}|\mathcal{S}^{k+1}(c_2) - \hat{\mathcal{S}}^{k+1}(c_2)| + \omega_{26}|\mathcal{I}^{k+1}(\tilde{c}_2) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_2)|. \end{aligned}$$

The conclusion of Theorem 5.12 becomes

$$\begin{aligned} \hat{E}^{i,k+1} \leq & \frac{1}{1-h_3\Delta t} \hat{E}^{i,k} + \frac{h_4}{1-h_3\Delta t} \left( |w^k| + |y^k| + |z^k| + |P^k - \hat{P}^k| + |Z^{i,k} - \hat{Z}^{i,k}| \right. \\ & \left. + |P^{k+1} - \hat{P}^{k+1}| + |\mathcal{S}^{k+1}(c_1) - \hat{\mathcal{S}}^{k+1}(c_1)| + |\mathcal{S}^{k+1}(c_2) - \hat{\mathcal{S}}^{k+1}(c_2)| \right. \\ & \left. + |\mathcal{I}^{k+1}(\tilde{c}_1) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_1)| + |\mathcal{I}^{k+1}(\tilde{c}_2) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_2)| \right) \Delta t, \end{aligned}$$

where  $\hat{E}^{i,k}$  is the same as in Theorem 5.12 and

$$h_3 = \max\{\omega_6 + \omega_{11}, \omega_{12}, \omega_{15} + \omega_{18}, \omega_{19} + \omega_{22}, \omega_{23}\}$$

$$h_4 = \max\{\omega_7, \omega_8 + \omega_{10} + \omega_{24} + \omega_{25}, \omega_{26}\}.$$

Equivalently,

$$\begin{aligned} \hat{E}^{i,k} \leq & \left( \frac{1}{1-h_3\Delta t} \right)^k \hat{E}^{i,0} + \frac{h_4\Delta t}{1-h_3\Delta t} \sum_{n=0}^{k-1} \left( \frac{1}{1-h_3\Delta t} \right)^{k-1-n} \left( |w^n| + |y^n| \right. \\ & \left. + |z^n| + |P^n - \hat{P}^n| + |Z^{i,n} - \hat{Z}^{i,n}| + |P^{n+1} - \hat{P}^{n+1}| \right. \\ & \left. + |\mathcal{S}^{n+1}(c_1) - \hat{\mathcal{S}}^{n+1}(c_1)| + |\mathcal{S}^{n+1}(c_2) - \hat{\mathcal{S}}^{n+1}(c_2)| \right. \\ & \left. + |\mathcal{I}^{n+1}(\tilde{c}_1) - \hat{\mathcal{I}}^{n+1}(\tilde{c}_1)| + |\mathcal{I}^{n+1}(\tilde{c}_2) - \hat{\mathcal{I}}^{n+1}(\tilde{c}_2)| \right). \end{aligned} \tag{26}$$

Using Theorem 5.10, we can take the limit in (26) to obtain

$$\begin{aligned} \hat{E}^i(t) \leq & e^{h_3 t} \hat{E}^i(0) + h_4 e^{h_3 t} \int_0^t \left( |B_a(\tau) - \hat{B}_a(\tau)| + |B_u(\tau) - \hat{B}_u(\tau)| \right. \\ & \left. + |M(\tau) - \hat{M}(\tau)| + 2|P(\tau) - \hat{P}(\tau)| + |Z^i(\tau) - \hat{Z}^i(\tau)| \right. \\ & \left. + |\mathcal{S}(\tau; c_1) - \hat{\mathcal{S}}(\tau; c_1)| + |\mathcal{S}(\tau; c_2) - \hat{\mathcal{S}}(\tau; c_2)| \right. \\ & \left. + |\mathcal{I}(\tau; \tilde{c}_1) - \hat{\mathcal{I}}(\tau; \tilde{c}_1)| + |\mathcal{I}(\tau; \tilde{c}_2) - \hat{\mathcal{I}}(\tau; \tilde{c}_2)| \right) d\tau, \end{aligned}$$

where  $(S^i, I^i, B_a, B_u, M), (\hat{S}^i, \hat{I}^i, \hat{B}_a, \hat{B}_u, \hat{M})$  are the unique solutions to (21)–(25) with the given functions  $(P^k, Z^{i,k}, \mathcal{I}^k(\rho), \mathcal{S}^k(c_1), \mathcal{I}^k(\tilde{c}_1), \mathcal{S}^k(c_2), \mathcal{I}^k(\tilde{c}_2))$  and  $(\hat{P}^k, \hat{Z}^{i,k}, \hat{\mathcal{I}}^k(\rho), \hat{\mathcal{S}}^k(c_1), \hat{\mathcal{I}}^k(\tilde{c}_1), \hat{\mathcal{S}}^k(c_2), \hat{\mathcal{I}}^k(\tilde{c}_2))$ , respectively, and

$$\begin{aligned} \hat{E}^i(t) = & \|S^i(t, \cdot) - \hat{S}^i(t, \cdot)\|_1 + \|I^i(t, \cdot) - \hat{I}^i(t, \cdot)\|_1 + |B_a(t) - \hat{B}_a(t)| \\ & + |B_u(t) - \hat{B}_u(t)| + |M(t) - \hat{M}(t)|. \end{aligned}$$

Then applying the estimate given in (26) to the corresponding solutions of (21)–(25), where for any continuous function  $\alpha(x)$ ,

$$\begin{aligned} P(t) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} (S^i(t, x) + I^i(t, x)) dx, \\ \hat{P}(t) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} (\hat{S}^i(t, x) + \hat{I}^i(t, x)) dx, \\ Z^i(t) &= \frac{1}{g^i(P, x_{\min})} \sum_{\ell=1}^m p^{i\ell} \int_{x_{\min}}^{x_{\max}} \left( \beta^\ell(P, x) S^\ell(t, x) + \tilde{\beta}^\ell(P, x) I^\ell(t, x) \right) dx, \\ \hat{Z}^i(t) &= \frac{1}{g^i(\hat{P}, x_{\min})} \sum_{\ell=1}^m p^{i\ell} \int_{x_{\min}}^{x_{\max}} \left( \beta^\ell(\hat{P}, x) \hat{S}^\ell(t, x) + \tilde{\beta}^\ell(\hat{P}, x) \hat{I}^\ell(t, x) \right) dx, \\ S(t; \alpha) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} \alpha(x) S^i(t, x) dx \\ \hat{S}(t; \alpha) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} \alpha(x) \hat{S}^i(t, x) dx \\ \mathcal{I}(t; \alpha) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} \alpha(x) I^i(t, x) dx \\ \hat{\mathcal{I}}(t; \alpha) &= \sum_{i=1}^m \int_{x_{\min}}^{x_{\max}} \alpha(x) \hat{I}^i(t, x) dx \end{aligned}$$

are defined in Theorem 5.10, we obtain the following result.

**Theorem 5.13.** *Suppose that  $(S^i, I^i, B_a, B_u, M)$ , and  $(\hat{S}^i, \hat{I}^i, \hat{B}_a, \hat{B}_u, \hat{M})$  are two weak solutions of (1)–(3) corresponding to the initial conditions  $S^{i,0}(x), I^{i,0}(x), B_a^0, B_u^0, M^0$  and  $\hat{S}^{i,0}(x), \hat{I}^{i,0}(x), \hat{B}_a^0, \hat{B}_u^0, \hat{M}^0$ , respectively. Then we have*

$$\begin{aligned} &\|S^i(t, \cdot) - \hat{S}^i(t, \cdot)\|_1 + \|I^i(t, \cdot) - \hat{I}^i(t, \cdot)\|_1 + |B_a(t) - \hat{B}_a(t)| + |B_u(t) - \hat{B}_u(t)| \\ &+ |M(t) - \hat{M}(t)| \leq h_4 e^{h_3 T} \exp(h_4 e^{h_3 T} t) \left\{ \|S_j^{i,0} - \hat{S}_j^{i,0}\|_1 + \|I_j^{i,0} - \hat{I}_j^{i,0}\|_1 \right. \\ &\quad \left. + |B_a^0 - \hat{B}_a^0| + |B_u^0 - \hat{B}_u^0| + |M^0 - \hat{M}^0| \right\}, \end{aligned}$$

which implies that the weak solution of (1)–(3) is unique.

Hence, from Theorem 5.13 it follows that the finite difference solution converges to the unique bounded variation solution of (1)–(3).

**6. Numerical simulations.** We begin this section by demonstrating that the convergence of the numerical scheme presented here (in Section 4) is indeed of first order. In Section 6.1, we first demonstrate convergence through direct computation of errors made from approximating the solution to a simplified version of the model with the numerical scheme. We also demonstrate, in Section 6.2 that convergence is maintained for the full model when we compute errors using an approximated solution with very small time and mesh sizes in place of the exact solution. We then, in Section 6.3 examine the effects of different forms of growth functions on the population dynamics. Lastly, in Section 6.4 we conduct preliminary studies on reproductive fitness and conditions for competitive exclusion within the context of our model as determined by the fecundity kernel as well as the selection-permutation matrix  $p$ . Throughout the remainder of these discussions, we will allow  $x_{\min} = 0$  and  $x_{\max} = 1$ , which can always be achieved by a simple transformation.

**6.1. Convergence for a simplified model.** In order to illustrate the first order convergence of this approximation scheme (presented in Section 4) we calculate the error between solutions computed with this scheme and an exact solution. Since we cannot analytically obtain a solution to the full model, we make some simplifications, essentially by eliminating all nonlinear terms, so that we can. We then use this exact solution for comparison with our approximated solution to the simplified model.

Without loss of generality, we take  $m = 1$  to consider only one physiological class and for simplicity, we denote  $S^1(t, x)$  by  $S(t, x)$  and use similar notation for



the other functions that have dependence on physiological class. We choose simple growth, death, and fecundity kernels,

$$g(P, x) = 1 - x, \quad \tilde{g}(P, x) = \frac{1}{2}(1 - x),$$

$$\mu(P, x) = \tilde{\mu}(P, x) = 1, \quad \beta(P, x) = \frac{1}{e - 1}, \quad \tilde{\beta}(P, x) = 0,$$

and we add the nonhomogeneous terms

$$f_1(t, x) = -xe^{x-t} + S(t, x) \left( \nu_1 \delta_1 B_u(t) + \nu_2 \delta_2 B_a(t) + \nu_3 \zeta c_2 M(t) + \nu_4 c_1 B_u(t) \right),$$

$$f_2(t, x) = -\frac{1}{4}xe^{x-t} + \frac{1}{4}e^{x-t} - \frac{1}{4}x^2e^{x-t} - S(t, x) \left( \nu_1 \delta_1 B_u(t) + \nu_2 \delta_2 B_a(t) + \nu_3 \zeta c_2 M(t) + \nu_4 c_1 B_u(t) \right),$$

to the righthand sides of the equations for the dynamics of the susceptible, and infected fish, respectively (first and second equations of (1)). Then the pde system governing the fish dynamics is linear, and simplifies to

$$\frac{\partial S}{\partial t} + \frac{\partial(gS)}{\partial x} + \mu S = -xe^{x-t},$$

$$\frac{\partial I}{\partial t} + \frac{\partial(\tilde{g}I)}{\partial x} + \tilde{\mu}I = -\frac{1}{4}xe^{x-t} + \frac{1}{4}e^{x-t} - \frac{1}{4}x^2e^{x-t}.$$

If we also then choose the initial conditions  $S(0, x) = e^x$ ,  $I(0, x) = \frac{1}{2}xe^x$ , and boundary conditions  $S(t, 0) = e^{-t}$ ,  $I(t, 0) = 0$ , then the linear system is readily solved to give the simple solutions

$$S(t, x) = e^{x-t}, \quad I(t, x) = \frac{1}{2}xe^{x-t}.$$

The activated Mm, unactivated Mm, carrier mosquito larvae equations, and total population equations can then be solved to obtain

$$B_a(t) = B_a^0 \exp\left(\frac{\delta_2}{2}(1 - 2e)(e^t - 1)e^{-t}\right),$$

$$B_u(t) = B_u^0 \exp\left(\frac{1}{2}(\delta_1 - 2\delta_1e + \delta_1e^{-t}(2e - 1) - 2c_M M^*t)\right),$$

$$M(t) = M^0 \exp(-\mu_M t), \quad P(t) = e^{1-t} - \frac{1}{2}e^{-t}.$$

We use the parameter values given in Table 2 and note that these parameters are chosen merely to demonstrate the achievement of the designed order of accuracy and are not biologically realistic.

We compute several solutions using the finite difference scheme (15)–(20), successively halving the time  $\Delta t$  and mesh  $\Delta x$  step (with a uniform mesh). The corresponding error and order of convergence, in the  $L^1$  norm, calculated from those approximations are presented in Table 3. The computed solutions with the numerical scheme clearly converge to the exact solution with order one, as anticipated.

**6.2. Convergence for the full model.** To demonstrate that first order convergence is maintained with the introduction of the nonlinearities in the model, we approximate the error of computed solutions for the full model by using a solution with very small time  $\Delta t = 3.90625 \times 10^{-5}$  and mesh  $\Delta x = 7.8125 \times 10^{-4}$  steps, which we refer to as the ‘reference solution’, in place of an exact solution to calculate the error. Again, we compute several solutions using the finite difference scheme (15)–(20) (with uniform mesh), successively halving the time and mesh steps. We

TABLE 2. Parameter values for the simplified (linear) model. Initial conditions are  $B_a(0) = 5$ ,  $B_u(0) = 3$ , and  $M(0) = 10$ .

| Parameter    | Value                | Parameter        | Value                  |
|--------------|----------------------|------------------|------------------------|
| $\nu_1$      | $1.0 \times 10^{-7}$ | $\nu_2$          | $0.125 \times 10^{-4}$ |
| $\delta_1$   | 1/500                | $\delta_2$       | 1/500                  |
| $c_M$        | 0.45                 | $\mu_M$          | 1/60                   |
| $\bar{\rho}$ | 0                    | $M^*$            | 20                     |
| $c_1(x)$     | 0                    | $\tilde{c}_1(x)$ | 0                      |
| $c_2(x)$     | 0                    | $\tilde{c}_2(x)$ | 0                      |
| $H(t)$       | 0                    | $\lambda$        | 0                      |
| $\epsilon$   | 0                    |                  |                        |

TABLE 3. Convergence of the method for the simplified linear model

| $\Delta t$           | $\Delta x$           | $S(2, x)$            |        | $I(2, x)$            |        |
|----------------------|----------------------|----------------------|--------|----------------------|--------|
|                      |                      | $L^1$ Error          | Order  | $L^1$ Error          | Order  |
| ( $\times 10^{-3}$ ) | ( $\times 10^{-3}$ ) | ( $\times 10^{-3}$ ) |        | ( $\times 10^{-5}$ ) |        |
| 6.25                 | 3.125                | 4.5859               |        | 3.1818               |        |
| 3.125                | 1.5625               | 2.2905               | 1.0015 | 1.5413               | 1.0457 |
| 1.5625               | 0.78125              | 1.1447               | 1.0008 | 0.7582               | 1.0234 |
| 0.78125              | 0.39063              | 0.5722               | 1.0004 | 0.3760               | 1.0119 |
| 0.39063              | 0.19531              | 0.2861               | 1.0002 | 0.1872               | 1.0060 |
| $\Delta t$           | $\Delta x$           | $B_a(t)$             |        | $B_u(t)$             |        |
|                      |                      | Max Error            | Order  | Max Error            | Order  |
| ( $\times 10^{-3}$ ) | ( $\times 10^{-3}$ ) | ( $\times 10^{-3}$ ) |        | ( $\times 10^{-7}$ ) |        |
| 6.25                 | 3.125                | 5.7287               |        | 2.8648               |        |
| 3.125                | 1.5625               | 2.8636               | 1.0004 | 1.2844               | 1.1573 |
| 1.5625               | 0.78125              | 1.4316               | 1.0002 | 0.6083               | 1.0783 |
| 0.78125              | 0.39063              | 0.7158               | 1.0001 | 0.2960               | 1.0390 |
| 0.39063              | 0.19531              | 0.3579               | 1.0000 | 0.1460               | 1.0195 |
| $\Delta t$           | $\Delta x$           | $M(t)$               |        |                      |        |
|                      |                      | Max Error            | Order  |                      |        |
| ( $\times 10^{-3}$ ) | ( $\times 10^{-3}$ ) | ( $\times 10^{-4}$ ) |        |                      |        |
| 6.25                 | 3.125                | 1.6791               |        |                      |        |
| 3.125                | 1.5625               | 0.8396               | 1.0000 |                      |        |
| 1.5625               | 0.78125              | 0.4198               | 1.0000 |                      |        |
| 0.78125              | 0.39063              | 0.2099               | 1.0000 |                      |        |
| 0.39063              | 0.19531              | 0.1049               | 1.0000 |                      |        |

use model parameters and auxiliary functions as displayed in Table 4. These were chosen in accordance with those used in [9], the focus of which, we reiterate, was primarily to study the Mm-medaka animal model, and produce biologically reasonable solutions for that scenario. There was no birth rate, however, in the solutions considered in [9] since the goal in that work was to achieve agreement with biological experiments, which were on a much shorter timescale (2–3 weeks). We continue to consider only one physiological class  $m = 1$  here. We note that the initial condition for the susceptible fish does not satisfy the boundary compatibility condition,

and therefore one does not expect solutions to be smooth; in fact a discontinuity is evident along the characteristic curve starting at the point  $(0, x_{\min})$ . Yet, the first order accuracy is still conserved, as can be seen in Table 5.

TABLE 4. Parameter values and forms of the rate functions for the full (nonlinear) model. Initial conditions are  $S(0, x) = \exp(-(5x - 2)^2)$ ,  $I(0, x) = 0$ ,  $B_a(0) = 1 \times 10^4$ ,  $B_u(0) = 1 \times 10^4$ , and  $M(0) = 1 \times 10^4$ .

| Parameter      | Value                  | Parameter             | Value                  |
|----------------|------------------------|-----------------------|------------------------|
| $\nu_1$        | $0.125 \times 10^{-4}$ | $\nu_2$               | $0.125 \times 10^{-4}$ |
| $\nu_3$        | $2.5 \times 10^{-5}$   | $\nu_4$               | $2.5 \times 10^{-5}$   |
| $\delta_1$     | 1/500                  | $\delta_2$            | 1/500                  |
| $\zeta$        | $2.4 \times 10^3$      | $\epsilon$            | 0.05                   |
| $c_M$          | 0.5                    | $M^*$                 | $2 \times 10^{30}$     |
| $\mu_M$        | 7/60                   | $\lambda$             | 2.0                    |
| $\bar{\rho}^i$ | $3 \times 10^4$        |                       |                        |
| Function       | Form                   | Function              | Form                   |
| $g(P, x)$      | $(x - 1) \ln(0.34)/13$ | $\tilde{g}(P, x)$     | $(x - 1) \ln(0.34)/26$ |
| $\mu(P, x)$    | 1/156                  | $\tilde{\mu}(P, x)$   | 2/156                  |
| $\beta(P, x)$  | $2x$                   | $\tilde{\beta}(P, x)$ | $x$                    |
| $c_1^i(x)$     | 0.5                    | $\tilde{c}_1^i(x)$    | 0.5                    |
| $c_2^i(x)$     | 0.5                    | $\tilde{c}_2^i(x)$    | 0.5                    |

We again note that because of the clever choice of mixed explicit and implicit approximations, the scheme is stable without a CFL condition. This is corroborated by the results in Tables 3 and 5.

**6.3. Effects of different growth rates.** We turn our focus to the preliminary implications of the model presented in this work, and specifically, to the exploration of features that are distinct from the model in [9]. Therefore, we are particularly interested in the role of size in the model. Again, we use parameters that have given biologically reasonable solutions in [9] (where possible), and are relevant for the Mm-medaka animal model, although we remind the reader that the model applies to more general situations as well.

To study the role of size in the dynamics of the model, it is natural to turn to the growth functions, as these determine how the fish size changes with time. Simple variations in the magnitude of the growth (for example, scaling by a constant multiple) would not be necessarily instructive as the resulting dynamics would be merely accelerated or decelerated. Rather, the manner in which a fish grows is of interest to us, as there is variability in the growth cycles between species, and in many cases, their rate of growth or development is unknown. Additionally, the growth function of the medaka is measurable in an experimental setting. For this discussion, we neglect crowding, or dependence of the growth functions on population size. We choose three different growth functions, all of which are potentially reasonable biologically, although we impose the condition

$$\int_{x_{\min}}^{x_{\max}} g^1(s)ds = \int_{x_{\min}}^{x_{\max}} g^2(s)ds = \int_{x_{\min}}^{x_{\max}} g^3(s)ds,$$

TABLE 5. Convergence of the method for the full (nonlinear) model

| $\Delta t$ | $\Delta x$ | $S(7, x)$                      |        | $I(7, x)$                          |        |
|------------|------------|--------------------------------|--------|------------------------------------|--------|
|            |            | $L^1$ Error                    | Order  | $L^1$ Error                        | Order  |
| 0.05       | 0.05       | 0.0781                         |        | 0.4612                             |        |
| 0.025      | 0.025      | 0.0318                         | 1.2962 | 0.2852                             | 0.6935 |
| 0.0125     | 0.0125     | 0.0177                         | 0.8456 | 0.1873                             | 0.6063 |
| 0.00625    | 0.00625    | 0.0096                         | 0.8848 | 0.1132                             | 0.7270 |
| 0.00313    | 0.00313    | 0.0048                         | 1.0281 | 0.0588                             | 0.9450 |
| $\Delta t$ | $\Delta x$ | $B_a(t)$                       |        | $B_u(t)$                           |        |
|            |            | Max Error<br>( $\times 10^3$ ) | Order  | Max Error<br>( $\times 10^{-27}$ ) | Order  |
| 0.05       | 0.05       | 1.2654                         |        | 2.5309                             |        |
| 0.025      | 0.025      | 0.5796                         | 1.1264 | 1.1593                             | 1.1264 |
| 0.0125     | 0.0125     | 0.2711                         | 1.0963 | 0.5421                             | 1.0965 |
| 0.00625    | 0.00625    | 0.1247                         | 1.1205 | 0.2493                             | 1.1205 |
| 0.00313    | 0.00313    | 0.0534                         | 1.2244 | 0.1067                             | 1.2244 |
| $\Delta t$ | $\Delta x$ | $M(t)$                         |        |                                    |        |
|            |            | Max Error                      | Order  |                                    |        |
| 0.05       | 0.05       | 20.8145                        |        |                                    |        |
| 0.025      | 0.025      | 9.0261                         | 1.2054 |                                    |        |
| 0.0125     | 0.0125     | 4.1063                         | 1.1363 |                                    |        |
| 0.00625    | 0.00625    | 1.8831                         | 1.1247 |                                    |        |
| 0.00313    | 0.00313    | 0.8312                         | 1.1798 |                                    |        |

in an attempt to maintain the total growth on the same scale, for the sake of comparing results. The three growth functions chosen can be found in Figure 1. The first function,  $g^1(x) = \frac{\ln(0.34)}{13}(x-1)$ , is the simplest representation of the observation that smaller (hatchling and juvenile) fish likely grow at much faster rates than larger (adult) fish. We take a simple decreasing linear function, and we use the information that they are approximately 66% of their maximum size [27, 33, 34] at the time at which fish are able to reproduce. At that size, fish are usually around 13 weeks old, and we therefore use 13 weeks as the generation time throughout the remainder of the paper. The second function,  $g^2(x) = -0.2398(x+0.01)(x-1)$  is consistent with the first in that large fish grow very slowly. But, if we consider that very small fish may grow slowly also, with an optimal period of growth in the middle (or juvenile) period, then this parabolic form is more appropriate. The third function,  $g^3(x) = -0.0519(x-0.5)^{1/3} + 0.0412$  is a modification of the first function to incorporate the idea from ecology that animals have finite energy and resources. Therefore there is a drastic shift in energy and resource expenditures from growth to reproduction as animals reach sexual maturity. Therefore, many animals of various species notably grow much slower, if at all, upon reaching sexual maturation. To emulate something similar, this function was chosen so that the growth rate would be high for small sizes, decreasing only slightly. For the mid-range sizes, the growth rate drops drastically, and remains low for all larger sizes. We take the growth rate functions for the infected fish to be half that of their uninfected counterparts, so  $\tilde{g}^i(P, x) = \frac{1}{2}g^i(P, x)$  for  $i = 1, 2, 3$ . Parameter values

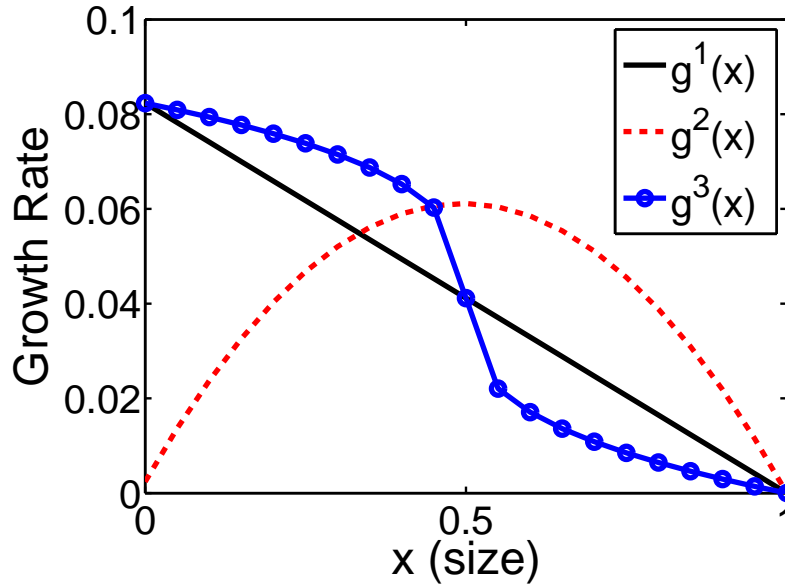


FIGURE 1. Growth rate functions for each class,  $i = 1, 2, 3$  as a function of size. These are:  $g^1(P, x) = \frac{\ln(0.34)}{13}(x - 1)$ ,  $g^2(P, x) = -0.2398(x + 0.01)(x - 1)$ ,  $g^3(P, x) = -0.0519(x - 0.5)^{1/3} + 0.0412$ .

and functions are the same as in Table 4 with the exception of the initial condition for susceptible fish  $S^{i,0}(x) = 10^6 \cdot \exp(-(5x - 2)^2)$ , for  $i = 1, 2, 3$ , and the fecundity kernels  $\beta(P, x) = \frac{bx}{1 + \nu P}$  and  $\tilde{\beta}(P, x) = \frac{1}{2}\beta(P, x)$  for the susceptible and infected fish, respectively. For the solutions shown in Figures 2 and 3,  $b = 5 \times 10^7$  and  $\nu = 5 \times 10^{-7}$ .

In Figure 2, we see the size distributions of each group after three generations ( $t \approx 39$  weeks). This gives us a sense of the size composition of each subpopulation (the proportion of the population that will be of the smaller, medium, larger, etc., sizes). Both strictly decreasing growth functions,  $g^1(x)$ ,  $g^3(x)$ , result in a relatively large proportion of the population being centered at large sizes ( $x \approx 0.6$  and  $x \approx 0.9$ , respectively). In both of these cases, the fish experience very low growth rates around these sizes, so it is reasonable that they grow past the smaller sizes quickly and do not progress past these larger sizes rapidly. Further, the sharp decrease in growth rate around  $x = 0.5$  in  $g^3(x)$ , as opposed to the linearly decreasing  $g^1(x)$ , results in the sharper peak of that size distribution in both the susceptible and infected populations. Also, it agrees with our intuition that the peak observed in the first subpopulation  $i = 1$  occurs at a larger size than that of the third subpopulation, since that group grows at a faster rate for larger sizes  $x > 0.5$ . The infected population of the third group appears to follow the same trend, in that there is a concentration of individuals around a large size as the growth rate decreases to very small values. Similar behavior is not obvious in the susceptible population of the second group; however, the (hatchling) fish at the boundary grow from there very slowly, and thus, a comparatively large concentration is evident at

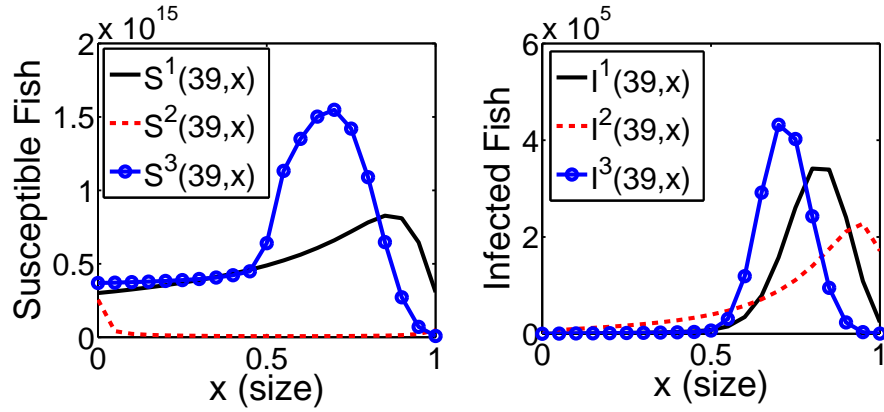


FIGURE 2. The densities of susceptible and infected fish as a function of size after 3 generations ( $t = 39$ ) using the growth functions shown in Figure 1.

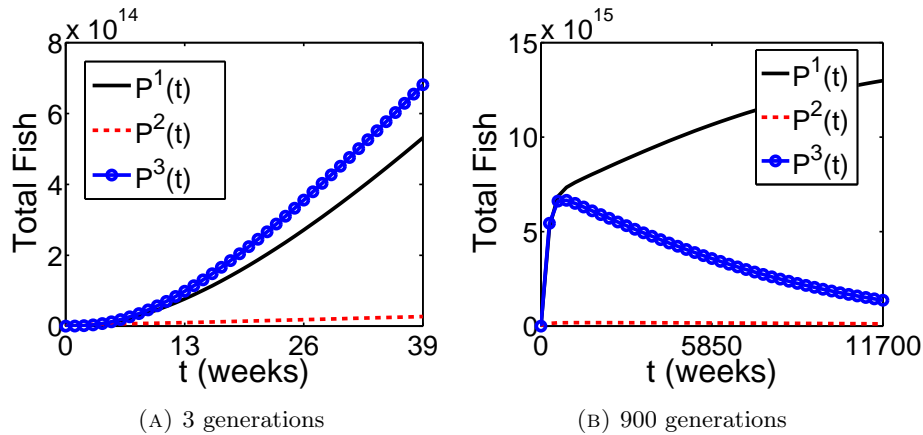


FIGURE 3. The total population size for each class where each class grows according to the growth functions shown in Figure 1 over a (a) shorter and (b) longer time interval.

the smallest size  $x_{\min} = 0$ . While these plots show the overall size composition of the subpopulations under the growth functions  $g^1(x)$ ,  $g^2(x)$ ,  $g^3(x)$ , we cannot, however, deduce which of these result in larger or smaller population sizes for each subpopulation. That is, we cannot immediately discern whether the subpopulation will flourish or languish under each growth scenario.

From the solutions shown in Figure 3, we see the differences in population sizes of each subgroup resulting from the different growth functions. We stress that the initial condition for each subgroup is the same, and also that they gave rise to progeny of the same subgroup. Therefore, any differences observed are simply due to the differences in growth and consequently, any subsequent effects of growth-dependent dynamics in this model. It appears that the third growth function  $g^3(x)$

gives that subgroup a slight advantage over the first subgroup (linearly decreasing growth rate  $g^1(x)$ ) after only three generations, as suggested by the trajectories in Figure 3a. Interestingly, we see that after an initial period (shown in Figure 3b), the first subgroup's population size actually increases substantially more than the third. During this first period in which the third group's population size is bigger, more of this subpopulation is at larger sizes (and hence reproducing faster), and fewer at smaller sizes as compared with the first group. This is due to  $g^3(x) > g^1(x)$  for small  $x$ , thereby growing faster to larger sizes. However, individuals in the first subpopulation overall grow faster (as can be seen by comparison of the two groups' peaks in Figure 2), and eventually, after several generations, this effect makes up for the differences in the size composition of the two populations in the earlier times. The second subgroup's population size is markedly lower as these individuals spend a substantially longer time at the lower sizes, and thus, the slower reproducing sizes.

**6.4. Spread of Genetic heterogeneity.** Another key feature of our model, that we explore here, is the ability to study reproductive fitness, and genetic spread throughout several generations. From the principal of competitive exclusion, we anticipate that when all other rates and parameters amongst the  $m$  classes are equal, that eventually, the only type remaining will be that which reproduces the most during its lifetime. For this model, there are competitive or crowding effects in the form of the birth rate, and limitless growth is not possible. Generally a physiological class would have a reproductive advantage if the largest proportion of progeny from each generation of any type is of that type. That is, if  $q^i$  for  $i = 1, \dots, m$  represents the proportion of the total new fish of type  $i$  for a fixed generation, then the subtype with the reproductive advantage is that with the largest  $q^i$ . If the growth rates are fixed, then this is determined by the fecundity kernels, and the selection-mutation matrix  $p$ .

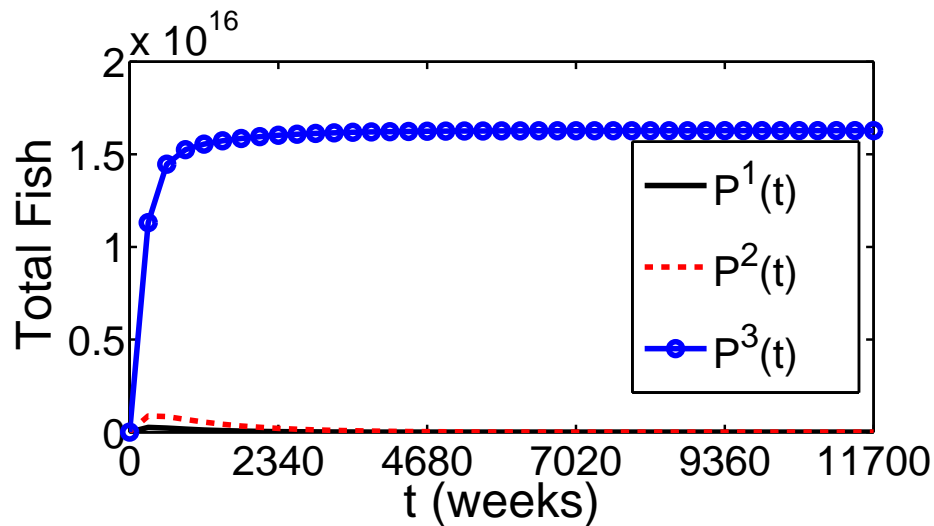


FIGURE 4. Competitive exclusion between classes with different birth rates.

In this section, all parameters and functions are equal within the three classes by using  $g^1(x)$  for the growth rate (as in Section 6.3) and the values and functions in Table 4. As in Section 6.3, we are using the modified initial condition,  $S^{i,0}(x) = 10^6 \cdot \exp(-(5x - 2)^2)$ , for  $i = 1, 2, 3$ . To study the effect of changes in values of parameter in the fecundity kernel, we choose

$$\beta^i(P, x) = \frac{b^i x}{1 + \nu P}, \quad \text{where } b^i = 5 \times 10^7, 5.3 \times 10^7, 5.6 \times 10^7 \quad \text{and } \nu = 5 \times 10^{-7}. \quad (27)$$

For this example, we use the identity matrix for  $p$ , so all progeny is of the same type as the progenitor to remove any genetic spread; each adult fish gives rise to individuals of the same type. With these values, the third class reproduces at the fastest rate, and therefore enjoys an advantage over the other two classes. The first class is the slowest to reproduce. The total population sizes of all three classes over 900 generations ( $t = 11,700$ ) are shown in Figure 4. As expected, the first physiological class is able to reproduce much faster, achieving and maintaining a high population size, while the other two classes go extinct. The second class is slower to go extinct than the first. So, not surprisingly, in the absence of genetic spread, the reproductive fitness of the individuals belonging to a physiological class is determined entirely by the birth rate. Thus, the principle of competitive exclusion holds, and the only surviving class is that with the highest birth rate.

If genetic spread occurs, or in other words, if a proportion of a fish's clutch (batches of eggs) are eggs of different type(s), then reproductive fitness of one subtype cannot be determined by birth rate alone. Further, it may be possible for this effect to counteract the dominant birth rate of one subgroup, which would otherwise result in that subgroup being the only one remaining, as seen in Figure 4. To examine the extent to which this spread, or mutation, may affect the simultaneous persistence of each type, we consider model solutions with different choices of the matrix  $p$ . In some instances, genetic spread may actually be the probability of mutations (although not exclusively so), and therefore, may be relatively rare. Therefore, the off-diagonal elements of the matrices considered here are small in comparison to the diagonal elements. The first three  $p$  matrices considered are reducible and the fourth one  $p$  is irreducible; these are given by

$$p_1 = \begin{bmatrix} 0.90 & 0.00 & 0.00 \\ 0.05 & 0.90 & 0.00 \\ 0.05 & 0.10 & 1.00 \end{bmatrix} \quad p_2 = \begin{bmatrix} 1.00 & 0.15 & 0.10 \\ 0.00 & 0.85 & 0.10 \\ 0.00 & 0.00 & 0.80 \end{bmatrix} \quad (28)$$

$$p_3 = \begin{bmatrix} 1.00 & 0.15 & 0.02 \\ 0.00 & 0.85 & 0.02 \\ 0.00 & 0.00 & 0.96 \end{bmatrix} \quad p_4 = \begin{bmatrix} 0.70 & 0.10 & 0.10 \\ 0.25 & 0.70 & 0.20 \\ 0.05 & 0.20 & 0.70 \end{bmatrix}.$$

We note that:

- By the first choice  $p_1$ , the offspring of individuals in the third class (with the largest birth rate) belong to that class only (pure selection). However, individuals in the second class can produce individuals of the second and third types, and individuals of the first type give rise to individuals of all three types.
- By the second choice  $p_2$ , the individuals in the third class with the highest birth rate produce individuals that belong to all three classes. Individuals in the second class give rise to individuals in the first (lowest birth rate) and



second classes. Individuals in class 1 produce individuals within their class only (pure selection for this class).

- The matrix  $p_3$  is similar to  $p_2$  but with reduced mutation rates for the third class, i.e., the fraction of offspring from individuals in class 3 being of the other two classes, is smaller in this case; the genetic spread of class 3 is less.
- The matrix  $p_4$  is irreducible, with all fish able to produce individuals belonging to any of the three classes, but with most progeny belonging to the same class as the progenitor.

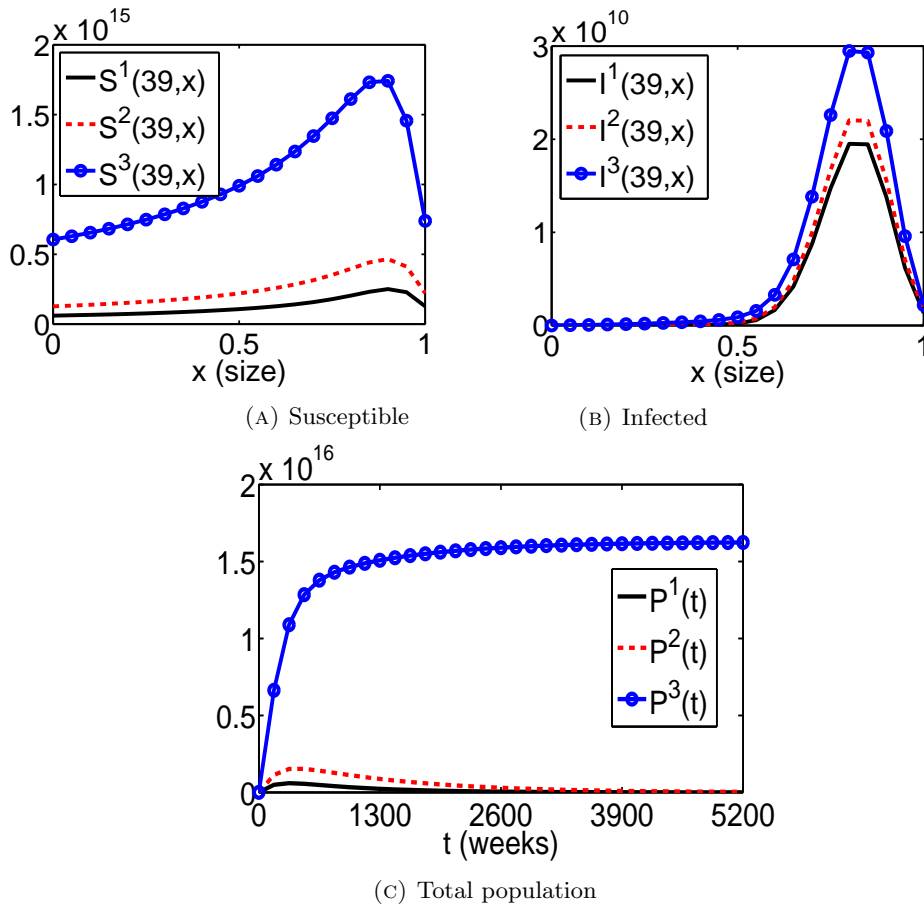


FIGURE 5. The susceptible (a) and infected fish (b) in each subgroup at  $t = 39$  (three generations), and the long term behavior of the subgroup total population (c) sizes with birth rates as in equation (27) and with the selection-mutation matrix  $p_1$  as in equation (28).

In Figure 5, we have the model solutions with  $p_1$  as the matrix  $p$ . Being that the third class, with the highest birth rate only produces progeny of its own kind, it is not surprising that the mutations, or genetic spread allowed between the first and second classes, with lower birth rates, are not able to compete effectively and go extinct. The model solutions using  $p_2$ , shown in Figure 6 in which the slowest

reproducing class (the first class) not only does not produce offspring of other types, but its population growth is enhanced by fish of the other types begetting fish of this type, albeit at lower rates. So, this is a clear case in which genetic spread can counteract the reproductive disadvantage of a low birth rate.

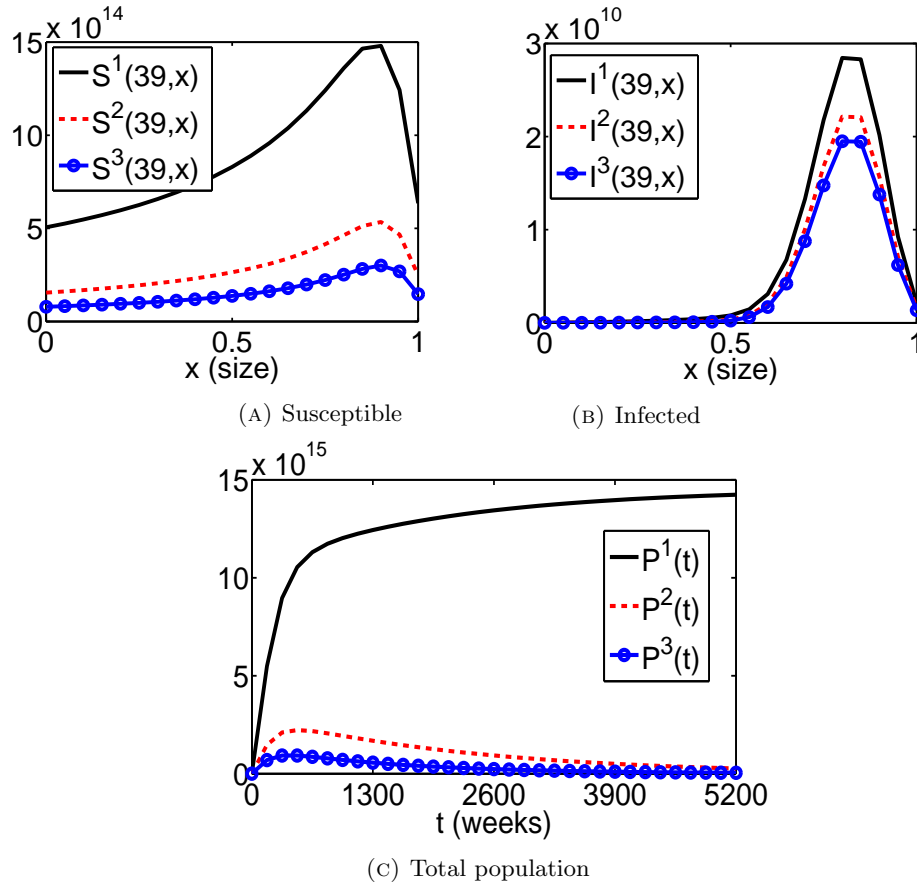


FIGURE 6. The susceptible (a) and infected fish (b) in each subgroup at  $t = 39$  (three generations), and the long term behavior of the subgroup total population (c) sizes with birth rates as in equation (27) and with the selection-mutation matrix  $p_2$  as in equation (28).

In Figure 7, we see the model solutions with  $p_3$ , which is only different from  $p_2$  in that there is less mutation by the fastest reproducing class. Here, class three again enjoys a reproductive advantage, as its genetic spread is less. This suggests that the determining factor of the first class' competitive advantage in Figure 6 was that the third class was disadvantaged, by allowing a higher proportion of its offspring than in  $p_3$  to be of the other classes. Thus, there appears to be a delicate balance between birth rate and genetic spread in determining reproductive fitness between the three subgroups.

While we see examples of competitive exclusion in Figures 5 – 7, we see coexistence of all three subgroups in Figure 8c with the use of  $p_4$  for the selection-mutation

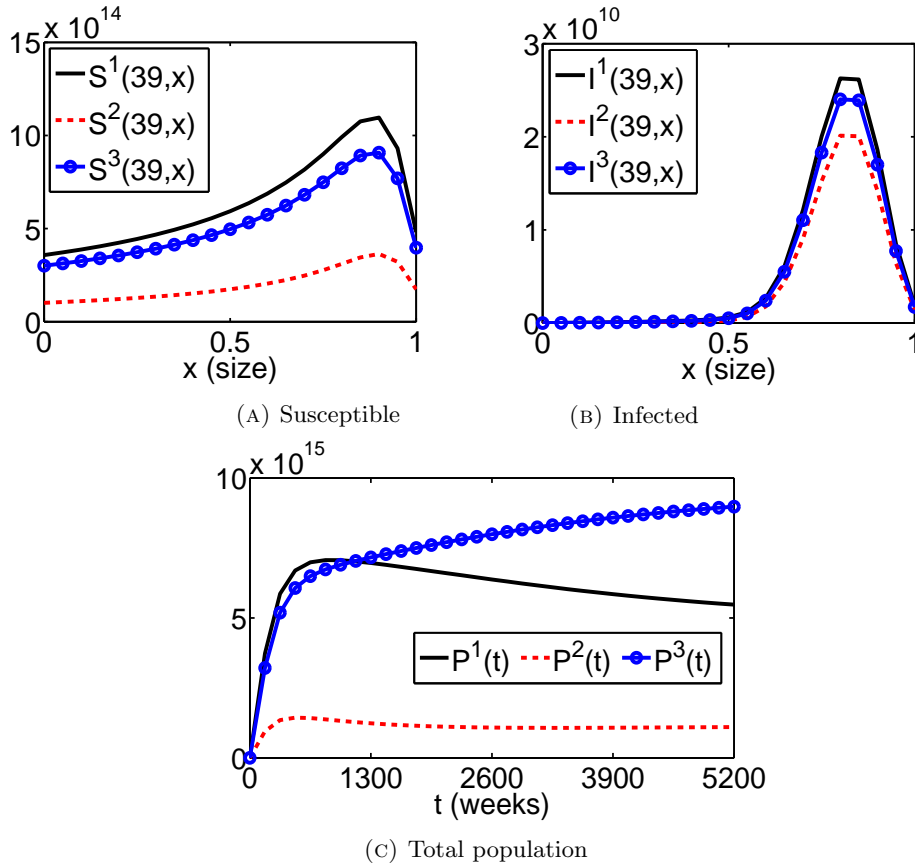


FIGURE 7. The susceptible (a) and infected fish (b) in each subgroup at  $t = 39$  (three generations), and the long term behavior of the subgroup total population (c) sizes with birth rates as in equation (27) and with the selection-mutation matrix  $p_3$  as in equation (28).

matrix. This is the only irreducible, and indeed the only positive matrix  $p$  considered. In this case, the extinction of any of the three subgroups is not a possibility, since the survival of either of the other two classes would result in new offspring of all the subgroups. Of the scenarios considered here, this matrix is the only one that does not involve pure selection of any of the three classes, and indeed, is the scenario in which genetic spread occurs to the greatest extent. This suggests that genetic spread can result in a situation in which the competitive exclusion principle does not hold, and can diminish reproductive advantages that would otherwise benefit fish of faster reproducing classes.

Note that the infection dynamics do not appear to play a key role here, as the susceptible populations at  $t = 39$  (Figures 5a, 6a, 7a, and 8a), and the infected populations (Figures 5b, 6b, 7b, and 8b) are qualitatively similar, with the only differences being the relative size of each subpopulation, which is likely simply due to the reproduction scenarios considered in each case. We would expect this to change if there are other differences between the subgroups' parameter values, such

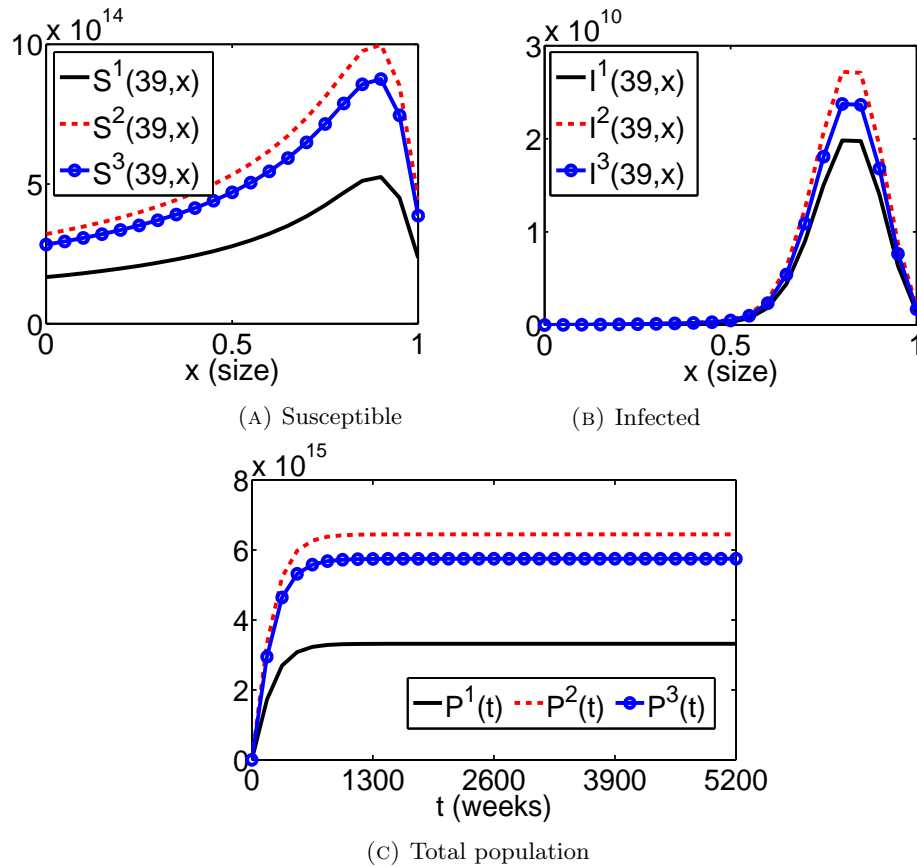


FIGURE 8. The susceptible (a) and infected fish (b) in each subgroup at  $t = 39$  (three generations), and the long term behavior of the subgroup total population (c) sizes with birth rates as in equation (27) and with the selection-mutation matrix  $p_4$  as in equation (28).

as those governing the Mm transmission, feeding behavior, etc. However, that is not the case in the examples presented here.

**7. Conclusion.** We developed a first attempt at a size-structured mathematical model to describe the spread of *Mycobacterium marinum* between aquatic animals. Our model consists of  $2m$  partial differential equations and three ordinary differential equations with nonlinear parameter functions, initial conditions, and boundary conditions. The scheme is designed as implicit, but can be solved explicitly in the order presented in (15)–(20) and is therefore numerically efficient. Convergence of the numerical approximation to the weak solution with bounded total variation was presented in Section 5. In Section 6 we demonstrated the convergence as time and mesh sizes decrease. We also illustrated some of the key features of the model that distinguish it from others. We explored the size composition under different forms of the growth function, and also the implications of that size composition on the population size of each physiological subgroup. Additionally, we explored questions

of reproductive fitness and genetic spread throughout generations and determined conditions under which the competitive exclusion principle would hold. Also, in this model, the reproductive advantage afforded one subpopulation via a high birth rate can be counteracted by sufficient permutation probability. We demonstrated that coexistence is possible when the permutation-selection matrix is irreducible, which amounts to each subpopulation eventually producing offspring of all other subpopulation types, so that long-term extinction of any subpopulation is not possible.

As the model developed here is complex, as a first attempt, we resorted to a first-order finite difference scheme. In the future, we plan to develop second-order high-resolution minmod based MUSCL schemes [23, 38]. Establishing convergence of such schemes will require significantly more complicated analysis because of the nonlocal nonlinearities and quadratic nonlinearities in the model (1). Future work will also include the design of higher order WENO schemes (e.g., see [39, 46] for fifth-order schemes) with suitable treatment for the boundary conditions and the quadratic terms modeling the disease transmission. Establishing stability (let alone convergence) results for such WENO schemes is in general very difficult. In fact, within the framework of size-structured models we only know of the result in [46], where the authors proved that the finite-volume scheme they developed is positivity-preserving and  $L^1$  stable.

**Appendix A. Proofs.**

**A.1. Proof of Lemma 5.1.** Uniqueness is obvious from (15)–(20). Note that  $S^{i,0}, I^{i,0}, B_a^0, B_u^0, M^0$  are nonnegative by assumption (A5). Now assume for some  $k > 0, S_j^{i,k}, I_j^{i,k} \geq 0$  for  $i = 1, \dots, m, j = 1, \dots, N$  and  $B_a^k, B_u^k, M^k \geq 0$ . By assumption (A3) and by (15) we have that  $S_0^{i,k+1} \geq 0$  and  $I_0^{i,k+1} = 0$ . Then it is clear from (16) and (17) that  $S_j^{i,k+1}, I_j^{i,k+1} \geq 0$  for  $j = 1, \dots, N$ , which ensures  $B_a^{k+1}, B_u^{k+1}, M^{k+1} \geq 0$ . This establishes the result.  $\square$

**A.2. Proof of Lemma 5.2.** By multiplying (9) by  $\Delta x \Delta t$ , summing over  $j = 1, \dots, N$  and  $i = 1, \dots, m$ , we have

$$\begin{aligned} \sum_{i=1}^m \sum_{j=1}^N (S_j^{i,k+1} - S_j^{i,k}) \Delta x + \Delta t \sum_{i=1}^m \sum_{j=1}^N (g_j^{i,k} S_j^{i,k+1} - g_{j-1}^{i,k} S_{j-1}^{i,k+1}) \\ + \sum_{i=1}^m \sum_{j=1}^N \mu_j^{i,k} S_j^{i,k+1} \Delta x \Delta t + \sum_{i=1}^m \sum_{j=1}^N L_j^{i,k} S_j^{i,k+1} \Delta x \Delta t = 0. \end{aligned}$$

Collapsing the telescoping sequence, incorporating the boundary condition from (14), and using the facts that  $g_N^{i,k} = 0$ , and  $\sum_{i=1}^m p^{i\ell} = 1$  we arrive at

$$\begin{aligned} \sum_{i=1}^m \sum_{j=1}^N S_j^{i,k+1} \Delta x \\ = \sum_{i=1}^m \sum_{j=1}^N S_j^{i,k} \Delta x + \Delta t \sum_{\ell=1}^m \sum_{j=1}^N \left[ \beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k} \right] \Delta x \end{aligned}$$

$$- \sum_{i=1}^m \sum_{j=1}^N (\mu_j^{i,k} + L_j^{i,k}) S_j^{i,k+1} \Delta x \Delta t.$$

Then by using (A2) and (A3), we determine

$$\begin{aligned} \sum_{i=1}^m \|S^{i,k+1}\|_1 &\leq \sum_{i=1}^m \|S^{i,k}\|_1 + c\Delta t \sum_{i=1}^m (\|S^{i,k}\|_1 + \|I^{i,k}\|_1) \\ &\quad - \sum_{i=1}^m \sum_{j=1}^N L_j^{i,k} S_j^{i,k+1} \Delta x \Delta t. \end{aligned} \quad (29)$$

Following similar arguments to those we used above for  $S_j^{i,+k+1}$  we have

$$\sum_{i=1}^m \|I^{i,k+1}\|_1 \leq \sum_{i=1}^m \|I^{i,k}\|_1 + \sum_{i=1}^m \sum_{j=1}^N L_j^{i,k} S_j^{i,k+1} \Delta x \Delta t. \quad (30)$$

Adding (29) and (30) we have

$$\begin{aligned} \sum_{i=1}^m (\|S^{i,k+1}\|_1 + \|I^{i,k+1}\|_1) &\leq (1 + c\Delta t) \sum_{i=1}^m (\|S^{i,k}\|_1 + \|I^{i,k}\|_1) \\ &\leq e^{cT} \sum_{i=1}^m (\|S^{i,0}\|_1 + \|I^{i,0}\|_1) \end{aligned}$$

and the result follows.  $\square$

**A.3. Proof of Lemma 5.3.** From equation (18), we determine

$$\begin{aligned} |B_a^{k+1}| &\leq \left| B_a^k + \Delta t \sum_{i=1}^m \sum_{j=1}^N \rho_j^i I_j^{i,k+1} \Delta x \right| \\ &\leq |B_a^k| + c\Delta t \sum_{i=1}^m \|I^{i,k+1}\|_1 \\ &\leq |B_a^k| + c\Delta t C_1 \\ &\leq |B_a^0| + c(k+1)\Delta t C_1. \end{aligned}$$

Then,

$$\begin{aligned} |B_a^k| &\leq |B_a^0| + cK\Delta t C_1 \\ &\leq |B_a^0| + cTC_1 \equiv C_{2,B_a}. \end{aligned}$$

Treating (19) similarly, we have

$$|B_u^{k+1}| \leq |B_u^0| + cT(1 + C_{2,B_a}) \equiv C_{2,B_u}.$$

Now, treating (20) similarly we have

$$|M^{k+1}| \leq |M^0| + c^3TC_{2,B_u} \equiv C_{2,M}.$$

Thus, letting  $C_2 = C_{2,B_a} + C_{2,B_u} + C_{2,M}$  we have our result.  $\square$

**A.4. Proof of Lemma 5.4.** Clearly,  $L_j^{i,k} \geq 0$ . Considering (8) and using (A4), (A7), and Lemma 5.3, we have

$$\begin{aligned} L_j^{i,k} &= \nu_1 \delta_1 B_u^k + \nu_2 \delta_2 B_a^k + \nu_3 \zeta c_{2,j}^i M^k + \nu_4 c_{1,j}^i B_u^k \\ &\leq 2c^2 B_u^k + c^2 B_a^k + c^3 M^k \\ &\leq (3c^2 + c^3)C_2 \equiv C_3. \end{aligned}$$

Using (A4), (A7), and Lemma 5.3, we obtain

$$\begin{aligned} |D_{\Delta x}^-(L_j^{i,k})| &= \left| \frac{L_j^{i,k} - L_{j-1}^{i,k}}{\Delta x} \right| \\ &\leq \left| c^2 M^k \left( \frac{c_{2,j}^i - c_{2,j-1}^i}{\Delta x} \right) + c B_u^k \left( \frac{c_{1,j}^i - c_{1,j-1}^i}{\Delta x} \right) \right| \\ &\leq c^3 C_2 + c^2 C_2 \equiv C_4. \end{aligned}$$

□

**A.5. Proof of Lemma 5.5.** If  $S_0^{i,k+1} = \|S^{i,k+1}\|_\infty$ , then from the boundary condition (15), the assumption (A3), and using the fact that  $p^{i\ell} \leq 1$ , we have

$$S_0^{i,k+1} \leq \frac{c}{g_0^{i,k}} \sum_{\ell=1}^m \sum_{j=1}^N [S_j^{\ell,k} + I_j^{\ell,k}] \Delta x.$$

Since  $0 \leq P^k \leq C_1$  for  $k = 0, \dots, K$ , we let  $\alpha \leq \min g^i(P, x_0)$  for  $P \in [0, C_1]$  and  $1 \leq i \leq m$ . Then

$$S_0^{i,k+1} \leq \frac{c}{\alpha} \sum_{\ell=1}^m [\|S^{\ell,k}\|_1 + \|I^{\ell,k}\|_1].$$

Using Lemma 5.2 we get

$$\|S^{i,k+1}\|_\infty \leq \frac{c}{\alpha} C_1.$$

If  $\|S^{i,k+1}\|_\infty$  is not obtained from the boundary, then there exists an integer,  $j_0$ ,  $1 \leq j_0 \leq N$  such that

$$S_{j_0}^{i,k+1} = \|S^{i,k+1}\|_\infty.$$

From (9) we have

$$\frac{S_{j_0}^{i,k+1} - S_{j_0}^{i,k}}{\Delta t} + \frac{g_{j_0}^{i,k} S_{j_0}^{i,k+1} - g_{j_0-1}^{i,k} S_{j_0-1}^{i,k+1}}{\Delta x} + \mu_{j_0}^{i,k} S_{j_0}^{i,k+1} + L_{j_0}^{i,k} S_{j_0}^{i,k+1} = 0.$$

Multiplying by  $\Delta t$ , combining like terms, and using the fact that  $S_{j_0-1}^{i,k+1} \leq S_{j_0}^{i,k+1}$  we obtain

$$S_{j_0}^{i,k+1} (1 + \Delta t \mu_{j_0}^{i,k} + \Delta t L_{j_0}^{i,k}) + \Delta t \frac{g_{j_0}^{i,k} - g_{j_0-1}^{i,k}}{\Delta x} S_{j_0}^{i,k+1} \leq S_{j_0}^{i,k}.$$

By (A1), (A2) and Lemma 5.4,

$$(1 - c\Delta t) \|S^{i,k+1}\|_\infty \leq \left( 1 + \Delta t \mu_{j_0}^{i,k} + \Delta t L_{j_0}^{i,k} + \Delta t \frac{g_{j_0}^{i,k} - g_{j_0-1}^{i,k}}{\Delta x} \right) \|S^{i,k+1}\|_\infty \leq \|S^{i,k}\|_\infty.$$

Thus,

$$\begin{aligned} \|S^{i,k+1}\|_\infty &\leq \left( \frac{1}{1 - c\Delta t} \right) \|S^{i,k}\|_\infty \\ &\leq \left( \frac{1}{1 - c\Delta t} \right)^{k+1} \|S^{i,0}\|_\infty. \end{aligned}$$

So we obtain

$$\|S^{i,k+1}\|_\infty \leq \max \left\{ \frac{c}{\alpha} C_1 \left( \frac{1}{1 - c\Delta t} \right)^k, \left( \frac{1}{1 - c\Delta t} \right)^{k+1} \|S^{i,0}\|_\infty \right\} < C_{5,S}.$$

If  $\|I^{i,k+1}\|_\infty$  is obtained at the left boundary, then  $\|I^{i,k+1}\|_\infty = 0$ . Thus, using arguments similar to those made above, we have

$$\|I^{i,k+1}\|_\infty \leq \left(\frac{1}{1-c\Delta t}\right)^{k+1} \|I^{i,0}\|_\infty + \sum_{l=1}^{k+1} \left(\frac{1}{1-c\Delta t}\right)^{k+1-l} \Delta t C_3 C_{5,S} < C_{5,I}.$$

Letting  $C_5 = C_{5,S} + C_{5,I}$  we obtain the result.  $\square$

**A.6. Proof of Lemma 5.6.** From the definition of  $P(t)$  we arrive at

$$\frac{P^{k+1} - P^k}{\Delta t} = \sum_{i=1}^m \sum_{j=1}^N \frac{S_j^{i,k+1} - S_j^{i,k}}{\Delta t} \Delta x + \sum_{i=1}^m \sum_{j=1}^N \frac{I_j^{i,k+1} - I_j^{i,k}}{\Delta t} \Delta x.$$

Incorporating (9) and (10) into the above, then collapsing the telescoping sums we acquire

$$\begin{aligned} \frac{P^{k+1} - P^k}{\Delta t} = \sum_{i=1}^m & \left[ g_0^{i,k} S_0^{i,k+1} - g_N^{i,k} S_N^{i,k+1} - \sum_{j=1}^N \mu_j^{i,k} S_j^{i,k+1} \Delta x \right. \\ & \left. + \tilde{g}_0^{i,k} I_0^{i,k+1} - \tilde{g}_N^{i,k} I_N^{i,k+1} - \sum_{j=1}^N \tilde{\mu}_j^{i,k} I_j^{i,k+1} \Delta x \right]. \end{aligned}$$

Since  $g_N^{i,k}, \tilde{g}_N^{i,k}, I_0^{i,k+1} = 0$  we obtain

$$\frac{P^{k+1} - P^k}{\Delta t} = \sum_{i=1}^m \left[ g_0^{i,k} S_0^{i,k+1} - \sum_{j=1}^N \mu_j^{i,k} S_j^{i,k+1} \Delta x - \sum_{j=1}^N \tilde{\mu}_j^{i,k} I_j^{i,k+1} \Delta x \right].$$

Incorporating the boundary condition (14) into the above we have

$$\begin{aligned} \frac{P^{k+1} - P^k}{\Delta t} &= \sum_{i=1}^m \left[ \sum_{\ell=1}^m p^{i\ell} \sum_{j=1}^N [\beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k}] \Delta x - \sum_{j=1}^N \mu_j^{i,k} S_j^{i,k+1} \Delta x \right. \\ & \quad \left. - \sum_{j=1}^N \tilde{\mu}_j^{i,k} I_j^{i,k+1} \Delta x \right] \\ \frac{P^{k+1} - P^k}{\Delta t} &= \sum_{\ell=1}^m \sum_{j=1}^N [\beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k}] \Delta x - \sum_{i=1}^m \sum_{j=1}^N \mu_j^{i,k} S_j^{i,k+1} \Delta x \\ & \quad - \sum_{i=1}^m \sum_{j=1}^N \tilde{\mu}_j^{i,k} I_j^{i,k+1} \Delta x. \end{aligned}$$

Thus, applying absolute value, and using (A2), (A3), and Lemma 5.2 we have

$$\left| \frac{P^{k+1} - P^k}{\Delta t} \right| \leq 2cC_1.$$

$\square$



A.7. **Proof of Lemma 5.7.** Observe that

$$\frac{g_0^{i,k} S_0^{i,k+1} - g_0^{i,k-1} S_0^{i,k}}{\Delta t} = g_0^{i,k} \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} + \frac{g_0^{i,k} - g_0^{i,k-1}}{\Delta t} S_0^{i,k}.$$

Incorporating the boundary condition (14) into the left-hand side of the above equation, we have

$$\begin{aligned} & g_0^{i,k} \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} + \frac{g_0^{i,k} - g_0^{i,k-1}}{\Delta t} S_0^{i,k} \\ &= \sum_{\ell=1}^m p^{i\ell} \sum_{j=1}^N \left[ \beta_j^{\ell,k} \frac{S_j^{\ell,k} - S_j^{\ell,k-1}}{\Delta t} + \frac{\beta_j^{\ell,k} - \beta_j^{\ell,k-1}}{\Delta t} S_j^{\ell,k-1} \right. \\ & \quad \left. + \tilde{\beta}_j^{\ell,k} \frac{I_j^{\ell,k} - I_j^{\ell,k-1}}{\Delta t} + \frac{\tilde{\beta}_j^{\ell,k} - \tilde{\beta}_j^{\ell,k-1}}{\Delta t} I_j^{\ell,k-1} \right] \Delta x. \end{aligned}$$

Using (9), (10) and the mean value theorem, we obtain

$$\begin{aligned} & g_0^{i,k} \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} + \frac{g_0^{i,k} - g_0^{i,k-1}}{\Delta t} S_0^{i,k} \\ &= \sum_{\ell=1}^m p^{i\ell} \sum_{j=1}^N \left[ -\beta_j^{\ell,k} \left( D_{\Delta x}^- (g_j^{\ell,k-1} S_j^{\ell,k}) + \mu_j^{\ell,k-1} S_j^{\ell,k} + L_j^{\ell,k-1} S_j^{\ell,k} \right) \right. \\ & \quad \left. + \beta_P^\ell(\bar{P}_1, x_j) \frac{P^k - P^{k-1}}{\Delta t} S_j^{\ell,k-1} + \tilde{\beta}_P^\ell(\bar{P}_2, x_j) \frac{P^k - P^{k-1}}{\Delta t} I_j^{\ell,k-1} \right] \Delta x \\ & \quad - \tilde{\beta}_j^{\ell,k} \left( D_{\Delta x}^- (\tilde{g}_j^{\ell,k-1} I_j^{\ell,k}) + \tilde{\mu}_j^{\ell,k-1} I_j^{\ell,k} - L_j^{\ell,k-1} S_j^{\ell,k} \right). \end{aligned}$$

where  $\bar{P}_1$  and  $\bar{P}_2$  are values (dependent on  $\ell$ ) between  $P^k$  and  $P^{k-1}$ .

Summing from  $i = 1, \dots, m$  then applying absolute value we have

$$\begin{aligned} & \left| \sum_{i=1}^m \left[ g_0^{i,k} \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} + \frac{g_0^{i,k} - g_0^{i,k-1}}{\Delta t} S_0^{i,k} \right] \right| \\ & \leq \left| \sum_{\ell=1}^m \sum_{j=1}^N \beta_j^{\ell,k} D_{\Delta x}^- (g_j^{\ell,k-1} S_j^{\ell,k}) \right| \Delta x + \left| \sum_{\ell=1}^m \sum_{j=1}^N \tilde{\beta}_j^{\ell,k} D_{\Delta x}^- (\tilde{g}_j^{\ell,k-1} I_j^{\ell,k}) \right| \Delta x \\ & \quad + \left| \sum_{\ell=1}^m \sum_{j=1}^N \left\{ \beta_j^{\ell,k} \left[ \mu_j^{\ell,k-1} S_j^{\ell,k} + L_j^{\ell,k-1} S_j^{\ell,k} \right] + \beta_P^\ell(\bar{P}_1, x_j) \frac{P^k - P^{k-1}}{\Delta t} S_j^{\ell,k-1} \right\} \right| \Delta x \\ & \quad + \left| \sum_{\ell=1}^m \sum_{j=1}^N \left\{ \tilde{\beta}_j^{\ell,k} \left[ \tilde{\mu}_j^{\ell,k-1} I_j^{\ell,k} - L_j^{\ell,k-1} S_j^{\ell,k} \right] + \tilde{\beta}_P^\ell(\bar{P}_2, x_j) \frac{P^k - P^{k-1}}{\Delta t} I_j^{\ell,k-1} \right\} \right| \Delta x. \end{aligned}$$

Using summation by parts and the facts that  $g_N^{i,k}, \tilde{g}_N^{i,k}, I_0^{\ell,k} = 0$  we obtain

$$\begin{aligned}
& \left| \sum_{i=1}^m \left[ g_0^{i,k} \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} + \frac{g_0^{i,k} - g_0^{i,k-1}}{\Delta t} S_0^{i,k} \right] \right| \\
& \leq \sum_{\ell=1}^m \left| \beta_0^{\ell,k} g_0^{\ell,k-1} S_0^{\ell,k} \right| + \sum_{\ell=1}^m \sum_{j=1}^N \left| D_{\Delta x}^- (\beta_j^{\ell,k}) g_{j-1}^{\ell,k-1} S_{j-1}^{\ell,k} \right| \Delta x \\
& \quad + \sum_{\ell=1}^m \sum_{j=1}^N \left| D_{\Delta x}^- (\tilde{\beta}_j^{\ell,k}) \tilde{g}_{j-1}^{\ell,k-1} I_{j-1}^{\ell,k} \right| \Delta x \\
& \quad + \sum_{\ell=1}^m \sum_{j=1}^N \left| \beta_j^{\ell,k} \left[ \mu_j^{\ell,k-1} S_j^{\ell,k} + L_j^{\ell,k-1} S_j^{\ell,k} \right] + \beta_P^\ell (\bar{P}_1, x_j) \frac{P^k - P^{k-1}}{\Delta t} S_j^{\ell,k-1} \right| \Delta x \\
& \quad + \sum_{\ell=1}^m \sum_{j=1}^N \left| \tilde{\beta}_j^{\ell,k} \left[ \tilde{\mu}_j^{\ell,k-1} I_j^{\ell,k} - L_j^{\ell,k-1} S_j^{\ell,k} \right] + \tilde{\beta}_P^\ell (\bar{P}_2, x_j) \frac{P^k - P^{k-1}}{\Delta t} I_j^{\ell,k-1} \right| \Delta x.
\end{aligned}$$

Hence,

$$\begin{aligned}
& \left| \sum_{i=1}^m \left[ g_0^{i,k} \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} + \frac{g_0^{i,k} - g_0^{i,k-1}}{\Delta t} S_0^{i,k} \right] \right| \\
& \leq mc^2 C_5 + \max_{\substack{1 \leq \ell \leq m \\ 1 \leq j \leq N}} |D_{\Delta x}^- (\beta_j^{\ell,k}) g_{j-1}^{\ell,k-1}| \sum_{\ell=1}^m (\|S^{\ell,k}\|_1 + \|S^{\ell,k}\|_\infty) \\
& \quad + \max_{\substack{1 \leq \ell \leq m \\ 1 \leq j \leq N}} |D_{\Delta x}^- (\tilde{\beta}_j^{\ell,k}) \tilde{g}_{j-1}^{\ell,k-1}| \sum_{\ell=1}^m (\|I^{\ell,k}\|_1 + \|I^{\ell,k}\|_\infty) + \max_{\substack{1 \leq \ell \leq m \\ 1 \leq j \leq N}} |\tilde{\beta}_j^{\ell,k} \tilde{\mu}_j^{\ell,k-1}| \sum_{\ell=1}^m \|I^{\ell,k}\|_1 \\
& \quad + \max_{\substack{1 \leq \ell \leq m \\ 1 \leq j \leq N}} \left( |\beta_j^{\ell,k} \mu_j^{\ell,k-1}| + |\beta_j^{\ell,k} L_j^{\ell,k-1}| + |\tilde{\beta}_j^{\ell,k} L_j^{\ell,k-1}| \right) \sum_{\ell=1}^m \|S^{\ell,k}\|_1 \\
& \quad + C_6 \max_{\substack{1 \leq \ell \leq m \\ (P,x) \in \mathbb{D}}} |\beta_P^\ell| \sum_{\ell=1}^m \|S^{\ell,k-1}\|_1 + C_6 \max_{\substack{1 \leq \ell \leq m \\ (P,x) \in \mathbb{D}}} |\tilde{\beta}_P^\ell| \sum_{\ell=1}^m \|I^{\ell,k-1}\|_1.
\end{aligned}$$

The result follows from (A1), (A2), (A3), Lemma 5.2, Lemma 5.4, and Lemma 5.6.  $\square$

**A.8. Proof of Lemma 5.8.** Set  $\eta_j^{i,k} = D_{\Delta x}^- (S_j^{i,k})$  and apply the operator  $D_{\Delta x}^-$  to (9) to get for  $2 \leq j \leq N$

$$\begin{aligned}
& \frac{\eta_j^{i,k+1} - \eta_j^{i,k}}{\Delta t} + D_{\Delta x}^- \left[ \frac{g_j^{i,k} S_j^{i,k+1} - g_{j-1}^{i,k} S_{j-1}^{i,k+1}}{\Delta x} \right] + D_{\Delta x}^- [\mu_j^{i,k} S_j^{i,k+1}] \\
& \quad + D_{\Delta x}^- [L_j^{i,k} S_j^{i,k+1}] = 0.
\end{aligned}$$

Multiplying the above by  $\text{sgn}(\eta_j^{i,k+1}) \Delta x$  and noting that  $-\eta_j^{i,k} \text{sgn}(\eta_j^{i,k+1}) \geq -|\eta_j^{i,k}|$  we have

$$\begin{aligned}
& \frac{|\eta_j^{i,k+1}| - |\eta_j^{i,k}|}{\Delta t} \Delta x + \left\{ D_{\Delta x}^- \left[ D_{\Delta x}^- (g_j^{i,k} S_j^{i,k+1}) \right] \right. \\
& \quad \left. + D_{\Delta x}^- (\mu_j^{i,k} S_j^{i,k+1}) + D_{\Delta x}^- (L_j^{i,k} S_j^{i,k+1}) \right\} \text{sgn}(\eta_j^{i,k+1}) \Delta x \leq 0,
\end{aligned} \tag{31}$$

for  $2 \leq j \leq N$ . When  $j = 1$  we have that

$$\frac{\eta_1^{i,k+1} - \eta_1^{i,k}}{\Delta t} = \frac{1}{\Delta x} \left( \frac{S_1^{i,k+1} - S_1^{i,k}}{\Delta t} - \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} \right).$$

Incorporating (9) into the above, we have

$$\frac{\eta_1^{i,k+1} - \eta_1^{i,k}}{\Delta t} = \frac{-1}{\Delta x} \left( \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} + \frac{g_1^{i,k} S_1^{i,k+1} - g_0^{i,k} S_0^{i,k+1}}{\Delta x} + \mu_1^{i,k} S_1^{i,k+1} + L_1^{i,k} S_1^{i,k+1} \right).$$

We set for notational convenience  $D_{\Delta x}^-(g_0^{i,k} S_0^{i,k+1}) = -\frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t}$  and multiply the above by  $\text{sgn}(\eta_1^{i,k+1})\Delta x$  to obtain

$$\begin{aligned} & \frac{|\eta_1^{i,k+1}| - |\eta_1^{i,k+1}|}{\Delta t} \Delta x + \left\{ D_{\Delta x}^- \left[ D_{\Delta x}^- (g_1^{i,k} S_1^{i,k+1}) \right] + D_{\Delta x}^- (\mu_1^{i,k} S_1^{i,k+1}) \right. \\ & \left. + \frac{\mu_0^{i,k} S_0^{i,k+1}}{\Delta x} + D_{\Delta x}^- (L_1^{i,k} S_1^{i,k+1}) - \frac{L_0^{i,k} S_0^{i,k+1}}{\Delta x} \right\} \text{sgn}(\eta_1^{i,k+1}) \Delta x \leq 0. \end{aligned} \quad (32)$$

Adding (31) and (32), then summing over the indices  $j = 1, 2, \dots, N$  we obtain

$$\begin{aligned} & \frac{\|\eta^{i,k+1}\|_1 - \|\eta^{i,k}\|_1}{\Delta t} + \sum_{j=1}^N \left\{ D_{\Delta x}^- \left[ D_{\Delta x}^- (g_j^{i,k} S_j^{i,k+1}) \right] + D_{\Delta x}^- (\mu_j^{i,k} S_j^{i,k+1}) \right. \\ & \left. + D_{\Delta x}^- (L_j^{i,k} S_j^{i,k+1}) \right\} \text{sgn}(\eta_j^{i,k+1}) \Delta x - \frac{1}{\Delta x} (L_0^{i,k} S_0^{i,k+1} \\ & - \mu_0^{i,k} S_0^{i,k+1}) \text{sgn}(\eta_j^{i,k+1}) \Delta x \leq 0. \end{aligned} \quad (33)$$

We consider the first term in the summation and find

$$\begin{aligned} & \sum_{j=1}^N D_{\Delta x}^- \left[ D_{\Delta x}^- (g_j^{i,k} S_j^{i,k+1}) \right] \text{sgn}(\eta_j^{i,k+1}) \Delta x \\ & = \sum_{j=2}^N D_{\Delta x}^- \left[ g_j^{i,k} \frac{S_j^{i,k+1} - S_{j-1}^{i,k+1}}{\Delta x} + \frac{g_j^{i,k} - g_{j-1}^{i,k}}{\Delta x} S_{j-1}^{i,k+1} \right] \text{sgn}(\eta_j^{i,k+1}) \Delta x \\ & \quad + D_{\Delta x}^- \left[ D_{\Delta x}^- (g_1^{i,k} S_1^{i,k+1}) \right] \text{sgn}(\eta_1^{i,k+1}) \Delta x \\ & = \sum_{j=2}^N D_{\Delta x}^- (g_j^{i,k} \eta_j^{i,k+1}) \text{sgn}(\eta_j^{i,k+1}) \Delta x \\ & \quad + \sum_{j=2}^N D_{\Delta x}^- \left[ \frac{g_j^{i,k} - g_{j-1}^{i,k}}{\Delta x} S_{j-1}^{i,k+1} \right] \text{sgn}(\eta_j^{i,k+1}) \Delta x \\ & \quad + D_{\Delta x}^- \left[ D_{\Delta x}^- (g_1^{i,k} S_1^{i,k+1}) \right] \text{sgn}(\eta_1^{i,k+1}) \Delta x. \end{aligned} \quad (34)$$

Using methods similar to those presented in [7], we obtain

$$\begin{aligned} & \sum_{j=2}^N D_{\Delta x}^- \left[ D_{\Delta x}^- (g_j^{i,k} S_j^{i,k+1}) \right] \operatorname{sgn}(\eta_j^{i,k+1}) \Delta x \\ & + D_{\Delta x}^- \left[ D_{\Delta x}^- (g_1^{i,k} S_1^{i,k+1}) \right] \operatorname{sgn}(\eta_1^{i,k+1}) \Delta x \\ & \geq \sum_{j=2}^N D_{\Delta x}^- \left[ D_{\Delta x}^- (g_j^{i,k} S_{j-1}^{i,k+1}) \right] \operatorname{sgn}(\eta_j^{i,k+1}) \Delta x \\ & \quad + D_{\Delta x}^- (g_1^{i,k}) S_0^{i,k+1} \operatorname{sgn}(\eta_1^{i,k+1}) + \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} \operatorname{sgn}(\eta_1^{i,k+1}), \end{aligned}$$

where  $\text{Jump} = \{j : \eta_j^{i,k+1} \eta_{j+1}^{i,k+1} < 0\}$ . Thus (33) becomes

$$\begin{aligned} & \frac{\|\eta^{i,k+1}\|_1 - \|\eta^{i,k}\|_1}{\Delta t} \\ & \leq \left( \max_{\substack{1 \leq i \leq m \\ 1 \leq j \leq N}} |D_{\Delta x}^- (g_j^{i,k})| + \max_{\substack{1 \leq i \leq m \\ 0 \leq j \leq N}} (\mu_j^i + L_j^{i,k}) \right) \|\eta^{i,k+1}\|_1 \\ & \quad + \left( \max_{\substack{1 \leq i \leq m \\ 2 \leq j \leq N}} |D_{\Delta x}^- [D_{\Delta x}^- (g_j^{i,k})]| + \max_{\substack{1 \leq i \leq m \\ 1 \leq j \leq N}} (|D_{\Delta x}^- (\mu_j^{i,k})| + |D_{\Delta x}^- (L_j^{i,k})|) \right) \|S^{i,k+1}\|_1 \\ & \quad + \left( \max_{\substack{1 \leq i \leq m \\ 1 \leq j \leq N}} |D_{\Delta x}^- (g_j^{i,k})| + \max_{\substack{1 \leq i \leq m \\ 0 \leq j \leq N}} (L_j^{i,k} + \mu_j^{i,k}) \right) \|S^{i,k+1}\|_\infty + \left| \frac{S_0^{i,k+1} - S_0^{i,k}}{\Delta t} \right|. \end{aligned}$$

Incorporating (A1), (A2), and Lemmas 5.2, 5.4, 5.5, and 5.7, we see that there are positive constants  $\omega_1$  and  $\omega_2$  such that

$$\frac{\|\eta^{i,k+1}\|_1 - \|\eta^{i,k}\|_1}{\Delta t} \leq \omega_1 \|\eta^{i,k}\|_1 + \omega_2. \quad (35)$$

Setting  $\xi_j^{i,k} = D_{\Delta x}^- (I_j^{i,k})$ , using similar arguments as above, and setting for notational convenience  $D_{\Delta x}^- (\tilde{g}_0^{i,k} I_0^{i,k+1}) = -\frac{I_0^{i,k+1} - I_0^{i,k}}{\Delta t}$ , we obtain

$$\begin{aligned} & \frac{\|\xi^{i,k+1}\|_1 - \|\xi^{i,k}\|_1}{\Delta t} + \sum_{j=1}^N \left( D_{\Delta x}^- \left( D_{\Delta x}^- (\tilde{g}_j^{i,k} I_j^{i,k+1}) \right) + D_{\Delta x}^- (\tilde{\mu}_j^i I_j^{i,k+1}) + \right. \\ & \quad \left. - D_{\Delta x}^- (L_j^{i,k} S_j^{i,k+1}) \right) \operatorname{sgn}(\xi_j^{i,k+1}) \Delta x - L_0^{i,k} S_0^{i,k+1} \operatorname{sgn}(\xi_1^{i,k+1}) \leq 0. \end{aligned} \quad (36)$$

Straightforward computations give

$$\begin{aligned} & \sum_{j=1}^N D_{\Delta x}^- \left( D_{\Delta x}^- (\tilde{g}_j^{i,k} I_j^{i,k+1}) \right) \operatorname{sgn}(\xi_j^{i,k+1}) \Delta x \\ & \geq \sum_{j=2}^N \left( D_{\Delta x}^- (D_{\Delta x}^- (\tilde{g}_j^{i,k})) I_{j-1}^{i,k+1} \right) \operatorname{sgn}(\xi_j^{i,k+1}) \Delta x. \end{aligned}$$

Thus, (36) becomes

$$\begin{aligned} & \frac{\|\xi^{i,k+1}\|_1 - \|\xi^{i,k}\|_1}{\Delta t} \\ & \leq \left( \max_{\substack{1 \leq i \leq m \\ 1 \leq j \leq N}} |D_{\Delta x}^-(\tilde{\mu}_j^{i,k})| + \max_{\substack{1 \leq i \leq m \\ 2 \leq j \leq N}} |D_{\Delta x}^-(D_{\Delta x}^-(\tilde{g}_j^{i,k}))| \right) \|I^{i,k+1}\|_1 \\ & \quad + \max_{\substack{1 \leq i \leq m \\ 0 \leq j \leq N}} (\tilde{\mu}_j^{i,k}) \|\xi^{i,k+1}\|_1 + \max_{\substack{1 \leq i \leq m \\ 0 \leq j \leq N}} (L_j^{i,k}) \left( \|\eta^{i,k+1}\|_1 + \|S^{i,k+1}\|_\infty \right) \\ & \quad + \max_{\substack{1 \leq i \leq m \\ 1 \leq j \leq N}} |D_{\Delta x}^-(L_j^{i,k})| \|S^{i,k+1}\|_1. \end{aligned}$$

Using (A1), (A2), and Lemmas 5.2, 5.4, and 5.5, we see that there are positive constants  $\omega_3, \omega_4$ , and  $\omega_5$  such that

$$\frac{\|\xi^{i,k+1}\|_1 - \|\xi^{i,k}\|_1}{\Delta t} \leq \omega_3 \|\xi^{i,k+1}\|_1 + \omega_4 \|\eta^{i,k+1}\|_1 + \omega_5. \quad (37)$$

The result now easily follows from (35) and (37).  $\square$

**A.9. Proof of Lemma 5.9.** Multiplying (9) by  $\Delta x$ , summing over  $j$ , then using Lemmas 5.2, 5.4, 5.8, and assumptions (A1) and (A2), we obtain

$$\begin{aligned} \sum_{j=1}^N \left| \frac{S_j^{i,k+1} - S_j^{i,k}}{\Delta t} \right| \Delta x &= \sum_{j=1}^N \left| -\frac{g_j^{i,k} S_j^{i,k} - g_{j-1}^{i,k} S_{j-1}^{i,k}}{\Delta x} - \mu_j^{i,k} S_j^{i,k+1} - L_j^{i,k} S_j^{i,k+1} \right| \Delta x \\ &\leq \sum_{j=1}^N \left| \frac{g_j^{i,k} - g_{j-1}^{i,k}}{\Delta x} S_j^{i,k} + g_{j-1}^{i,k} \frac{S_j^{i,k} - S_{j-1}^{i,k}}{\Delta x} \right| \Delta x \\ &\quad + c \|S^{i,k+1}\|_1 + C_5 \|S^{i,k+1}\|_1 \\ &\leq C_1 \max_{\substack{1 \leq i \leq m \\ 1 \leq j \leq N}} |D_{\Delta x}^-(g_j^{i,k})| + cC_8 + cC_1 + C_5 C_1 \equiv C_9. \end{aligned}$$

Thus,

$$\sum_{j=1}^N \left| \frac{S_j^{i,r} - S_j^{i,q}}{\Delta t} \right| \Delta x \leq \sum_{k=q}^{r-1} \sum_{j=1}^N \left| \frac{S_j^{i,k+1} - S_j^{i,k}}{\Delta t} \right| \Delta x \leq C_9(r-q).$$

The result for  $I$  can be established similarly.

Applying absolute value to (12), and using Lemmas 5.2, 5.3, 5.6, and assumptions (A4), (A6), (A7) we get

$$\begin{aligned} \left| \frac{B_u^{k+1} - B_u^k}{\Delta t} \right| &\leq |H^k| + |\lambda B_a^k| + |c_M M^* B_u^{k+1}| + |\delta_1 B_u^{k+1} P^{k+1}| \\ &\quad + \sum_{i=1}^m \sum_{j=1}^N |c_{1,j}^i B_u^{k+1} S_j^{i,k+1}| \Delta x + \sum_{i=1}^m \sum_{j=1}^N |\tilde{c}_{1,j}^i B_u^{k+1} I_j^{i,k+1}| \Delta x \\ &\leq c + cC_2 + (c^2 + 2cC_1)C_2 \equiv C_{11}. \end{aligned}$$

Thus,

$$\left| \frac{B_u^r - B_u^q}{\Delta t} \right| \leq \sum_{k=q}^{r-1} \left| \frac{B_u^{k+1} - B_u^k}{\Delta t} \right| \leq C_{11}(r-q).$$

The results for  $B_a$  and  $M$  can be established similarly.  $\square$

A.10. **Proof of Theorem 5.10.** The results for  $S^i(t, x)$  and  $I^i(t, x)$  follow from Lemmas 5.2–5.9 and the proof of Lemma 16.7 (p. 276) in [40]. The results for  $B_a(t)$ ,  $B_u(t)$ , and  $M(t)$  follow from the Ascoli-Arzelà Theorem (p. 74) in [45].  $\square$

A.11. **Proof of Theorem 5.11.** Let  $\varphi^i \in C^1([0, T], [x_{\min}, x_{\max}])$  and  $\varsigma^i \in C^1([0, T], [x_{\min}, x_{\max}])$  for  $i = 1, \dots, m$ . We denote the finite difference approximations of  $\varphi^i(t_k, x_j)$  by  $\varphi_j^{i,k}$  and  $\varsigma^i(t_k, x_j)$  by  $\varsigma_j^{i,k}$ . Multiplying (9) by  $\varphi_j^{i,k+1} \Delta x$ , rearranging terms, then summing over  $j = 1, \dots, N$ , and over  $k = 0, \dots, K-1$  we get

$$\begin{aligned} & \sum_{j=1}^N (S_j^{i,K} \varphi_j^{i,K} - S_j^{i,0} \varphi_j^{i,0}) \Delta x \\ &= \sum_{k=0}^{K-1} \sum_{j=1}^N \left( S_j^{i,k} (\varphi_j^{i,k+1} - \varphi_j^{i,k}) \Delta x + g_{j-1}^{i,k} S_{j-1}^{i,k+1} (\varphi_j^{i,k+1} - \varphi_{j-1}^{i,k+1}) \Delta t \right. \\ & \quad \left. - \varphi_j^{i,k+1} \mu_j^{i,k} S_j^{i,k+1} \Delta t \Delta x - \varphi_j^{i,k+1} L_j^{i,k} S_j^{i,k+1} \Delta t \Delta x \right) \\ & \quad + \sum_{k=0}^{K-1} \varphi_0^{i,k+1} \left( \sum_{\ell=1}^m p^{i\ell} \sum_{j=1}^N [\beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k}] \Delta x \right) \Delta t. \end{aligned}$$

In a similar manner, we multiply (10) by  $\varsigma_j^{i,k+1} \Delta x$ , rearrange terms, then sum over  $j = 1, \dots, N$ , and over  $k = 0, \dots, K-1$ , to obtain

$$\begin{aligned} \sum_{j=1}^N (I_j^{i,K} \varsigma_j^{i,K} - I_j^{i,0} \varsigma_j^{i,0}) \Delta x &= \sum_{k=0}^{K-1} \sum_{j=1}^N \left( I_j^{i,k} (\varsigma_j^{i,k+1} - \varsigma_j^{i,k}) \Delta x \right. \\ & \quad \left. + \tilde{g}_{j-1}^{i,k} I_{j-1}^{i,k+1} (\varsigma_j^{i,k+1} - \varsigma_{j-1}^{i,k+1}) \Delta t \right. \\ & \quad \left. - \varsigma_j^{i,k+1} \tilde{\mu}_j^{i,k} I_j^{i,k+1} \Delta t \Delta x + \varsigma_j^{i,k+1} L_j^{i,k} S_j^{i,k+1} \Delta t \Delta x \right). \end{aligned}$$

Using the above and then by a similar argument to those in the proof of Lemma 16.9 (p. 279) in [40], it can be shown that the limit of the difference approximations defined in Theorem 5.10 is a weak solution to (1)–(3) by allowing  $N, K \rightarrow \infty$ . The bounds on the functions are found by taking the limit in the bounds of the difference approximations in Lemmas 5.2, 5.3, and 5.5.  $\square$

A.12. **Proof of Theorem 5.12.** Recall that we let  $u_j^{i,k} = S_j^{i,k} - \hat{S}_j^{i,k}$ ,  $v_j^{i,k} = I_j^{i,k} - \hat{I}_j^{i,k}$ ,  $w^k = B_a^k - \hat{B}_a^k$ ,  $y^k = B_u^k - \hat{B}_u^k$ , and  $z^k = M^k - \hat{M}^k$ . Denote the corresponding approximations of the total fish population by  $P^k$  and  $\hat{P}^k$  and let  $g_j^{i,k} = g^i(P^k, x_j)$  and  $\hat{g}_j^{i,k} = g^i(\hat{P}^k, x_j)$ . Similar notation is used for the other model parameters. Also, we let  $\mathcal{S}^k(\alpha)$  and  $\mathcal{I}^k(\alpha)$  to denote the approximation at  $t^k$  of  $\mathcal{S}(t^k; \alpha)$  and  $\mathcal{I}(t^k; \alpha)$ , respectively. Then we have from (9)–(13)

$$\begin{aligned} & \frac{u_j^{i,k+1} - u_j^{i,k}}{\Delta t} + D_{\Delta x}^- (g_j^{i,k} S_j^{i,k+1} - \hat{g}_j^{i,k} \hat{S}_j^{i,k+1}) + \mu_j^{i,k} u_j^{i,k+1} \\ & \quad + (\mu_j^{i,k} - \hat{\mu}_j^{i,k}) \hat{S}_j^{i,k+1} + L_j^{i,k} u_j^{i,k+1} + (L_j^{i,k} - \hat{L}_j^{i,k}) \hat{S}_j^{i,k+1} = 0, \\ & \frac{v_j^{i,k+1} - v_j^{i,k}}{\Delta t} + D_{\Delta x}^- (\tilde{g}_j^{i,k} I_j^{i,k+1} - \hat{\tilde{g}}_j^{i,k} \hat{I}_j^{i,k+1}) + \tilde{\mu}_j^{i,k} v_j^{i,k+1} \\ & \quad + (\tilde{\mu}_j^{i,k} - \hat{\tilde{\mu}}_j^{i,k}) \hat{I}_j^{i,k+1} - L_j^{i,k} u_j^{i,k+1} - (L_j^{i,k} - \hat{L}_j^{i,k}) \hat{S}_j^{i,k+1} = 0, \end{aligned} \quad (38)$$

$$\begin{aligned}
\frac{w^{k+1} - w^k}{\Delta t} &= (\mathcal{I}^{k+1}(\rho) - \hat{\mathcal{I}}^{k+1}(\rho)) - \delta_2 B_a^{k+1}(P^{k+1} - \hat{P}^{k+1}) \\
&\quad - \delta_2 \hat{P}^{k+1} w^{k+1} - \lambda w^{k+1}, \\
\frac{y^{k+1} - y^k}{\Delta t} &= -\lambda w^{k+1} - c_M M^* y^{k+1} - \delta_1 B_u^{k+1}(P^{k+1} - \hat{P}^{k+1}) \\
&\quad - \delta_1 \hat{P}^{k+1} y^{k+1} - B_u^{k+1}(\mathcal{S}^{k+1}(c_1) - \hat{\mathcal{S}}^{k+1}(c_1)) \\
&\quad - \hat{\mathcal{S}}^{k+1}(c_1) y^{k+1} - B_u^{k+1}(\mathcal{I}^{k+1}(\tilde{c}_1) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_1)) \\
&\quad - \hat{\mathcal{I}}^{k+1}(\tilde{c}_1) y^{k+1}, \\
\frac{z^{k+1} - z^k}{\Delta t} &= \epsilon c_M M^* y^{k+1} - \epsilon c_M (\hat{M}^{k+1} y^{k+1} + B_u^{k+1} z^{k+1}) - \mu_M z^{k+1} \\
&\quad - M^{k+1}(\mathcal{S}^{k+1}(c_2) - \hat{\mathcal{S}}^{k+1}(c_2)) - \hat{\mathcal{S}}^{k+1}(c_2) z^{k+1} \\
&\quad - M^{k+1}(\mathcal{I}^{k+1}(\tilde{c}_2) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_2)) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_2) z^{k+1}.
\end{aligned}$$

Multiplying the first equation of (A.12) by  $\text{sgn}(u_j^{i,k+1})\Delta x$ , and summing over  $j = 1, \dots, N$ , we get

$$\begin{aligned}
&\frac{\|u^{i,k+1}\|_1 - \|u^{i,k}\|_1}{\Delta t} + \sum_{j=1}^N D_{\Delta x}^-(g_j^{i,k} S_j^{i,k+1} - \hat{g}_j^{i,k} \hat{S}_j^{i,k+1}) \text{sgn}(u_j^{i,k+1}) \Delta x \\
&\quad + \sum_{j=1}^N ((\mu_j^{i,k} - \hat{\mu}_j^{i,k}) \hat{S}_j^{i,k+1} + (L_j^{i,k} - \hat{L}_j^{i,k}) \hat{S}_j^{i,k+1}) \text{sgn}(u_j^{i,k+1}) \Delta x \\
&\quad + \sum_{j=1}^N \mu_j^{i,k} |u_j^{i,k+1}| \Delta x + \sum_{j=1}^N |L_j^{i,k} u_j^{i,k+1}| \Delta x \leq 0.
\end{aligned}$$

Using methods similar to those found in [7] we obtain

$$\begin{aligned}
&\sum_{j=1}^N D_{\Delta x}^-(g_j^{i,k} S_j^{i,k+1} - \hat{g}_j^{i,k} \hat{S}_j^{i,k+1}) \text{sgn}(u_j^{i,k+1}) \Delta x \\
&\geq -g_0^{i,k} u_0^{i,k+1} \text{sgn}(u_1^{i,k+1}) + \sum_{j=1}^N D_{\Delta x}^-(\hat{S}_j^{i,k+1} (g_j^{i,k} - \hat{g}_j^{i,k})) \text{sgn}(u_j^{i,k+1}) \Delta x.
\end{aligned}$$

Thus,

$$\begin{aligned}
&\frac{\|u^{i,k+1}\|_1 - \|u^{i,k}\|_1}{\Delta t} \\
&\leq g_0^{i,k} u_0^{i,k+1} \text{sgn}(u_1^{i,k+1}) + \sum_{j=1}^N D_{\Delta x}^-(\hat{S}_j^{i,k+1} (g_j^{i,k} - \hat{g}_j^{i,k})) \text{sgn}(u_j^{i,k+1}) \Delta x \\
&\quad - \sum_{j=1}^N ((\mu_j^{i,k} - \hat{\mu}_j^{i,k}) \hat{S}_j^{i,k+1} + (L_j^{i,k} - \hat{L}_j^{i,k}) \hat{S}_j^{i,k+1}) \text{sgn}(u_j^{i,k+1}) \Delta x \\
&\quad + \sum_{j=1}^N \mu_j^{i,k} |u_j^{i,k+1}| \Delta x + \sum_{j=1}^N |L_j^{i,k} u_j^{i,k+1}| \Delta x.
\end{aligned} \tag{39}$$

We next establish a bound on the terms on the right of (39), beginning with the first. Using the definition of  $u_j^{i,k}$  and (15) we realize

$$\begin{aligned}
g_0^{i,k} u_0^{i,k+1} \text{sgn}(u_1^{i,k+1}) &= (Z^{i,k} - \hat{Z}^{i,k} - \hat{S}_0^{i,k+1} (g_0^{i,k} - \hat{g}_0^{i,k})) \text{sgn}(u_1^{i,k+1}) \\
&\leq |Z^{i,k} - \hat{Z}^{i,k}| + \hat{S}_0^{i,k+1} |g_0^{i,k} - \hat{g}_0^{i,k}| \\
&\leq |Z^{i,k} - \hat{Z}^{i,k}| + C_5 \left( \max_{\substack{1 \leq i \leq m \\ (P,x) \in \mathbb{D}}} |g_P^i| \right) |P^k - \hat{P}^k|.
\end{aligned} \tag{40}$$

Using (A1), (A2), Lemmas 5.2, 5.4, 5.8, and the mean value theorem for the second term in (39), we obtain

$$\begin{aligned} & - \sum_{j=1}^N D_{\Delta x}^- (\hat{S}_j^{i,k+1} (g_j^{i,k} - \hat{g}_j^{i,k})) \operatorname{sgn}(u_j^{i,k+1}) \Delta x \\ & \leq \left( C_8 \max_{\substack{1 \leq i \leq m \\ (P,x) \in \mathbb{D}}} |g_P^i| + C_1 \max_{\substack{1 \leq i \leq m \\ (P,x) \in \mathbb{D}}} |g_{P_x}^i| \right) |P^k - \hat{P}^k|, \end{aligned} \quad (41)$$

and for the third term

$$\begin{aligned} & - \sum_{j=1}^N ((\mu_j^{i,k} - \hat{\mu}_j^{i,k}) \hat{S}_j^{i,k+1} + (L_j^{i,k} - \hat{L}_j^{i,k}) \hat{S}_j^{i,k+1}) \operatorname{sgn}(u_j^{i,k+1}) \Delta x \\ & \leq C_1 \max_{\substack{1 \leq i \leq m \\ (P,x) \in \mathbb{D}}} |\mu_P^i| |P^k - \hat{P}^k| + c^3 C_1 (|y^k| + |w^k| + |z^k|). \end{aligned} \quad (42)$$

Incorporating (40), (41), and (42) into (39) we see that there are positive constants  $\omega_6, \omega_7$ , and  $\omega_8$  such that

$$\begin{aligned} \frac{\|u^{i,k+1}\|_1 - \|u^{i,k}\|_1}{\Delta t} & \leq \omega_6 \|u^{i,k+1}\|_1 + \omega_7 (|y^k| + |w^k| + |z^k|) + \omega_8 |P^k - \hat{P}^k| \\ & \quad + |Z^{i,k} - \hat{Z}^{i,k}|. \end{aligned} \quad (43)$$

We note here that

$$|Z^{i,k} - \hat{Z}^{i,k}| \leq \sum_{\ell=1}^m (c(\|u^{\ell,k}\|_1 + \|v^{\ell,k}\|_1) + 2cC_1 |P^k - \hat{P}^k|), \quad (44)$$

$$|P^k - \hat{P}^k| \leq \sum_{i=1}^m (\|u^{i,k}\|_1 + \|v^{i,k}\|_1). \quad (45)$$

Incorporating (44) and (45) into (43), we see that there is a positive constant  $\omega_9$  such that

$$\begin{aligned} \frac{\|u^{i,k+1}\|_1 - \|u^{i,k}\|_1}{\Delta t} & \leq \omega_9 \|u^{i,k}\|_1 + \omega_9 \|v^{i,k}\|_1 + \omega_6 \|u^{i,k+1}\|_1 \\ & \quad + \omega_7 (|y^k| + |w^k| + |z^k|). \end{aligned} \quad (46)$$

Using similar arguments as above, we determine

$$\begin{aligned} & \frac{\|v^{i,k+1}\|_1 - \|v^{i,k}\|_1}{\Delta t} \\ & \leq \left( C_8 \max_{\substack{1 \leq i \leq m \\ (P,x) \in \mathbb{D}}} |\tilde{g}_P^i| + C_1 \max_{\substack{1 \leq i \leq m \\ (P,x) \in \mathbb{D}}} |\tilde{g}_{P_x}^i| + C_1 \max_{\substack{1 \leq i \leq m \\ (P,x) \in \mathbb{D}}} |\tilde{\mu}_P^i| \right) |P^k - \hat{P}^k| \\ & \quad + c^3 C_1 (|y^k| + |w^k| + |z^k|) + C_3 \|u^{i,k+1}\|_1 + c \|v^{i,k+1}\|_1. \end{aligned} \quad (47)$$

Hence, there are positive constants  $\omega_{10}, \omega_{11}$ , and  $\omega_{12}$ , such that

$$\begin{aligned} \frac{\|v^{i,k+1}\|_1 - \|v^{i,k}\|_1}{\Delta t} & \leq \omega_{10} \|u^{i,k}\|_1 + \omega_{10} \|v^{i,k}\|_1 + \omega_{11} \|u^{i,k+1}\|_1 \\ & \quad + \omega_{12} \|v^{i,k+1}\|_1 + \omega_7 (|y^k| + |w^k| + |z^k|). \end{aligned} \quad (48)$$

We now multiply the third, fourth, and fifth equations of (A.12) by  $\operatorname{sgn}(w^{k+1})$ ,  $\operatorname{sgn}(y^{k+1})$ , and  $\operatorname{sgn}(z^{k+1})$ , respectively, to get

$$\begin{aligned} \frac{|w^{k+1}| - |w^k|}{\Delta t} & \leq |\mathcal{I}^{k+1}(\rho) - \hat{\mathcal{I}}^{k+1}(\rho)| + \delta_2 B_a^{k+1} |P^{k+1} - \hat{P}^{k+1}| \\ & \quad + \delta_2 \hat{P}^{k+1} |w^{k+1}| + \lambda |w^{k+1}|, \end{aligned} \quad (49)$$



$$\begin{aligned} \frac{|y^{k+1}| - |y^k|}{\Delta t} \leq & \lambda|w^{k+1}| + c_M M^* |y^{k+1}| + \delta_1 B_u^{k+1} |P^{k+1} - \hat{P}^{k+1}| \\ & + \delta_1 \hat{P}^{k+1} |y^{k+1}| + B_u^{k+1} |\mathcal{S}^{k+1}(c_1) - \hat{\mathcal{S}}^{k+1}(c_1)| \\ & + \hat{\mathcal{S}}^{k+1}(c_1) |y^{k+1}| + B_u^{k+1} |\mathcal{I}^{k+1}(\tilde{c}_1) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_1)| \\ & + \hat{\mathcal{I}}^{k+1}(\tilde{c}_1) |y^{k+1}| \end{aligned} \tag{50}$$

$$\begin{aligned} \frac{|z^{k+1}| - |z^k|}{\Delta t} \leq & \epsilon c_M M^* |y^{k+1}| + \epsilon c_M M^{k+1} |y^{k+1}| + \epsilon c_M \hat{B}_u^{k+1} |z^{k+1}| \\ & + \mu_M |z^{k+1}| + M^{k+1} |\mathcal{S}^{k+1}(c_2) - \hat{\mathcal{S}}^{k+1}(c_2)| \\ & + \hat{\mathcal{S}}^{k+1}(c_2) |z^{k+1}| + M^{k+1} |\mathcal{I}^{k+1}(\tilde{c}_2) - \hat{\mathcal{I}}^{k+1}(\tilde{c}_2)| \\ & + \hat{\mathcal{I}}^{k+1}(\tilde{c}_2) |z^{k+1}|. \end{aligned} \tag{51}$$

We note here that for any continuous  $\alpha$ ,

$$\begin{aligned} |\mathcal{S}^k(\alpha) - \hat{\mathcal{S}}^k(\alpha)| & \leq \sum_{i=1}^m c \|u^{i,k+1}\|_1, \\ |\mathcal{I}^k(\alpha) - \hat{\mathcal{I}}^k(\alpha)| & \leq \sum_{i=1}^m c \|v^{i,k+1}\|_1, \end{aligned} \tag{52}$$

Incorporating (45) and (52) into the above equations, along with (A7), Lemma 5.2, and Lemma 5.3 we see that there are positive constants  $\omega_{13}, \omega_{14}, \omega_{15}, \omega_{16}, \omega_{17}, \omega_{18}, \omega_{19}, \omega_{20}, \omega_{21}, \omega_{22}$ , and  $\omega_{23}$  such that

$$\frac{|w^{k+1}| - |w^k|}{\Delta t} \leq \omega_{13} \|u^{i,k+1}\|_1 + \omega_{14} \|v^{i,k+1}\|_1 + \omega_{15} |w^{k+1}|, \tag{53}$$

$$\frac{|y^{k+1}| - |y^k|}{\Delta t} \leq \omega_{16} \|u^{i,k+1}\|_1 + \omega_{17} \|v^{i,k+1}\|_1 + \omega_{18} |w^{k+1}| + \omega_{19} |y^{k+1}|, \tag{54}$$

$$\frac{|z^{k+1}| - |z^k|}{\Delta t} \leq \omega_{20} \|u^{i,k+1}\|_1 + \omega_{21} \|v^{i,k+1}\|_1 + \omega_{22} |y^{k+1}| + \omega_{23} |z^{k+1}|. \tag{55}$$

Multiplying (46), (48), (53), (54), and (55) by  $\Delta t$  and then adding the resulting inequalities, we have

$$(1 - h_1 \Delta t) \hat{E}^{i,k+1} \leq (1 + h_2 \Delta t) \hat{E}^{i,k},$$

for each  $i = 1, \dots, m$  and where

$$h_1 = \max\{\omega_6 + \omega_{11} + \omega_{13} + \omega_{16} + \omega_{20}, \omega_{11} + \omega_{14} + \omega_{17} + \omega_{21}, \omega_{15} + \omega_{18}, \omega_{19} + \omega_{22}, \omega_{23}\},$$

$$h_2 = \max\{\omega_9, \omega_{10}, \omega_7\},$$

and the result is established. □

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