A second-order high-resolution finite difference scheme for a size-structured model for the spread of Mycobacterium marinum

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Published online: 01 Oct 2014.

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A second-order high-resolution finite difference scheme for a size-structured model for the spread of *Mycobacterium marinum*

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We present a second-order high-resolution finite difference scheme to approximate the solution of a mathematical model of the transmission dynamics of *Mycobacterium marinum* (Mm) in an aquatic environment. This work extends the numerical theory and continues the preliminary studies on the model first developed in Ackleh *et al.* [*Structured models for the spread of Mycobacterium marinum: foundations for a numerical approximation scheme*, Math. Biosci. Eng. 11 (2014), pp. 679–721]. Numerical simulations demonstrating the accuracy of the method are presented, and we compare this scheme to the first-order scheme developed in Ackleh *et al.* [*Structured models for the spread of Mycobacterium marinum: foundations for a numerical approximation scheme*, Math. Biosci. Eng. 11 (2014), pp. 679–721] to show that the first-order method requires significantly more computational time to provide solutions with a similar accuracy. We also demonstrated that the model can be a tool to understand surprising or nonintuitive phenomena regarding competitive advantage in the context of biologically realistic growth, birth and death rates.

1. Introduction

Mycobacterium marinum (Mm), a fish pathogen, is one of the closest related species to *Mycobacterium tuberculosis* (Mtb), the aetiological agent of human tuberculosis (TB). Mm shares many of the same bacterial virulence genes required by Mtb complex to infect, grow, spread, and cause disease in humans [16,29,41]. Mm has recently become a tractable surrogate pathogen to study TB-like infections [16,17,29,34,38,39,41], since it grows much faster than Mtb, represents less risk to researchers, similarly infects host macrophages (both human and fish), and many Mm and Mtb genes are interchangeable. The magnitude of the human TB burden is paralleled by a variety of mycobacterial pathogens in fish, and in particular by Mm [14,16,18,20,22]. As in human TB, it appears that there is a similarly large pool of chronically Mm-infected fish with similar implications for the overall disease impact; that is, even though there is only a small proportion of the chronically infected animals that become acute, it results in a large number of fatalities. Mm is known to infect at least 200 fish species in marine and fresh water environments [16,18,27]. 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 [22,24,27].

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Despite the large economic impact, the mode(s) of Mm infection and transmission between fish have remained speculative, with proposed modes including vertical transmission, horizontal transmission, and infection by ingestion of Mm-laced foods [27,28]. Until recently, little experimental research has been conducted to offer concrete support to one or more of these postulated transmission models. Recently, chronic infections have been successfully induced in medaka [15–17,32,36], thereby establishing this as an experimental species in which to study this crucial stage of infection, and the hypothesized modes of transmission between animals. These and other related studies revealed that Mm retrieved from infected tissues were also considerably more infectious, likely because these bacteria reside in the caustic intracellular environment of host macrophages of the target organs [16,19,21,30,34]. We are referring to this inducible enhanced virulence state for Mm as 'activated'.

Recently, two mathematical models were developed to study Mm [8,9]. In [9], a bacterial load-structured model was created to incorporate the differences in fish behavior as a function of infection severity, since chronic infection plays such a crucial role and these infections are asymptomatic. Solutions of this model provided reasonable agreement with experimental data, establishing the model's potential as a tool within which to interpret experimental findings and guide further experimental design. In [8], a size-structured model was developed to study key metabolic features such as growth rates and consumption activity on disease dynamics. The authors used this model to illustrate conditions for competitive exclusion or coexistence as determined by reproductive fitness and genetic spread in the population. The models in [8,9] were both discretized using a first-order finite difference method. In [8], the authors proved convergence of their method to a bounded variation weak solution for Equation (2); these results can readily be extended to the model and scheme from [9]. Here, we develop for the model in [8] a novel second-order high-resolution scheme in the spirit of those developed in [5,7,23,35,40]. To establish convergence of this method, a substantial modification of the techniques used in [5,7] is necessary due to the explicit modelling of the genetic or phenotypic heterogeneity between individuals, nonlocal nonlinearities, and quadratic nonlinearities.

There has been substantial research using numerical methods to solve structured models [3,4, 6,8,9] using first-order finite difference methods. These methods have been successfully applied to size-structured models which incorporate all nonlinear vital rates. Other methods used to study size-structured models include finite element methods [11,13,31], monotone approximations [3], integration along characteristics [1,10,25,26,33], and semigroup theory [12]. Several different methods for numerically solving structured population models are reviewed and compared in [2].

In this paper, we first (Section 2) succinctly describe the model and relevant biological processes. In Section 3, we introduce the weak solution and the finite difference scheme along with notation that is used throughout the paper. In Section 4, we give the estimates for the finite difference approximations, and in Section 5, we show that the finite difference scheme converges to the unique weak solution of the model. In Section 6, we confirm the second-order convergence established previously, and illustrate some features of the model. We begin by showing the order of the method by applying the scheme to a linear model with a smooth solution, and then to the full nonlinear model. Next, we compare the results from the first-order scheme designed in [8] to the second-order scheme designed here and close Section 6 with an exploration of biologically tenable growth, birth, and death rates, and demonstrate the model's utility in the resulting outcomes, which are not immediately intuitive. Finally, we make our concluding remarks in Section 7.

2. The structured model

We consider m distinct physiological groups, $i = 1, \ldots, m$, of fish with identical characteristics within each group. Within each physiological group, fish are either infected with Mm, or not

infected and susceptible to Mm. In this model, infected fish and susceptible fish grow, die, and procreate at different rates. Let $S^i(t, x)$ be the density of susceptible fish and $I^i(t, x)$ be the density of infected fish in class i of size $x \in [x_{\min}, x_{\max}]$ at time $t \in [0, T]$, where T is some arbitrary finite time. Other model variables include the number of carrier mosquito larvae, $M(t)$, activated bacteria (Mm) in the environment, $B_a(t)$, and unactivated bacteria (Mm) in the environment, $B_u(t)$.

The growth, death, and procreation rates are represented by $g^i(P, x)$, $\mu^i(P, x)$, and $\beta^i(P, x)$ for susceptible fish and $\tilde{g}^i(P, x)$, $\tilde{\mu}^i(P, x)$, and $\tilde{\beta}^i(P, x)$ for infected fish. The dependence on $P(t)$ represents the possible impact of crowding on a fish's ability to grow, survive, and reproduce, where the total population is

$$P(t) = \sum_{i=1}^{m} \int_{x_{\min}}^{x_{\max}} (S^i(t, x) + I^i(t, x))\, dx. \tag{1}$$

There are four modes of transmission for susceptible fish to become infected (per capita): (i) consumption of food sources that may contain unactivated bacteria, $\nu_1 \delta_1 B_u$, and (ii) activated bacteria, $\nu_2 \delta_2 B_a$, (iii) consumption of mosquito larvae that are carrying an *effective* load of bacteria, $\nu_3 \zeta c_2^i M$, and (iv) consumption of biofilms that may contain unactivated Mm, $\nu_4 c_1^i B_u$. The parameters ν_1, ν_2, ν_3, and ν_4 are effective transmission rates, δ_1 and δ_2 are the rates at which fish encounter unactivated and activated bacteria, respectively, ζ represents the bacterial dose within a 'typical' mosquito larvae, while $c_1^i(x)$ and $c_2^i(x)$ are fish consumption rates.

In accordance with experimental studies [16,17], there is no vertical transmission in this model and therefore there is zero flux of fish at the minimum size. Thus, the flux condition for susceptible fish are the 'births' (hatchlings) from susceptible fish as well as infected fish. Incorporated into the total birth rates is a selection-mutation matrix, p, which represents the probability of a fish of type ℓ giving birth to a fish of type i and is the (i, ℓ)th entry. We construct the matrix so that the entries are ordered according to similarity, so that adjacent indices represent physiologically similar classes. We observe that $\sum_{i=1}^{m} p^{i\ell} = 1$, the fractions of births of all types i from an individual of type ℓ sum to one.

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 $1/\lambda$. We also note that unactivated and activated bacteria are taken up through a fish's gills at rates of $\delta_1 B_u P$ and $\delta_2 B_a P$, respectively. We use $H(t)$ to represent the actions of humans that may provide a source of unactivated bacteria. The rates $\mathcal{S}(t; c_1)$ and $\mathcal{I}(t; \tilde{c}_1)$ represent the loss of unactivated bacteria in biofilms by consumption from susceptible and infected fish, respectively. Mosquito larvae consume unactivated bacteria at a rate of $c_M M^* B_u$, where c_M is the consumption rate of bacteria per capita mosquito larva and M^* denotes the (assumed in excess and therefore constant) total larval population. In the above, we have used the notation

$$\mathcal{S}(t; c_1) = \sum_{i=1}^{m} \int_{x_{\min}}^{x_{\max}} c_1^i(x) S^i(t, x)\, dx,$$

$$\mathcal{I}(t; \tilde{c}_1) = \sum_{i=1}^{m} \int_{x_{\min}}^{x_{\max}} \tilde{c}_1^i(x) I^i(t, x)\, dx,$$

$$\mathcal{I}(t; \rho) = \sum_{i=1}^{m} \int_{x_{\min}}^{x_{\max}} \rho^i(x) I^i(t, x)\, dx \quad \text{where } \rho^i(x) = \bar{\rho}^i \frac{x - x_{\min}}{x_{\max} - x_{\min}},$$

and $\bar{\rho}^i$ is a positive constant. We note that $\mathcal{S}(t; c_2)$ and $\mathcal{I}(t; \tilde{c}_2)$ are defined similarly.

While the total mosquito larvae population is constant, the number of those that are carriers of Mm, however, is a dynamically changing quantity. As mosquito larvae consume Mm-laden biofilms, and other common food sources, they become effective carriers of Mm at rate $\epsilon c_M (M^* - M) B_u$, where ϵ scales for the effective number of unactivated bacteria needed to consider mosquito larvae as a carrier of *Mm*. Note that $M^* - M$ represents the population of mosquito larvae that are not carriers of Mm. Carrier mosquito larvae are lost through maturation out of the larval stage at rate $\mu_M M$ and through consumption by susceptible and infected fish at rates $\mathcal{S}(t; c_2)$ and $\mathcal{I}(t; \tilde{c}_2)$, respectively.

The model equations are then given by

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

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

$$\frac{\mathrm{d} B_a}{\mathrm{d}t} = \mathcal{I}(t; \rho) - \delta_2 B_a P - \lambda B_a, \tag{2}$$

$$\frac{\mathrm{d} B_u}{\mathrm{d}t} = H + \lambda B_a - c_M M^* B_u - \delta_1 B_u P - \mathcal{S}(t; c_1) B_u - \mathcal{I}(t; \tilde{c}_1) B_u,$$

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

with boundary conditions

$$g^i(P, x_{\min}) S^i(t, x_{\min}) = \sum_{\ell=1}^{m} p^{il} \int_{x_{\min}}^{x_{\max}} [\beta^\ell(P, x) S^\ell(t, x) + \tilde{\beta}^\ell(P, x) I^\ell(t, x)] \, \mathrm{d}x, \tag{3}$$

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

and initial conditions

$$S^i(0, x) = S^{i,0}(x), \quad I^i(0, x) = I^{i,0}(x), \quad B_a(0) = B_a^0, \quad B_u(0) = B_u^0, \quad M(0) = M^0, \tag{4}$$

for $0 \le t \le T$, $x \in [x_{\min}, x_{\max}]$, and $i = 1, \ldots, m$.

For simplicity of notation, we let the function

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

throughout the paper.

3. Weak solutions and a second-order high-resolution scheme

Throughout the discussion we let $c > 1$ be a sufficiently large positive constant. We assume that the parameters in Equations (2)–(4) satisfy the following assumptions:

(A1) The functions $g^i(P, x)$ and $\tilde{g}^i(P, x)$ are twice continuously differentiable with respect to x and P. Also, $0 < g^i(P, x) \le c$, $0 < \tilde{g}^i(P, x) \le c$ 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, $0 \le \mu^i(P, x) \le c$, $0 \le \tilde{\mu}^i(P, x) \le c$ 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 $c_1^i(x)$, $c_2^i(x)$, $\tilde{c}_1^i(x)$, and $\tilde{c}_2^i(x)$ are continuously differentiable and $0 \leq c_1^i(x) \leq c$, $0 \leq c_2^i(x) \leq c$, $0 \leq \tilde{c}_1^i(x) \leq c$, and $0 \leq \tilde{c}_2^i(x) \leq c$ 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 $B_a(0)$, $B_u(0)$, and $M(0)$ 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) ν_1, ν_2, ν_3, ν_4, δ_1, δ_2, ζ, c_M, λ, $\bar{\rho}^i$, ϵ, M^*, and μ_M are nonnegative constants less than c.

We let the vectors $\vec{S} = (S^1, \ldots, S^m)^{\mathrm{T}}$ and $\vec{I} = (I^1, \ldots, I^m)^{\mathrm{T}}$ denote the susceptible and infected fish densities, respectively, for all m physiological groups. Multiplying the first and second equations of Equation (2) by $\phi(t,x)$ and $\psi(t,x)$, respectively, and formally integrating by parts, we define a weak solution of our system (2)–(4) 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 the following equations:

$$\int_{x_{\min}}^{x_{\max}} S^i(t,x)\phi(t,x)\,\mathrm{d}x - \int_{x_{\min}}^{x_{\max}} S^{i,0}(x)\phi(0,x)\,\mathrm{d}x$$

$$= \int_0^t \left(\sum_{\ell=1}^m p^{i\ell} \int_{x_{\min}}^{x_{\max}} [\beta^\ell(P(\tau),x)S^\ell(\tau,x) + \tilde{\beta}(P(\tau),x)I^\ell(\tau,x)]\,\mathrm{d}x \right) \phi(\tau, x_{\min})\,\mathrm{d}\tau$$

$$+ \int_0^t \int_{x_{\min}}^{x_{\max}} S^i(\tau,x)(\phi_\tau(\tau,x) + g^i(P(\tau),x)\phi_x(\tau,x) - \mu^i(P(\tau),x)\phi(\tau,x))\,\mathrm{d}x\,\mathrm{d}\tau$$

$$- \int_0^t \int_{x_{\min}}^{x_{\max}} S^i(\tau,x)L^i(B_a(\tau), B_u(\tau), M(\tau), x)\phi(\tau,x)\,\mathrm{d}x\,\mathrm{d}\tau,$$

$$\int_{x_{\min}}^{x_{\max}} I^i(t,x)\psi(t,x)\,\mathrm{d}x - \int_{x_{\min}}^{x_{\max}} I^{i,0}(x)\psi(0,x)\,\mathrm{d}x$$

$$= \int_0^t \int_{x_{\min}}^{x_{\max}} I^i(\tau,x)(\psi_\tau(\tau,x) + \tilde{g}^i(P(\tau),x)\psi_x(\tau,x) - \tilde{\mu}^i(P(\tau),x)\psi(\tau,x))\,\mathrm{d}x\,\mathrm{d}\tau$$

$$+ \int_0^t \int_{x_{\min}}^{x_{\max}} S^i(\tau,x)L^i(B_a(\tau), B_u(\tau), M(\tau), x)\psi(x,\tau)\,\mathrm{d}x\,\mathrm{d}\tau,$$

$$B_a(t) = B_a(0) + \int_0^t [\mathcal{I}(\tau;\rho) - \delta_2 B_a(\tau)P(\tau) - \lambda B_a(\tau)]\,\mathrm{d}\tau,$$

$$B_u(t) = B_u(0) + \int_0^t [H(\tau) + \lambda B_a(\tau) - c_M M^* B_u(\tau) - \delta_1 B_u(\tau)P(\tau)$$

$$- \mathcal{S}(\tau;c_1)B_u(\tau) - \mathcal{I}(\tau;\tilde{c}_1)B_u(\tau)]\,\mathrm{d}\tau,$$

$$M(t) = M(0) + \int_0^t [\epsilon c_M(M^* - M(\tau))B_u(\tau) - \mu_M M(\tau) - \mathcal{S}(\tau;c_2)M(\tau) - \mathcal{I}(\tau;\tilde{c}_2)M(\tau)]\,\mathrm{d}\tau,$$

(6)

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

As was presented in [8], we assume that there is a smallest size $x_{\min}$ (average birth size) and a largest size $x_{\max}$ (we may assume $x_{\max} \leq c$) for the fish population(s) being 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 $j = 0, 1, \ldots, N$

$(x_0 = x_{\min}, x_N = x_{\max})$. 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 $k = 0, 1, \ldots, K$ and $\Delta t = T/K$.

We denote by $S_j^{i,k}$ and $I_j^{i,k}$ the numerical approximations of the densities of susceptible and infected fish, $S^i(t_k, x_j)$ and $I^i(t_k, x_j)$, respectively. 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, and I^i, 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 ρ_j^i the values of $g^i(P^k, x_j)$, $\tilde{g}^i(P^k, x_j)$, $\mu^i(P^k, x_j)$, $\tilde{\mu}^i(P^k, x_j)$, $\beta^i(P^k, x_j)$, $\tilde{\beta}^i(P^k, x_j)$, $c_1^i(x_j)$, $\tilde{c}_1^i(x_j)$, $c_2^i(x_j)$, $\tilde{c}_2^i(x_j)$, and $\rho^i(x_j)$, respectively.

We define the finite difference operators

$$\Delta_+ u_j^{i,k} = u_{j+1}^{i,k} - u_j^{i,k}, \quad 0 \le j \le N - 1, \quad \Delta_- u_j^{i,k} = u_j^{i,k} - u_{j-1}^{i,k}, \quad 1 \le j \le N.$$

We define total variation, the ℓ_1 norm, and the ℓ_∞ norm by

$$\mathrm{TV}(u^{i,k}) = \sum_{j=0}^{N-1} |u_{j+1}^{i,k} - u_j^{i,k}|,$$

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

A special summation notation will be used throughout the paper and is defined by

$$\sum_{j=j_1}^{j_2}{}^{\star} a_j^{i,k} = \frac{3}{2}a_{j_1}^{i,k} + \frac{1}{2}a_{j_2}^{i,k} + \sum_{j=j_1+1}^{j_2-1} a_j^{i,k}. \tag{7}$$

We develop the discretization of Equation (2) by using the discretization of Equation (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 the result is

$$\frac{S_j^{i,k+1} - S_j^{i,k}}{\Delta t} + \frac{h_{j+1/2}^{i,k} - h_{j-1/2}^{i,k}}{\Delta x} + \mu_j^{i,k} S_j^{i,k+1} + L_j^{i,k} S_j^{i,k+1} = 0,$$

$$\frac{I_j^{i,k+1} - I_j^{i,k}}{\Delta t} + \frac{\hat{h}_{j+1/2}^{i,k} - \hat{h}_{j-1/2}^{i,k}}{\Delta x} + \tilde{\mu}_j^{i,k} I_j^{i,k+1} - L_j^{i,k} S_j^{i,k+1} = 0,$$

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

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

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

$$\tag{9}$$

where $0 \le k \le K - 1$ and $1 \le j \le N$.

The numerical fluxes, $h_{j+1/2}^{i,k}$ and $\hat{h}_{j+1/2}^{i,k}$, are given by

$$
h_{j+1/2}^{i,k} = \begin{cases} g_j^{i,k} S_j^{i,k} + \dfrac{g_{j+1}^{i,k} - g_j^{i,k}}{2} S_j^{i,k} + \dfrac{g_j^{i,k}}{2} mm(\Delta_+ S_j^{i,k}, \Delta_- S_j^{i,k}), & j = 2, \ldots, N-2, \\ g_j^{i,k} S_j^{i,k}, & j = 0, 1, N-1, N, \end{cases}
$$

$$
\hat{h}_{j+1/2}^{i,k} = \begin{cases} \tilde{g}_j^{i,k} I_j^{i,k} + \dfrac{\tilde{g}_{j+1}^{i,k} - \tilde{g}_j^{i,k}}{2} I_j^{i,k} + \dfrac{\tilde{g}_j^{i,k}}{2} mm(\Delta_+ I_j^{i,k}, \Delta_- I_j^{i,k}), & j = 2, \ldots, N-2, \\ \tilde{g}_j^{i,k} I_j^{i,k}, & j = 0, 1, N-1, N, \end{cases}
\tag{10}
$$

where $mm(a,b) = ((sign(a) + sign(b))/2) \, \min(|a|, |b|)$. We would like the reader to note that

$$
0 \le \frac{mm(a,b)}{a} \le 1, \quad 0 \le \frac{mm(a,b)}{b} \le 1, \quad \forall a, b \ne 0.
\tag{11}
$$

Clearly, the scheme (9) is second-order accurate in space except at the boundary, where it is first-order accurate. This guarantees second-order accuracy in space in the L^1 norm. In order to calculate the values at the boundary for susceptible fish, and the total population at each time step, t_k, we use a right-hand rectangular rule on the first interval and the trapezoid rule on the remaining intervals. This gives the following quadrature rules:

$$
g_0^{i,k} S_0^{i,k} = \sum_{\ell=1}^{m} p^{i\ell} \sum_{j=1}^{N} {}^{\star} (\beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k}) \Delta x,
\tag{12}
$$

$$
P^k = \sum_{i=1}^{m} \sum_{j=1}^{N} {}^{\star} (S_j^{i,k} + I_j^{i,k}) \Delta x.
\tag{13}
$$

We note that the approximations (12) and (13) are second-order accurate in space. Additionally, as previously mentioned, there is no vertical transmission of the disease and therefore the boundary condition for infected fish is given as

$$
I_0^{i,k} = 0.
\tag{14}
$$

The five equations of Equation (9) can be written as follows:

$$
S_j^{i,k+1}(1 + \Delta t \mu_j^{i,k} + \Delta t L_j^{i,k}) = S_j^{i,k} - \frac{\Delta t}{\Delta x}(h_{j+1/2}^{i,k} - h_{j-1/2}^{i,k}),
$$

$$
I_j^{i,k+1}(1 + \Delta t \tilde{\mu}_j^{i,k}) = I_j^{i,k} - \frac{\Delta t}{\Delta x}(\hat{h}_{j+1/2}^{i,k} - \hat{h}_{j-1/2}^{i,k}) + \Delta t L_j^{i,k} S_j^{i,k+1},
$$

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

$$
B_u^{k+1}\left(1 + \Delta t c_M M^* + \Delta t \delta_1 P^{k+1} + \Delta t \sum_{i=1}^{m} \sum_{j=1}^{N} {}^{\star} (c_{1,j}^i S_j^{i,k+1} + \tilde{c}_{1,j}^i I_j^{i,k+1}) \Delta x \right)
\tag{15}
$$

$$
= B_u^k + \Delta t H^k + \Delta t \lambda B_a^{k+1},
$$

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

$$
= M^k + \Delta t \epsilon c_M M^* B_u^{k+1},
$$

for $i = 1, \ldots, m, \ k = 1, \ldots, K - 1$. We shall denote by

$$
F_j^{i,k} =
\begin{cases}
g_j^{i,k}, & j = 1, N, \\[2mm]
\dfrac{1}{2}\left(g_{j+1}^{i,k} + g_j^{i,k} + g_j^{i,k} \dfrac{mm(\Delta_+ S_j^{i,k}, \Delta_- S_j^{i,k})}{\Delta_- S_j^{i,k}} \right), & j = 2, \\[4mm]
\dfrac{1}{2}\left(g_{j+1}^{i,k} + g_j^{i,k} + g_j^{i,k} \dfrac{mm(\Delta_+ S_j^{i,k}, \Delta_- S_j^{i,k})}{\Delta_- S_j^{i,k}}, \right. \\[4mm]
\qquad \left. - g_{j-1}^{i,k} \dfrac{mm(\Delta_- S_j^{i,k}, \Delta_- S_{j-1}^{i,k})}{\Delta_- S_j^{i,k}} \right), & j = 3, \ldots, N - 2, \\[4mm]
\dfrac{1}{2}\left(2 g_j^{i,k} - g_{j-1}^{i,k} \dfrac{mm(\Delta_- S_j^{i,k}, \Delta_- S_{j-1}^{i,k})}{\Delta_- S_j^{i,k}} \right), & j = N - 1,
\end{cases}
$$

and

$$
G_j^{i,k} =
\begin{cases}
\Delta_- g_j^{i,k}, & j = 1, N, \\[1mm]
\frac{1}{2}\Delta_+ g_j^{i,k} + \Delta_- g_j^{i,k}, & j = 2, \\[1mm]
\frac{1}{2}(\Delta_+ g_j^{i,k} + \Delta_- g_j^{i,k}), & j = 3, \ldots, N - 2, \\[1mm]
\frac{1}{2}\Delta_- g_j^{i,k}, & j = N - 1.
\end{cases}
$$

We use similar definitions for $\tilde{F}_j^{i,k}$ and $\tilde{G}_j^{i,k}$. Simple calculations show that

$$
0 \le F_j^{i,k}, \tilde{F}_j^{i,k} \le \tfrac{3}{2}c, \tag{16}
$$

and

$$
2(F_j^{i,k} - G_j^{i,k}) =
\begin{cases}
2 g_{j-1}^{i,k}, & j = 1, N, \\[2mm]
g_j^{i,k} + g_{j-1}^{i,k}\left(1 - \dfrac{mm(\Delta_- S_j^{i,k}, \Delta_- S_{j-1})}{\Delta_- S_j^{i,k}} \right), & j = N - 1, \\[3mm]
2 g_{j-1}^{i,k} + g_j^{i,k} \dfrac{mm(\Delta_+ S_j^{i,k}, \Delta_- S_j^{i,k})}{\Delta_- S_j^{i,k}}, & j = 2, \\[3mm]
g_j^{i,k}\left(1 + \dfrac{mm(\Delta_+ S_j^{i,k}, \Delta_- S_j^{i,k})}{\Delta_- S_j^{i,k}} \right), & j = 3, \ldots, N - 2.
\end{cases}
$$

A similar expression can be derived for $2(\tilde{F}_j^{i,k} - \tilde{G}_j^{i,k})$. Thus,

$$
F_j^{i,k} - G_j^{i,k} \ge 0 \quad \text{and} \quad \tilde{F}_j^{i,k} - \tilde{G}_j^{i,k} \ge 0. \tag{17}
$$

Introducing the above into Equation (15), one can compute the approximate solution explicitly in the order specified below. Beginning with Equation (15), then computing the approximations

in Equation (12) and finally the boundary condition for infected fish, we have

$$S_j^{i,k+1} = \frac{(1 - (\Delta t/\Delta x)F_j^{i,k})S_j^{i,k} + (\Delta t/\Delta x)(F_j^{i,k} - G_j^{i,k})S_{j-1}^{i,k}}{1 + \Delta t\mu_j^{i,k} + \Delta t L_j^{i,k}},$$

$$I_j^{i,k+1} = \frac{(1 - (\Delta t/\Delta x)\tilde{F}_j^{i,k})I_j^{i,k} + (\Delta t/\Delta x)(\tilde{F}_j^{i,k} - \tilde{G}_j^{i,k})I_{j-1}^{i,k} + \Delta t L_j^{i,k}S_j^{i,k+1}}{1 + \Delta t\tilde{\mu}_j^{i,k}},$$

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

$$B_u^{k+1} = \frac{B_u^k + \Delta t H^k + \Delta t\lambda B_a^{k+1}}{1 + \Delta t c_M M^* + \Delta t\delta_1 P^{k+1} + \Delta t \sum_{i=1}^m \sum_{j=1}^N {}^\star (c_{1,j}^i S_j^{i,k+1} + \tilde{c}_{1,j}^i I_j^{i,k+1})\Delta x}, \qquad (18)$$

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

$$S_0^{i,k+1} = \frac{1}{g_0^{i,k+1}} \sum_{\ell=1}^m p^{i\ell} \sum_{j=1}^N {}^\star (\beta_j^{\ell,k+1} S_j^{\ell,k+1} + \tilde{\beta}_j^{\ell,k+1} I_j^{\ell,k+1})\Delta x,$$

$$I_0^{i,k+1} = 0.$$

Within this paper, we will use the following CFL-type condition concerning Δt and Δx:

(A8)

$$\frac{1}{c} \geq \frac{\Delta t}{\Delta x}\frac{3}{2}.$$

4. Estimates for the finite difference approximations

We begin this section by showing that the system has a unique nonnegative solution and that the difference approximations are bounded in the ℓ_1 norm.

LEMMA 1 *The system* (9)–(12) *has a unique nonnegative solution.*

Proof Uniqueness is obvious from Equation (18). From (A5), we have that $S_j^{i,0}, I_j^{i,0}, B_a^0, B_u^0, M^0$ are nonnegative. Assume, for some $k > 0$, that $S_j^{i,k}, I_j^{i,k} \geq 0$ for $i = 1, \ldots, m, j = 1, \ldots, N$ and $B_a^k, B_u^k, M^k \geq 0$. By (A1), (A8), and Equation (16), we have

$$1 - \frac{\Delta t}{\Delta x}F_j^{i,k} \geq 1 - \frac{\Delta t}{\Delta x}c\frac{3}{2} \geq 0,$$

$$1 - \frac{\Delta t}{\Delta x}\tilde{F}_j^{i,k} \geq 1 - \frac{\Delta t}{\Delta x}c\frac{3}{2} \geq 0.$$

Hence, from Equations (17), (18), and Assumptions (A1)–(A7), $S_j^{i,k+1}, I_j^{i,k+1}, B_a^{k+1}, B_u^{k+1}, M^{k+1} \geq 0$ for $j = 1, \ldots, N$. From (A1) and (A3) and the last two equations of Equation (18), it follows that $S_0^{i,k+1} \geq 0$ and $I_0^{i,k+1} = 0$. This establishes the result. ∎

The next lemma shows that S^i and I^i are bounded in the ℓ_1 norm for $i = 1, \ldots, m$ and that the model variables, $B_a(t), B_u(t),$ and $M(t)$ are also bounded.

LEMMA 2 *There is a positive constant C_1 such that*

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

Proof We begin by multiplying the first equation of Equation (9) by $\Delta x \Delta t$ and collect like terms. Summing over $j = 1, \ldots, N$ and $i = 1, \ldots, m$ gives

$$\sum_{i=1}^{m}\sum_{j=1}^{N} S_j^{i,k+1}(1 + \Delta t \mu_j^{i,k})\Delta x = \sum_{i=1}^{m}\sum_{j=1}^{N} S_j^{i,k}\Delta x - \Delta t \sum_{i=1}^{m}\sum_{j=1}^{N}(h_{j+1/2}^{i,k} - h_{j-1/2}^{i,k})$$

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

Using (A1), (A2), Equation (12), the fact that $1 + \Delta t \mu_j^{i,k} \geq 1$, and collapsing the telescoping sum, we have

$$\sum_{i=1}^{m}\|S^{i,k+1}\|_1 \leq \sum_{i=1}^{m}\|S^{i,k}\|_1 + \Delta t \sum_{i=1}^{m}\sum_{\ell=1}^{m} p^{i\ell}\sum_{j=1}^{N}{}^{\star}(\beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k})\Delta x$$

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

By (A3), the definition in Equation (7), and since $\sum_{i=1}^{m} p^{i\ell} = 1$, we have

$$\sum_{i=1}^{m}\|S^{i,k+1}\|_1 \leq \left(1 + \frac{3}{2}c\Delta t\right)\sum_{i=1}^{m}\|S^{i,k}\|_1 + \frac{3}{2}c\Delta t \sum_{i=1}^{m}\|I^{i,k}\|_1 - \Delta t \sum_{i=1}^{m}\sum_{j=1}^{N} L_j^{i,k} S_j^{i,k+1}\Delta x. \quad (19)$$

Using similar techniques on the second equation of Equation (9), we have

$$\sum_{i=1}^{m}\|I^{i,k+1}\|_1 \leq \sum_{i=1}^{m}\|I^{i,k}\|_1 + \Delta t \sum_{i=1}^{m}\sum_{j=1}^{N} L_j^{i,k} S_j^{i,k+1}\Delta x. \quad (20)$$

Adding Equations (19) and (20), we obtain by Assumption (A5),

$$\sum_{i=1}^{m}(\|S^{i,k+1}\|_1 + \|I^{i,k+1}\|_1) \leq \left(1 + \frac{3}{2}c\Delta t\right)\sum_{i=1}^{m}(\|S^{i,k}\|_1 + \|I^{i,k}\|_1)$$

$$\leq e^{(3/2)cT}\sum_{i=1}^{m}(\|S^{i,0}\|_1 + \|I^{i,0}\|_1) \equiv C_{SI}. \quad (21)$$

Focusing on the third equation of Equation (18), we use Assumption (A7) and the definition in Equation (7) to determine

$$|B_a^{k+1}| \leq \left|B_a^k + \Delta t \sum_{i=1}^{m}\sum_{j=1}^{N}{}^{\star}\rho_j^i I_j^{i,k+1}\Delta x\right|$$

$$\leq |B_a^k| + \Delta t \frac{3}{2}c \sum_{i=1}^{m}\|I^{i,k+1}\|_1.$$

Thus,

$$|B_a^k| \leq |B_1^0| + T\frac{3}{2}cC_{SI}.$$

The bounds for B_u and M are established similarly. Hence, the result follows. ■

As a consequence of the above lemma, we now have that $0 \leq P^k \leq C_1$ for $k = 1, \ldots, K$. Hence, $g^i(P, x)$ is defined on a compact set and attains its minimum here. We let $0 < \alpha \leq \min g^i(P, x_0)$ for $P \in [0, C_1]$ and $i = 1, \ldots, m$. We denote $\mathbb{D} = [0, C_1] \times [x_{\min}, x_{\max}]$ and we will use this throughout the remainder of the paper. Now, we establish the bound on the infinity norms of the approximations $S_j^{i,k}$ and $I_j^{i,k}$.

LEMMA 3 *There exists a constant C_2 such that*

$$\|S^{i,k}\|_\infty + \|I^{i,k}\|_\infty \leq C_2.$$

Proof If $S_0^{i,k+1} = \|S^{i,k+1}\|_\infty$, then from the sixth equation of Equation (18), (A3), and using the fact that $p^{i\ell} \leq 1$, we have

$$S_0^{i,k+1} = \frac{1}{g_0^{i,k+1}} \sum_{\ell=1}^m p^{i\ell} \sum_{j=1}^N {}^\star (\beta_j^{\ell,k+1} S_j^{\ell,k+1} + \tilde{\beta}_j^{\ell,k+1} I_j^{\ell,k+1}) \Delta x$$

$$\leq \frac{3c}{2\alpha} \sum_{\ell=1}^m \sum_{j=1}^N (S_j^{\ell,k+1} + I_j^{\ell,k+1}) \Delta x,$$

$$\leq \frac{3c}{2\alpha} \sum_{\ell=1}^m (\|S^{\ell,k+1}\|_1 + \|I^{\ell,k+1}\|_1).$$

By Lemma 2

$$\|S^{i,k+1}\|_\infty \leq \frac{3c}{2\alpha} C_1.$$

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

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

Beginning with the first equation in Equation (18), using (A2), and Lemma 4, we have

$$S_{j_0}^{i,k+1} \leq \left(1 - \frac{\Delta t}{\Delta x} F_{j_0}^{i,k}\right) S_{j_0}^{i,k} + \frac{\Delta t}{\Delta x}(F_{j_0}^{i,k} - G_{j_0}^{i,k}) S_{j_0-1}^{i,k}.$$

Using the facts that $S_{j_0-1}^{i,k} \leq S_{j_0}^{i,k}$ and $F_{j_0}^{i,k} - G_{j_0}^{i,k} \geq 0$, we reach

$$S_{j_0}^{i,k+1} \leq S_{j_0}^{i,k} - \frac{\Delta t}{\Delta x} G_{j_0}^{i,k} S_{j_0}^{i,k}.$$

Note that for $1 \leq j \leq N$,

$$-G_j^{i,k} \leq \frac{3}{2} \max_{1 \leq j \leq N} (g_{j-1}^{i,k} - g_j^{i,k}).$$

Hence,

$$\|S^{i,k+1}\|_\infty \leq \|S^{i,k}\|_\infty + \frac{\Delta t}{\Delta x}\left(\frac{3}{2}\max_{1\leq j\leq N}(g_{j-1}^{i,k} - g_j^{i,k})\right)\|S^{i,k}\|_\infty,$$

$$\leq \|S^{i,k}\|_\infty + \frac{3}{2}\Delta t \max_{(P,x)\in\mathbb{D}}|g_x^i(P,x)|\|S^{i,k}\|_\infty,$$

$$\leq \left(1 + \frac{3}{2}c\Delta t\right)\|S^{i,k}\|_\infty.$$

Thus,

$$\|S^{i,k}\|_\infty \leq \max\left\{\frac{3c}{2\alpha}C_1\left(1 + \frac{3}{2}c\Delta t\right)^{k-1}, \left(1 + \frac{3}{2}c\Delta t\right)^k\|S^{i,0}\|_\infty\right\} < C_{2,S}. \tag{22}$$

We similarly consider $\|I^{i,k+1}\|_\infty$. Since $I_0^{i,k} = 0$ for $k = 1, \ldots, K$, $\|I^{i,k}\|_\infty$ cannot be obtained at the left boundary. Using (A1), Equations (16), (17), (22), Lemma 4, and methods similar to the above, we have

$$\|I^{i,k+1}\|_\infty \leq \left(1 + \frac{3}{2}c\Delta t\right)\|I^{i,k}\|_\infty + \Delta t 4c^3 C_1 C_{2,S}.$$

Therefore, we have

$$\|I^{i,k}\|_\infty \leq \left(1 + \frac{3}{2}c\Delta t\right)^k\|I^{i,0}\|_\infty + \sum_{\ell=0}^{k-1}\left(1 + \frac{3}{2}c\Delta t\right)^{k-1-\ell}\Delta t 4c^3 C_1 C_{2,S} < C_{2,I}. \tag{23}$$

Combining Equations (22) and (23) and letting $C_2 > C_{2,S} + C_{2,I}$, we obtain the result. ∎

The results contained in the following lemma are all necessary to show that the approximations $S_j^{i,k}$ and $I_j^{i,k}$ have bounded total variation.

LEMMA 4 *There exists positive constants C_3, C_4, C_5, and C_6 such that the following bounds hold*:

$$0 \leq L_j^{i,k} \leq C_3, \quad \mathrm{TV}(L^{i,k}) \leq C_4,$$

$$\left|\frac{P^{k+1} - P^k}{\Delta t}\right| \leq C_5, \quad \left|\sum_{i=1}^m(S_0^{i,k+1} - S_0^{i,k})\right| \leq C_6.$$

Proof It is easy to verify that $L_j^{i,k} \geq 0$ from Lemma 1 and Assumptions (A4) and (A7). Then from Equation (8) and incorporating Lemma 2 we have

$$L_j^{i,k} \leq c^2 C_1 + c^2 C_1 + c^3 C_1 + c^2 C_1 \equiv C_3.$$

From Equation (8), we have

$$L_{j+1}^{i,k} - L_j^{i,k} = \nu_3\zeta M^k(c_{2,j+1}^i - c_{2,j}^i) + \nu_4 B_u^k(c_{1,j+1}^i - c_{1,j}^i).$$

Applying absolute value and summing from $j = 0, \ldots, N-1$, we have

$$\sum_{j=0}^{N-1}|L_{j+1}^{i,k} - L_j^{i,k}| \leq \nu_3\zeta M^k\sum_{j=0}^{N-1}|c_{2,j+1}^i - c_{2,j}^i| + \nu_4 B_u^k\sum_{j=0}^{N-1}|c_{1,j+1}^i - c_{1,j}^i|.$$

Thus, from (A4), (A7), and Lemma 2

$$
\begin{aligned}
\mathrm{TV}(L^{i,k}) &\leq c^2 C_1 \, \mathrm{TV}(c_2^i) + c C_1 \, \mathrm{TV}(c_1^i) \\
&\leq c^3 C_1 + c^2 C_1 \equiv C_4.
\end{aligned}
$$

By Equation (13)

$$
P^{k+1} - P^k = \sum_{i=1}^{m} \sum_{j=1}^{N} {}^{\star} (S_j^{i,k+1} - S_j^{i,k})\Delta x + \sum_{i=1}^{m} \sum_{j=1}^{N} {}^{\star} (I_j^{i,k+1} - I^{i,k})\Delta x.
$$

Incorporating the first two equations of Equation (9), applying absolute value to both sides, then collecting like terms, we have

$$
\begin{aligned}
|P^{k+1} - P^k| \leq \frac{3}{2} \sum_{i=1}^{m} \Bigg\{ &\sum_{j=1}^{N} \left[\frac{\Delta t}{\Delta x} |h_{j+1/2}^{i,k} - h_{j-1/2}^{i,k}| + \Delta t \mu_j^{i,k} S_j^{i,k+1} \right] \\
&+ \sum_{j=1}^{N} \left[\frac{\Delta t}{\Delta x} |\hat{h}_{j+1/2}^{i,k} - \hat{h}_{j-1/2}^{i,k}| + \Delta t \tilde{\mu}_j^{i,k} I_j^{i,k+1} \right] \Bigg\} \Delta x.
\end{aligned}
$$

Collapsing the telescoping sums, acknowledging $g_N^{i,k}, \tilde{g}_N^{i,k}, I_0^{i,k+1} = 0$, and incorporating the boundary condition from Equation (12) result in

$$
\begin{aligned}
|P^{k+1} - P^k| \leq \frac{3}{2} \sum_{i=1}^{m} \Bigg\{ &\sum_{\ell=1}^{m} p^{i\ell} \sum_{j=1}^{N} {}^{\star} (\beta_j^{\ell,k} S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k} I_j^{\ell,k}) \Delta x \Delta t + \sum_{j=1}^{N} \mu_j^{i,k} S_j^{i,k+1} \Delta t \Delta x \\
&+ \sum_{j=1}^{N} \tilde{\mu}_j^{i,k} I_j^{i,k+1} \Delta t \Delta x \Bigg\}.
\end{aligned}
$$

Using (A2), (A3) and the fact that $\sum_{i=1}^{m} p^{i\ell} = 1$ secures

$$
\begin{aligned}
|P^{k+1} - P^k| &\leq \frac{3}{2} \Bigg\{ \frac{3}{2} c \sum_{\ell=1}^{m} (\|S^{\ell,k}\|_1 + \|I^{\ell,k}\|_1)\Delta t + c \sum_{i=1}^{m} (\|S^{i,k+1}\|_1 + \|I^{i,k+1}\|_1)\Delta t \Bigg\} \\
&\leq \frac{15}{4} c C_1 \Delta t \equiv C_5 \Delta t.
\end{aligned}
$$

From the sixth equation of Equation (18), we have

$$
\begin{aligned}
\sum_{i=1}^{m} (S_0^{i,k+1} - S_0^{i,k}) \leq \frac{1}{\alpha} \sum_{i=1}^{m} \sum_{\ell=1}^{m} p^{i\ell} \Bigg[&\frac{3}{2} (\beta_1^{\ell,k+1} S_1^{\ell,k+1} - \beta_1^{\ell,k} S_1^{\ell,k})\Delta x + \frac{3}{2} (\tilde{\beta}_1^{\ell,k+1} I_1^{\ell,k+1} - \tilde{\beta}_1^{\ell,k} I_1^{\ell,k})\Delta x \\
&+ \frac{1}{2} (\beta_N^{\ell,k+1} S_N^{\ell,k+1} - \beta_N^{\ell,k} S_N^{\ell,k})\Delta x + \frac{1}{2} (\tilde{\beta}_N^{\ell,k+1} I_N^{\ell,k+1} - \tilde{\beta}_N^{\ell,k} I_N^{\ell,k})\Delta x \\
&+ \sum_{j=2}^{N-1} (\beta_j^{\ell,k+1} S_j^{\ell,k+1} - \beta_j^{\ell,k} S_j^{\ell,k})\Delta x) + \sum_{j=2}^{N-1} (\tilde{\beta}_j^{\ell,k+1} I_j^{\ell,k+1} - \tilde{\beta}_j^{\ell,k} I_j^{\ell,k})\Delta x \Bigg].
\end{aligned}
$$

$$(24)$$

By a simple manipulation, we have

$$\sum_{i=1}^{m}(S_0^{i,k+1} - S_0^{i,k}) \leq \frac{3}{2\alpha} \sum_{i=1}^{m}\sum_{\ell=1}^{m} p^{i\ell} \sum_{j=1}^{N}(\beta_j^{\ell,k+1}S_j^{\ell,k+1} - \beta_j^{\ell,k}S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k+1}I_j^{\ell,k+1} - \tilde{\beta}_j^{\ell,k}I_j^{\ell,k})\Delta x.$$

Using similar methods from the proof of Lemma 7 in [8], we see that there is a positive constant ω_1 such that

$$\left|\sum_{i=1}^{m}\sum_{\ell=1}^{m} p^{i\ell} \sum_{j=1}^{N}(\beta_j^{\ell,k+1}S_j^{\ell,k+1} - \beta_j^{\ell,k}S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k+1}I_j^{\ell,k+1} - \tilde{\beta}_j^{\ell,k}I_j^{\ell,k})\Delta x\right|$$

$$= \left|\sum_{\ell=1}^{m} \sum_{j=1}^{N}(\beta_j^{\ell,k+1}S_j^{\ell,k+1} - \beta_j^{\ell,k}S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k+1}I_j^{\ell,k+1} - \tilde{\beta}_j^{\ell,k}I_j^{\ell,k})\Delta x\right|,$$

$$\leq \omega_1\Delta t.$$

Hence,

$$\left|\sum_{i=1}^{m}(S_0^{i,k+1} - S_0^{i,k})\right| \leq \frac{3}{2\alpha}\omega_1\Delta t \equiv C_6\Delta t.$$

∎

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

LEMMA 5 *There exists a positive constant C_7 such that*

$$\mathrm{TV}(S^{i,k}) + \mathrm{TV}(I^{i,k}) \leq C_7.$$

Proof We begin by rewriting the first equation of Equation (18) as

$$S_j^{i,k+1}(1 + \Delta t\mu_j^{i,k} + \Delta tL_j^{i,k}) = S_j^{i,k} - \frac{\Delta t}{\Delta x}F_j^{i,k}(S_j^{i,k} - S_{j-1}^{i,k}) - \frac{\Delta t}{\Delta x}G_j^{i,k}S_{j-1}^{i,k}.$$

Then,

$$S_{j+1}^{i,k+1}(1 + \Delta t\mu_{j+1}^{i,k} + \Delta tL_{j+1}^{i,k}) - S_j^{i,k+1}(1 + \Delta t\mu_j^{i,k} + \Delta tL_j^{i,k})$$

$$= S_{j+1}^{i,k} - \frac{\Delta t}{\Delta x}F_{j+1}^{i,k}(S_{j+1}^{i,k} - S_j^{i,k}) - \frac{\Delta t}{\Delta x}G_{j+1}^{i,k}S_j^{i,k}$$

$$- S_j^{i,k} + \frac{\Delta t}{\Delta x}F_j^{i,k}(S_j^{i,k} - S_{j-1}^{i,k}) + \frac{\Delta t}{\Delta x}G_j^{i,k}S_{j-1}^{i,k}.$$

Grouping terms in an appropriate way, we have

$$(1 + \Delta t\mu_{j+1}^{i,k} + \Delta tL_{j+1}^{i,k})(S_{j+1}^{i,k+1} - S_j^{i,k+1}) + \Delta tS_j^{i,k+1}(\mu_{j+1}^{i,k} - \mu_j^{i,k}) + \Delta tS_j^{i,k+1}(L_{j+1}^{i,k} - L_j^{i,k})$$

$$= (S_{j+1}^{i,k} - S_j^{i,k}) - \frac{\Delta t}{\Delta x}F_{j+1}^{i,k}(S_{j+1}^{i,k} - S_j^{i,k}) - \frac{\Delta t}{\Delta x}G_{j+1}^{i,k}S_j^{i,k}$$

$$+ \frac{\Delta t}{\Delta x}F_j^{i,k}(S_j^{i,k} - S_{j-1}^{i,k}) + \frac{\Delta t}{\Delta x}G_j^{i,k}S_{j-1}^{i,k}.$$

Rearranging the terms in the previous equation yields

$$
(1 + \Delta t \mu_{j+1}^{i,k} + \Delta t L_{j+1}^{i,k})(S_{j+1}^{i,k+1} - S_j^{i,k+1})
$$

$$
= (S_{j+1}^{i,k} - S_j^{i,k})\left(1 - \frac{\Delta t}{\Delta x}F_{j+1}^{i,k}\right) + \frac{\Delta t}{\Delta x}(F_j^{i,k} - G_j^{i,k})(S_j^{i,k} - S_{j-1}^{i,k})
$$

$$
- \frac{\Delta t}{\Delta x}S_j^{i,k}(G_{j+1}^{i,k} - G_j^{i,k}) - \Delta t S_j^{i,k+1}(\mu_{j+1}^{i,k} - \mu_j^{i,k}) - \Delta t S_j^{i,k+1}(L_{j+1}^{i,k} - L_j^{i,k}).
$$

We now apply the absolute value, then sum over $j = 1, \ldots, N - 1$ and use the fact that $1 + \Delta t \mu_{j+1}^{i,k} + \Delta t L_{j+1}^{i,k} \geq 1$ to obtain

$$
\mathrm{TV}(S^{i,k+1}) \leq (1 + \Delta t \mu_1^{i,k} + \Delta t L_1^{i,k})|S_1^{i,k+1} - S_0^{i,k+1}|
$$

$$
+ \sum_{j=1}^{N-1}\left|(S_{j+1}^{i,k} - S_j^{i,k})\left(1 - \frac{\Delta t}{\Delta x}F_{j+1}^{i,k}\right) + \frac{\Delta t}{\Delta x}(F_j^{i,k} - G_j^{i,k})(S_j^{i,k} - S_{j-1}^{i,k})\right|
$$

$$
+ \frac{\Delta t}{\Delta x}\sum_{j=1}^{N-1}S_j^{i,k}|G_{j+1}^{i,k} - G_j^{i,k}|
$$

$$
+ \Delta t \sum_{j=1}^{N-1}S_j^{i,k+1}(|\mu_{j+1}^{i,k} - \mu_j^{i,k}| + |L_{j+1}^{i,k} - L_j^{i,k}|). \tag{25}
$$

We now estimate each term separately. Incorporating the first equation from Equation (18), (A1), (A2), and Lemma 4 into the first term on the right-hand side of Equation (25), we have

$$
(1 + \Delta t \mu_1^{i,k} + \Delta t L_1^{i,k})|S_1^{i,k+1} - S_0^{i,k+1}|
$$

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

$$
\leq |S_1^{i,k} - S_0^{i,k}|\left(1 - \frac{\Delta t}{\Delta x}g_1^{i,k}\right) + |S_0^{i,k+1} - S_0^{i,k}|
$$

$$
+ \frac{\Delta t}{\Delta x}S_0^{i,k}|g_1^{i,k} - g_0^{i,k}| + \Delta t S_0^{i,k}(\mu_1^{i,k} + L_1^{i,k})
$$

$$
\leq |S_1^{i,k} - S_0^{i,k}|\left(1 - \frac{\Delta t}{\Delta x}g_1^{i,k}\right) + C_6\Delta t + cC_2\Delta t + C_2(c + C_3)\Delta t. \tag{26}
$$

For the second term on the right-hand side of Equation (25), we use (A1) to realize

$$
\sum_{j=1}^{N-1}\left|(S_{j+1}^{i,k} - S_j^{i,k})\left(1 - \frac{\Delta t}{\Delta x}F_{j+1}^{i,k}\right) + \frac{\Delta t}{\Delta x}(F_j^{i,k} - G_j^{i,k})(S_j^{i,k} - S_{j-1}^{i,k})\right|
$$

$$
\leq \sum_{j=1}^{N-1}|S_{j+1}^{i,k} - S_j^{i,k}| - \frac{\Delta t}{\Delta x}\sum_{j=1}^{N-1}(F_{j+1}^{i,k}|S_{j+1}^{i,k} - S_j^{i,k}| - F_j^{i,k}|S_j^{i,k} - S_{j-1}^{i,k}|)
$$

$$
+ \Delta t \sum_{j=1}^{N-1}\frac{3}{2}\max_{(P,x)\in\mathbb{D}}|g_x^i(P,x)||S_j^{i,k} - S_{j-1}^{i,k}|
$$

$$
\leq \sum_{j=1}^{N-1}|S_{j+1}^{i,k} - S_j^{i,k}| + \frac{\Delta t}{\Delta x}g_1^{i,k}|S_1^{i,k} - S_0^{i,k}| + \frac{3}{2}c\Delta t\sum_{j=1}^{N-1}|S_j^{i,k} - S_{j-1}^{i,k}|. \tag{27}
$$

Adding Equations (26) and (27), we determine

$$(1 + \Delta t \mu_1^{i,k} + \Delta t L_1^{i,k})|S_1^{i,k+1} - S_0^{i,k+1}|$$

$$+ \sum_{j=1}^{N-1} \left| (S_{j+1}^{i,k} - S_j^{i,k}) \left(1 - \frac{\Delta t}{\Delta x} F_{j+1}^{i,k} \right) + \frac{\Delta t}{\Delta x} (F_j^{i,k} - G_j^{i,k})(S_j^{i,k} - S_{j-1}^{i,k}) \right|$$

$$\leq \text{TV}(S^{i,k}) \left(1 + \frac{3}{2} c \Delta t \right) + C_6 \Delta t + c C_2 \Delta t + C_2 (c + C_3) \Delta t.$$

Incorporating (A1), and Lemmas 2 and 3 into the third term on the right-hand side of Equation (25), we have

$$\frac{\Delta t}{\Delta x} \sum_{j=1}^{N-1} S_j^{i,k} |G_{j+1}^{i,k} - G_j^{i,k}| = \frac{\Delta t}{\Delta x} \sum_{j=3}^{N-3} S_j^{i,k} |G_{j+1}^{i,k} - G_j^{i,k}| + \frac{\Delta t}{\Delta x} \sum_{j=1,2,N-1,N-2} S_j^{i,k} |G_{j+1}^{i,k} - G_j^{i,k}|$$

$$\leq \frac{\Delta t}{\Delta x} \sum_{j=3}^{N-3} S_j^{i,k} \frac{1}{2} |(g_{j+2}^{i,k} - 2g_{j+1}^{i,k} + g_j^{i,k}) + (g_{j+1}^{i,k} - 2g_j^{i,k} + g_{j-1}^{i,k})|$$

$$+ 8 \frac{\Delta t}{\Delta x} \frac{3}{2} \sum_{j=1,2,N-1,N-2} S^{i,k} \max_{0 \leq j \leq N-1} |g_{j+1}^{i,k} - g_j^{i,k}|$$

$$\leq \Delta t \|S^{i,k}\|_1 \max_{(P,x) \in \mathbb{D}} |g_{xx}^i(P,x)| + 8 \Delta t \frac{3}{2} \|S^{i,k}\|_\infty \max_{(P,x) \in \mathbb{D}} |g_x^i(P,x)|$$

$$\leq c C_1 \Delta t + 12 c C_2 \Delta t.$$

For the last term on the right-hand side of Equation (25), we use (A2), and Lemmas 4 and 3 to obtain

$$\Delta t \sum_{j=1}^{N-1} S_j^{i,k+1} \left(\left| \frac{\mu_{j+1}^{i,k} - \mu_j^{i,k}}{\Delta x} \right| \Delta x + |L_{j+1}^{i,k} - L_j^{i,k}| \right)$$

$$\leq \Delta t \|S^{i,k+1}\|_1 \max_{(P,x) \in \mathbb{D}} |\mu_x^i(P,x)| + \Delta t \|S^{i,k+1}\|_\infty \text{TV}(L^{i,k})$$

$$\leq c C_1 \Delta t + C_2 C_3 \Delta t.$$

We let

$$C_{7,S} = C_6 + c C_2 + C_2(c + C_3) + c C_1 + 12 c C_2 + c C_1 + C_2 C_3,$$

and therefore have

$$\text{TV}(S^{i,k+1}) \leq \text{TV}(S^{i,k}) \left(1 + \frac{3}{2} c \Delta t \right) + C_{7,S} \Delta t$$

$$\leq \text{TV}(S^{i,0}) \left(1 + \frac{3}{2} c \Delta t \right)^{k+1} + \sum_{l=1}^{k+1} C_{7,S} \left(1 + \frac{3}{2} c \Delta t \right)^{k+1-l} \Delta t. \tag{28}$$

Using similar methods beginning with the fourth equation of Equation (18), then using (A1), (A2), Lemmas 2 and 4, and letting

$$C_{7,I} = C_3 C_2 + c C_1 + 12 c C_2 + C_2 C_4 + \text{TV}(S^{i,k+1}) C_3 + c C_4,$$

we find that

$$
\begin{aligned}
\mathrm{TV}(I^{i,k+1}) &\le \mathrm{TV}(I^{i,k})\left(1 + \frac{3}{2}c\right) + C_{7,I}\Delta t \\
&\le \mathrm{TV}(I^{i,0})\left(1 + \frac{3}{2}c\Delta t\right) + \sum_{l=1}^{k+1} C_{7,I}\left(1 + \frac{3}{2}c\Delta t\right)^{k+1-l}\Delta t.
\end{aligned}
\tag{29}
$$

Combining Equations (28) and (29), we have established the result. ■

The next lemma shows that the numerical approximations satisfy a Lipschitz-type condition in t.

LEMMA 6　*There is a positive constant C_8 such that for any integers $q_1 > q_2 \ge 0$*

$$
\sum_{j=1}^{N}\left|\frac{S_j^{i,q_1} - S_j^{i,q_2}}{\Delta t}\right|\Delta x \le C_8(q_1 - q_2), \quad \sum_{j=1}^{N}\left|\frac{I_j^{i,q_1} - I_j^{i,q_2}}{\Delta t}\right|\Delta x \le C_8(q_1 - q_2),
$$

$$
\left|\frac{B_a^{q_1} - B_a^{q_2}}{\Delta t}\right| \le C_8(q_1 - q_2), \quad \left|\frac{B_u^{q_1} - B_u^{q_2}}{\Delta t}\right| \le C_8(q_1 - q_2), \quad \left|\frac{M^{q_1} - M^{q_2}}{\Delta t}\right| \le C_8(q_1 - q_2).
$$

Proof　From the first equation of Equation (18), applying (A1), (16), and Lemmas 2–5, we have

$$
\begin{aligned}
\sum_{j=1}^{N}\left|\frac{S_j^{i,k+1} - S_j^{i,k}}{\Delta t}\right|\Delta x &= \sum_{j=1}^{N}\left|\frac{F_j^{i,k}(S_j^{i,k} - S_{j-1}^{i,k}) + G_j^{i,k}S_{j-1}^{i,k} + S_j^{i,k}(\mu_j^{i,k} + L_j^{i,k})\Delta x}{1 + \Delta t\mu_j^{i,k} + \Delta t L_j^{i,k}}\right|, \\
&\le \sum_{j=1}^{N}(F_j^{i,k}|S_j^{i,k} - S_{j-1}^{i,k}| + |G_j^{i,k}|S_{j-1}^{i,k} + S_j^{i,k}(\mu_j^{i,k} + L_j^{i,k})\Delta x), \\
&\le \frac{3}{2}c\,\mathrm{TV}(S^{i,k}) + \frac{3}{2}\max_{(P,x)\in\mathbb{D}}|g_x^i(P,x)|\|S^{i,k}\|_1 + \|S^{i,k}\|_1(c + C_2), \\
&\le \frac{3}{2}cC_7 + \left(\frac{5}{2}c + C_3\right)C_1 \equiv C_{8,S}.
\end{aligned}
$$

Therefore,

$$
\begin{aligned}
\sum_{j=1}^{N}\left|\frac{S_j^{i,q_1} - S_j^{i,q_2}}{\Delta t}\right|\Delta x &\le \sum_{k=q_2}^{q_1}\sum_{j=1}^{N}\left|\frac{S_j^{i,k+1} - S_j^{i,k}}{\Delta t}\right|\Delta x, \\
&\le C_{8,S}(q_1 - q_2).
\end{aligned}
\tag{30}
$$

Turning our attention to the second equation of Equation (18), and following similar arguments as above, we obtain

$$
\begin{aligned}
\sum_{j=1}^{N}\left|\frac{I_j^{i,k+1} - I_j^{i,k}}{\Delta t}\right|\Delta x &\le \sum_{j=1}^{N}\left|\frac{\tilde{F}_j^{i,k}(I_j^{i,k} - I_{j-1}^{i,k}) + \tilde{G}_j^{i,k}I_{j-1}^{i,k} + \Delta t\tilde{\mu}_j^{i,k}I_j^{i,k} + \Delta t L_j^{i,k}S_j^{i,k}}{1 + \Delta t\tilde{\mu}_j^{i,k}}\right|, \\
&\le \sum_{j=1}^{N}(\tilde{F}_j^{i,k}|I_j^{i,k} - I_{j-1}^{i,k}| + |\tilde{G}_j^{i,k}|I_{j-1}^{i,k} + \Delta t\tilde{\mu}_j^{i,k}I_j^{i,k} + \Delta t L_j^{i,k}S_j^{i,k}),
\end{aligned}
$$

$$\leq \frac{3}{2} c \, \mathrm{TV}(I^{i,k}) + \frac{3}{2} \max_{(P,x) \in \mathbb{D}} |\tilde{g}_x^i(P,x)| \|I^{i,k}\|_1 + c\|I^{i,k}\|_1 + C_2 \|S^{i,k+1}\|_1,$$

$$\leq \frac{3}{2} c C_7 + \left(\frac{5}{2} c + C_3\right) C_1 \equiv C_{8,I}.$$

Thus,

$$\sum_{j=1}^{N} \left| \frac{I_j^{i,q_1} - I_j^{i,q_2}}{\Delta t} \right| \Delta x \leq \sum_{k=q_2}^{q_1} \sum_{j=1}^{N} \left| \frac{I_j^{i,k+1} - I_j^{i,k}}{\Delta t} \right| \Delta x$$

$$\leq C_{8,I}(q_1 - q_2). \tag{31}$$

The bounds for the third, fourth, and fifth equations of Equation (18) are established in a very similar manner as was used in [8] and are

$$\left| \frac{B_a^{q_1} - B_a^{q_2}}{\Delta t} \right| = \sum_{k=q_2}^{q_1} \left| \frac{B_a^{k+1} - B_a^k}{\Delta t} \right| \leq c C_1 \left(\frac{5}{2} + C_1\right)(q_1 - q_2),$$

$$\left| \frac{B_u^{q_1} - B_u^{q_2}}{\Delta t} \right| = \sum_{k=q_2}^{q_1} \left| \frac{B_u^{k+1} - B_u^k}{\Delta t} \right| \leq (c + cC_1 + c^2 C_1 + 2cC_1^2)(q_1 - q_2), \tag{32}$$

$$\left| \frac{M^{q_1} - M^{q_2}}{\Delta t} \right| = \sum_{k=q_2}^{q_1} \left| \frac{M^{k+1} - M^k}{\Delta t} \right| \leq cC_1(c^2 + cC_1 + C_1 + 1)(q_1 - q_2).$$

Hence, the result follows.   ∎

5. Convergence of the difference approximations to the unique weak solution

Following [37], 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

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

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

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

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

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

for $x \in [x_j, x_{j+1})$, $t \in [t_k, t_{k+1})$, where $j = 0, \ldots, N-1$ and $k = 0, \ldots, K-1$. 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 $i = 1, \ldots, m$. Also, $\{\mathbb{B}_{a_{\Delta t}}\}$, $\{\mathbb{B}_{u_{\Delta t}}\}$, and $\{\mathbb{M}_{\Delta t}\}$ are compact in the topology of $C(0, T)$.

THEOREM 7   *There exist sequences* $\{\mathbb{S}_{\Delta t_l, \Delta x_l}^i\} \subset \{\mathbb{S}_{\Delta t, \Delta x}^i\}$ *and* $\{\mathbb{I}_{\Delta t_l, \Delta x_l}^i\} \subset \{\mathbb{I}_{\Delta t, \Delta x}^i\}$ *that converge to* $BV([0, T] \times [x_{\min}, x_{\max}])$ *functions* $S^i(t, x)$ *and* $I^i(t, x)$, *respectively, for each* $i = i, \ldots, m$. *There are also sequences* $\{\mathbb{B}_{a_{\Delta t_l}}\} \subset \{\mathbb{B}_{a_{\Delta t}}\}$, $\{\mathbb{B}_{u_{\Delta t_l}}\} \subset \{\mathbb{B}_{u_{\Delta t}}\}$, *and* $\{\mathbb{M}_{\Delta t_l}\} \subset \{\mathbb{M}_{\Delta t}\}$ *that converge,*

respectively, to functions $B_a(t)$, $B_u(t)$, and $M(t) \in C[0, T]$. This happens in the sense that for all $t > 0$

$$\int_{x_{\min}}^{x_{\max}} |\mathbb{S}_{\Delta t_l, \Delta x_l}^i(t, x) - S^i(t, x)| \, dx \to 0,$$

$$\int_{x_{\min}}^{x_{\max}} |\mathbb{I}_{\Delta t_l, \Delta x_l}^i(t, x) - I^i(t, x)| \, dx \to 0,$$

$$\int_0^T \int_{x_{\min}}^{x_{\max}} |\mathbb{S}_{\Delta t_l, \Delta x_l}^i(t, x) - S^i(t, x)| \, dx \, dt \to 0,$$

$$\int_0^T \int_{x_{\min}}^{x_{\max}} |\mathbb{I}_{\Delta t_l, \Delta x_l}^i(t, x) - I^i(t, x)| \, dx \, dt \to 0,$$

and

$$\max_{t \in [0,T]} |\mathbb{B}_{a_{\Delta t_l}}(t) - B_a(t)| \to 0, \quad \max_{t \in [0,T]} |\mathbb{B}_{u_{\Delta t_l}}(t) - B_u(t)| \to 0, \quad \max_{t \in [0,T]} |\mathbb{M}_{\Delta t_l}(t) - M(t)| \to 0,$$

for each i and as $l \to \infty$. Furthermore, there exists a positive constant C_8 such that the limit functions satisfy

$$\|S\|_{BV([0,T] \times [x_{\min}, x_{\max}])} + \|I\|_{BV([0,T] \times [x_{\min}, x_{\max}])} + \|B_a\|_{C[0,T]} + \|B_u\|_{C[0,T]} + \|M\|_{C[0,T]} \le C_8.$$

Proof The results for $S^i(t, x)$ and $I^i(t, x)$ follow from Lemmas 2 to 6 and the proof of Lemma 16.7 in [37, p. 276]. The results for $B_a(t)$, $B_u(t)$, and $M(t)$ follow from the Ascoli-Arzela theorem [42, p. 74]. ∎

In the next theorem, we show that the set of limit functions $S^i(t, x)$, $I^i(t, x)$, $B_a(t)$, $B_u(t)$, and $M(t)$ constructed from our difference scheme is a weak solution of Equations (2)–(4).

THEOREM 8 *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 7 is a weak solution of Equations (2)–(4) and satisfies*

$$\|S^i(t, \cdot)\|_1 + \|I^i(t, \cdot)\|_1 + |B_a(t)| + |B_u(t)| + |M(t)| \le C_9$$

and

$$\|S^i\|_{L^\infty((0,T) \times (x_{\min}, x_{\max}))} + \|L^i\|_{L^\infty((0,T) \times (x_{\min}, x_{\max}))} + \|B_a\|_{C[0,T]} + \|B_u\|_{C[0,T]} + \|M\|_{C[0,T]} \le C_{10},$$

for some positive constants C_9 and C_{10}.

Proof Let $\varphi^i, \varsigma^i \in C^1([0, T] \times [x_{\min}, x_{\max}])$ for $i = 1, \ldots, m$ and denote the finite difference approximations of $\varphi^i(t_k, x_j)$, $\varsigma^i(t_k, x_j)$ by $\varphi_j^{i,k}$ and $\varsigma_j^{i,k}$, respectively. Multiplying the first equation of (9) by $\varphi_j^{i,k+1}$ and rearranging terms, we arrive at

$$S_j^{i,k+1} \varphi_j^{i,k+1} - S_j^{i,k} \varphi_j^{i,k} = S_j^{i,k} (\varphi_j^{i,k+1} - \varphi_j^{i,k}) - \Delta t \varphi_j^{i,k+1} S_j^{i,k+1} (\mu_j^{i,k} + L_j^{i,k})$$
$$+ \frac{\Delta t}{\Delta x} (h_{j-1/2}^{i,k} (\varphi_j^{i,k+1} - \varphi_{j-1}^{i,k+1}) + \varphi_{j-1}^{i,k+1} h_{j-1/2}^{i,k} - \varphi_j^{i,k+1} h_{j+1/2}^{i,k}).$$

Multiplying the above by Δx then summing over $j = 1, \ldots, N$, summing over $k = 0, \ldots, K - 1$, then using (A1) and incorporating the boundary condition from Equation (12), we have

$$
\sum_{j=1}^{N}(S_j^{i,K}\varphi_j^{i,k} - S_j^{i,0}\varphi_j^{i,0})\Delta x = \sum_{k=0}^{K-1}\sum_{j=1}^{N}[S_j^{i,k}(\varphi_j^{i,k+1} - \varphi_j^{i,k}) - \varphi_j^{i,k+1}S_j^{i,k+1}(\mu_j^{i,k} + L_j^{i,k})\Delta t]\Delta x
$$

$$
+ \sum_{k=0}^{K-1}\sum_{j=0}^{N-1}h_{j+1/2}^{i,k}\frac{\varphi_{j+1}^{i,k+1} - \varphi_j^{i,k}}{\Delta x}\Delta x\Delta t
$$

$$
+ \sum_{k=0}^{K-1}\varphi_0^{i,k+1}\sum_{\ell=1}^{m}p^{i\ell}\sum_{j=1}^{N}{}^{\star}(\beta_j^{\ell,k}S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k}I_j^{\ell,k})\Delta x\Delta x. \tag{33}
$$

Note that by Equation (10), we have

$$
\sum_{k=0}^{K-1}\sum_{j=0}^{N-1}h_{j+1/2}^{i,k}\frac{\varphi_{j+1}^{i,k+1} - \varphi_j^{i,k}}{\Delta x}\Delta t\Delta x = \sum_{k=0}^{K-1}\left[g_0^{i,k}S_0^{i,k} + g_1^{i,k}S_1^{i,k} + g_{N-1}^{i,k}S_{N-1}^{i,k} + \sum_{j\in J_1}\frac{1}{2}(g_{j+1}^{i,k} + g_j^{i,k})S_j^{i,k}\right.
$$

$$
+ \sum_{j\in J_2}\frac{1}{2}(g_{j+1}^{i,k}S_j^{i,k} + g_j^{i,k}S_{j+1}^{i,k})
$$

$$
\left. + \sum_{j\in J_3}\frac{1}{2}(g_{j+1}^{i,k}S_j^{i,k} + 2g_j^{i,k}S_j^{i,k} - g_j^{i,k}S_{j-1}^{i,k})\right]\frac{\varphi_{j+1}^{i,k+1} - \varphi_j^{i,k}}{\Delta x}\Delta t\Delta x, \tag{34}
$$

where $J_1 = \{2 \leq j \leq N - 2 : sign(\Delta_+S_j^{i,k})sign(\Delta_-S_j^{i,k}) = -1$, or $sign(\Delta_+S_j^{i,k})sign(\Delta_-S_j^{i,k}) = 0\}$, $J_2 = \{2 \leq j \leq N - 2 : \Delta_-S_j^{i,k} \geq \Delta_+S_j^{i,k} > 0$, or $\Delta_-S_j^{i,k} \leq \Delta_+S_j^{i,k} < 0\}$, and $J_3 = \{2 \leq j \leq N - 2 : \Delta_+S_j^{i,k} > \Delta_-S_j^{i,k} > 0$, or $\Delta_+S_j^{i,k} < \Delta_-S_j^{i,k} < 0\}$. Therefore, we can rewrite Equation (33) as

$$
\sum_{j=1}^{N}(S_j^{i,K}\varphi_j^{i,k} - S_j^{i,0}\varphi_j^{i,0})\Delta x = \sum_{k=0}^{K-1}\sum_{j=1}^{N}[S_j^{i,k}(\varphi_j^{i,k+1} - \varphi_j^{i,k}) - \Delta t\varphi_j^{i,k+1}S_j^{i,k+1}(\mu_j^{i,k} + L_j^{i,k})]\Delta x
$$

$$
+ \sum_{k=0}^{K-1}\left[g_0^{i,k}S_0^{i,k} + g_1^{i,k}S_1^{i,k} + g_{N-1}^{i,k}S_{N-1}^{i,k} + \sum_{j\in J_1}\frac{1}{2}(g_{j+1}^{i,k} + g_j^{i,k})S_j^{i,k}\right.
$$

$$
+ \sum_{j\in J_2}\frac{1}{2}(g_{j+1}^{i,k}S_j^{i,k} + g_j^{i,k}S_{j+1}^{i,k})
$$

$$
\left. + \sum_{j\in J_3}\frac{1}{2}(g_{j+1}^{i,k}S_j^{i,k} + 2g_j^{i,k}S_j^{i,k} - g_j^{i,k}S_{j-1}^{i,k})\right]\frac{\varphi_{j+1}^{i,k+1} - \varphi_j^{i,k}}{\Delta x}\Delta x\Delta t
$$

$$
+ \sum_{k=0}^{K-1}\varphi_0^{i,k+1}\sum_{\ell=1}^{m}p^{i\ell}\sum_{j=1}^{N}{}^{\star}(\beta_j^{\ell,k}S_j^{\ell,k} + \tilde{\beta}_j^{\ell,k}I_j^{\ell,k})\Delta x\Delta x. \tag{35}
$$

Similarly, we multiply the second equation of Equation (9) by $\varsigma_j^{i,k+1}$ and rearrange terms to acquire

$$
\begin{aligned}
I_j^{i,k+1}\varsigma_j^{i,k+1} - I_j^{i,k}\varsigma_j^{i,k} &= I_j^{i,k}(\varsigma_j^{i,k+1} - \varsigma_j^{i,k}) - \Delta t\varsigma_j^{i,k+1}(\tilde{\mu}_j^{i,k}I_j^{i,k+1} - L_j^{i,k}S_j^{i,k+1}) \\
&\quad + \frac{\Delta t}{\Delta x}(\hat{h}_{j-1/2}^{i,k}(\varsigma_j^{i,k+1} - \varsigma_{j-1}^{i,k+1}) + \varsigma_{j-1}^{i,k+1}\hat{h}_{j-1/2}^{i,k} - \varsigma_j^{i,k+1}\hat{h}_{j+1/2}^{i,k}).
\end{aligned}
$$

We multiply the above by Δx then sum over $j = 1, \ldots, N$, sum over $k = 0, \ldots, K-1$, then using (A1) and incorporating the boundary condition for infected fish (14) we have

$$
\begin{aligned}
\sum_{j=1}^{N}(I_j^{i,K}\varsigma_j^{i,K} - I_j^{i,0}\varsigma_j^{i,0})\Delta x &= \sum_{k=0}^{K-1}\sum_{j=1}^{N}[I_j^{i,k}(\varsigma_j^{i,k+1} - \varsigma_j^{i,k}) - \varsigma_j^{i,k+1}(\tilde{\mu}_j^{i,k}I_j^{i,k+1} - L_j^{i,k+1}S_j^{i,k+1})\Delta t]\Delta x \\
&\quad + \sum_{k=0}^{K-1}\sum_{j=0}^{N-1}\hat{h}_{j+1/2}^{i,k}\frac{\varsigma_{j+1}^{i,k+1} - \varsigma_j^{i,k+1}}{\Delta x}\Delta x\Delta t.
\end{aligned}
\tag{36}
$$

Note that by Equations (10) and (14), we have

$$
\begin{aligned}
\sum_{k=0}^{K-1}\sum_{j=0}^{N-1}\hat{h}_{j+1/2}^{i,k}\frac{\varsigma_{j+1}^{i,k+1} - \varphi_j^{i,k}}{\Delta x}\Delta t\Delta x &= \sum_{k=0}^{K-1}\Bigg[\hat{g}_1^{i,k}I_1^{i,k} + \hat{g}_{N-1}^{i,k}I_{N-1}^{i,k} + \sum_{j\in\tilde{J}_1}\frac{1}{2}(\hat{g}_{j+1}^{i,k} + \hat{g}_j^{i,k})I_j^{i,k} \\
&\quad + \sum_{j\in\tilde{J}_2}\frac{1}{2}(\hat{g}_{j+1}^{i,k}I_j^{i,k} + \hat{g}_j^{i,k}I_{j+1}^{i,k}) \\
&\quad + \sum_{j\in\tilde{J}_3}\frac{1}{2}(\hat{g}_{j+1}^{i,k}I_j^{i,k} + 2\hat{g}_j^{i,k}I_j^{i,k} - \hat{g}_j^{i,k}I_{j-1}^{i,k})\Bigg]\frac{\varsigma_{j+1}^{i,k+1} - \varsigma_j^{i,k}}{\Delta x}\Delta t\Delta x,
\end{aligned}
\tag{37}
$$

where $\tilde{J}_1$, $\tilde{J}_2$, and $\tilde{J}_3$ are defined in a similar manner as was done for $S_j^{i,k}$. Therefore, we can rewrite Equation (36) as

$$
\begin{aligned}
\sum_{j=1}^{N}(I_j^{i,K}\varsigma_j^{i,K} - I_j^{i,0}\varsigma_j^{i,0})\Delta x &= \sum_{k=0}^{K-1}\sum_{j=1}^{N}[I_j^{i,k}(\varsigma_j^{i,k+1} - \varsigma_j^{i,k}) - \varsigma_j^{i,k+1}(\tilde{\mu}_j^{i,k}I_j^{i,k+1} - L_j^{i,k+1}S_j^{i,k+1})\Delta t]\Delta x \\
&\quad + \sum_{k=0}^{K-1}\Bigg[\hat{g}_1^{i,k}I_1^{i,k} + \hat{g}_{N-1}^{i,k}I_{N-1}^{i,k} + \sum_{j\in J_1}\frac{1}{2}(\hat{g}_{j+1}^{i,k} + \hat{g}_j^{i,k})I_j^{i,k} \\
&\quad + \sum_{j\in J_2}\frac{1}{2}(\hat{g}_{j+1}^{i,k}I_j^{i,k} + \hat{g}_j^{i,k}I_{j+1}^{i,k}) \\
&\quad + \sum_{j\in J_3}\frac{1}{2}(\hat{g}_{j+1}^{i,k}I_j^{i,k} + 2\hat{g}_j^{i,k}I_j^{i,k} - \hat{g}_j^{i,k}I_{j-1}^{i,k})\Bigg]\frac{\varsigma_{j+1}^{i,k+1} - \varsigma_j^{i,k}}{\Delta x}\Delta t\Delta x.
\end{aligned}
\tag{38}
$$

Using Equations (35) and (38) and then following a similar argument to those in the proof of Lemma 16.9 (p. 279) in [37], it can be shown that the limit of the difference approximations defined in Theorem 7 is a weak solution to Equations (2)–(4) by allowing $N, K \to \infty$. The

bounds on $\|S^i\|_{L^\infty}$ and $\|I^i\|_{L^\infty}$ are obtained by taking the limit in the bounds of the difference approximations in Lemmas 2 and 3. ∎

Remark 1 Using arguments similar to those in [8], it follows that the weak solution to the model (2)–(4) is unique. From Theorems 7, 8 and the uniqueness of the weak solution, we determine that the finite difference approximation (18) converges to the unique weak solution of the system (2)–(4).

Note that the scheme (18) is of second-order accuracy in space but only first-order in time. In order to develop second-order accuracy in time, we apply a second-order Richardson extrapolation. We indicate the time step in parentheses, for example, $S_j^{i,k}(\Delta t)$ is the approximated model solution for susceptible fish using a given Δt. A similar notation will be used for all variables. To this end, let the vectors

$$u^k(\Delta t) = [S_0^{1,k}(\Delta t), \ldots, S_N^{m,k}(\Delta t), I_0^{1,k}(\Delta t), \ldots, I_N^{m,k}(\Delta t), B_a^k(\Delta t), B_u^k(\Delta t), M^k(\Delta t)]^{\mathrm{T}}$$

denote the solution of the system (18) at time t_k when the time mesh is Δt. We denote the second-order Richardson extrapolation iteration, $\tilde{u}^k$, at time t_k for $k = 1, \ldots, K$ as

$$\tilde{u}^k = 2u^{2k}\left(\frac{\Delta t}{2}\right) - u^k(\Delta t). \tag{39}$$

From Theorems 7 and 8, it follows that the Richardson extrapolation iteration, $\tilde{u}^k$ in Equation (39), converges to the unique weak solution of the system (2)–(4) in the sense given in Theorem 7.

6. Numerical results

In this section, we demonstrate numerically the performance of the second-order scheme (9). Throughout this discussion, we will use uniform mesh points for x and t. Using the Taylor expansion, we find that (cf. [35])

$$\frac{h_{2+1/2}^{i,k} - h_{2-1/2}^{i,k}}{\Delta x} = \frac{3}{2}(gS)_x + O(\Delta x), \quad \frac{h_{N-1+1/2}^{i,k} - h_{N-1-1/2}^{i,k}}{\Delta x} = \frac{1}{2}(gS)_x + O(\Delta x),$$

$$\frac{\hat{h}_{2+1/2}^{i,k} - \hat{h}_{2-1/2}^{i,k}}{\Delta x} = \frac{3}{2}(\tilde{g}I)_x + O(\Delta x), \quad \frac{\hat{h}_{N-1+1/2}^{i,k} - \hat{h}_{N-1-1/2}^{i,k}}{\Delta x} = \frac{1}{2}(\tilde{g}I)_x + O(\Delta x).$$

Based on this analysis, it is more accurate to adjust the second interval $x_2 - x_1$ from Δx to $(3/2)\Delta x$, and to adjust the second to the last interval $x_{N-1} - x_{N-2}$ from Δx to $(1/2)\Delta x$. This is done in the scheme only and is done without changing the values of x_3 or x_{N-2}. One could show using the arguments in the previous sections that the stability and convergence of the scheme would not be affected. Additionally, for all the computations presented here $x_{\min} = 0$ and $x_{\max} = 1$.

6.1. *Convergence of a simplified linear model*

To illustrate that our approximation scheme that is presented in Section 3 is in fact second order, we calculate the error between the scheme and an exact solution. We cannot obtain a solution to the full model by analytic means, so we make some simplifications by eliminating the nonlinear

Table 1. Nonzero parameter values for the simplified (linear) model.

Parameter	Value	Parameter	Value
δ_1	1/2	δ_2	1/2
c_M	1/4	μ_M	1
M^*	20	B_a^0	5
B_u^0	3	M^0	10

Table 2. Simple growth, death, and fecundity functions.

Growth	Death	Fecundity
$g(P,x) = 1 - x$	$\mu(P,x) = 1$	$\beta(P,x) = \dfrac{1}{e-1}$
$\tilde{g}(P,x) = 0.5(1-x)$	$\tilde{\mu}(P,x) = 1$	$\tilde{\beta}(P,x) = 0$

terms. We will use this exact solution for comparison with our approximated solution to the simplified model.

The exact solution to the linear version of the model (2)–(4) was developed in [8] and we will provide a summary here. Without loss of generality, we take $m = 1$ (one physiological class) and we will denote $S^1(t,x)$ by $S(t,x)$ (similar notation will be used for the other functions with dependency on physiological class) for simplicity. We have included the parameter values for the simplified system in Table 1. Only the parameters needed in the simplified system are included, as the other parameters were given a value of zero to simplify the model (2)–(4). The values were chosen purely to demonstrate the achievement of the designed order of accuracy and are not biologically relevant. Simple growth, death, and fecundity kernels are given in Table 2. We add the nonhomogeneous terms

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

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

to the right-hand side of the first two equations of Equation (2). This simplifies the pde system governing fish dynamics to a linear system given by

$$S_t + (gS)_x + \mu S = -x\,e^{x-t},$$

$$I_t + (\tilde{g}I)_x + \tilde{\mu}I = -\tfrac{1}{4}x\,e^{x-t} + \tfrac{1}{4}\,e^{x-t} - \tfrac{1}{4}x^2\,e^{x-t}.$$

We choose initial conditions $S(0,x) = e^x$, $I(0,x) = \tfrac{1}{2}x\,e^x$ and boundary conditions $S(t,0) = e^{-t}$, $I(t,0) = 0$. With these choices, it can easily be verified that

$$S(t,x) = e^{x-t}, \quad I(t,x) = \tfrac{1}{2}x\,e^{x-t}, \quad P(t) = e^{1-t} - \tfrac{1}{2}\,e^{-t},$$

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

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

$$M(t) = M^0 \exp(-\mu_M t)$$

is the solution to Equation (2). Next, we ran five simulations of Equations (15) and (12) with step sizes being halved with each successive iteration. We then calculated the L^1 norms of the errors

Table 3. Convergence of the second-order method (linear case).

Δt $\times 10^{-3}$	Δx $\times 10^{-2}$	$S(2,x)$ L_1 error $\times 10^{-3}$	Order	$I(2,x)$ L_1 error $\times 10^{-5}$	Order
2.5000	5.0000	5.7089		2.5140	
1.2500	2.5000	1.4105	2.0170	0.6400	1.9738
0.6250	1.2500	0.3505	2.0086	0.1616	1.9858
0.3125	0.6250	0.0873	2.0051	0.0406	1.9927
0.1565	0.3125	0.0218	2.0034	0.0102	1.9963

Δt $\times 10^{-3}$	Δx $\times 10^{-2}$	$B_a(t)$ Max error $\times 10^{-3}$	Order	$B_u(t)$ Max error $\times 10^{-18}$	Order
2.5000	5.0000	7.2172		5.4716	
1.2500	2.5000	1.8000	2.0034	1.2665	2.1111
0.6250	1.2500	0.4499	2.0005	0.3047	2.0556
0.3125	0.6250	0.1125	2.0000	0.0747	2.0278
0.1565	0.3125	0.0281	1.9999	0.0185	2.0139

Δt $\times 10^{-3}$	Δx $\times 10^{-2}$	$M(t)$ Max error $\times 10^{-7}$	Order
2.5000	5.0000	1.0813	
1.2500	2.5000	0.2702	2.0005
0.6250	1.2500	0.0675	2.0003
0.3125	0.6250	0.0169	2.0001
0.1565	0.3125	0.0042	2.0006

in $S(2,x)$ and $I(2,x)$ and the maximum error for $P(t)$, $B_a(t)$, $B_u(t)$, and $M(t)$. Finally, we found $\log_2$ of the ratios of consecutive errors to determine the order of accuracy. The results in Table 3 clearly demonstrate that the method achieves second-order accuracy.

6.2. *Convergence for the full nonlinear model*

To demonstrate that second-order convergence is maintained with the introduction of the model nonlinearities, we compute the error of the approximated solutions for the full model by using a solution with a very small time $\Delta t = 9.765625 \times 10^{-7}$ and mesh $\Delta x = 1.953125 \times 10^{-4}$ steps, and we will refer to this as the 'reference solution' in place of an exact solution to calculate the error. We compute several solutions using the finite difference scheme (15) (with uniform mesh), successively halving the time and mesh steps. We use the model parameters and auxiliary functions as in Tables 4 and 5. The parameters and functions used here are not biological in nature, but were used to show the order of the method. We have continued 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 (a discontinuity is evident along the characteristic curve starting at the point $(0, x_{\min})$).

Table 4. Nonzero parameter values for the full (nonlinear) model.

Parameter	Value	Parameter	Value
ν_1	0.125×10^{-6}	ν_2	0.125×10^{-6}
ν_3	2.5×10^{-7}	ν_4	2.5×10^{-7}
δ_1	$1/500$	δ_2	$1/500$
ζ	2.4×10^3	ϵ	0.05
c_M	0.5	M^*	2×10^{30}
μ_M	$7/60$	λ	2.0
$\bar{\rho}$	3×10^4		

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

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
$c_1(x)$	0.5	$\tilde{c}_1(x)$	0.5
$c_2(x)$	0.5	$\tilde{c}_2(x)$	0.5

In spite of this discontinuity, we still converge to second-order accuracy since the scheme, being of high resolution, approximates solutions involving discontinuities well.

### 6.3. *Comparison of first-order and second-order methods*

Our next example is included to illustrate the computational savings found when using the second-order high-resolution method (SOHR) instead of the first-order implicit (FOI) scheme developed in [8]. Using the values and functions in Tables 4 and 5, we obtain the results for the model solutions shown in Table 6. The error and order of convergence (in the L^1 norm) resulting from the SOHR scheme and those resulting from the FOI scheme are given in Table 7. We included the computational time for the approximate solutions using the built-in MATLAB commands *tic* and *toc*. It is clear that to obtain a similar accuracy, the SOHR scheme requires less CPU time. The FOI scheme requires 120.4340 s to compute an approximation solution with the L^1 norm of the error equal to 0.0046647. However, when using the SOHR scheme, we can get a more accurate approximation (with the L^1 norm of the error equal to 0.0018335) in just 32.1365 s. This clearly shows that the SOHR scheme saves 73.32% CPU time in this case (Figure 1).

Table 6. Convergence of the second-order method (nonlinear case).

Δt $\times 10^{-3}$	Δx $\times 10^{-2}$	$S(2,x)$ L_1 error	Order	$I(2,x)$ L_1 error	Order
2.5000	2.5000	2.4761		0.1311	
1.2500	1.2500	0.6797	1.8651	0.0392	1.7422
0.6250	0.6250	0.1817	1.9030	0.0122	1.6868
0.3125	0.3125	0.0509	1.8373	0.0036	1.7482
0.1563	0.1563	0.0119	2.1015	0.0009	1.9793

Δt $\times 10^{-3}$	Δx $\times 10^{-2}$	$B_a(t)$ Max error $\times 10^{-3}$	Order	$B_u(t)$ Max error $\times 10^{-5}$	Order
2.5000	5.0000	5.4425		1.2045	
1.2500	2.5000	1.3921	1.9670	0.3080	1.9672
0.6250	1.2500	0.3474	2.0026	0.0769	2.0027
0.3125	0.6250	0.0831	2.0631	0.0184	2.0631
0.1563	0.3125	0.0167	2.3182	0.0037	2.3182

Δt $\times 10^{-3}$	Δx $\times 10^{-2}$	Max error $\times 10^{-3}$	$M(t)$ Order
2.5000	5.0000	4.5586	
1.2500	2.5000	1.2366	1.8222
0.6250	1.2500	0.3363	1.8784
0.3125	0.6250	0.0817	2.0412
0.1563	0.3125	0.0165	2.3123

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Table 7. L^1 errors, orders of accuracy, and computational time (in seconds) for the FOI and SOHR schemes.

Δt	Δx	$P(t)$ FOI Max error	Order	Time	$P(t)$ SOHR Max error	Order	Time
0.01	0.1	0.5591134		0.0896	0.5179306		0.2054
0.005	0.05	0.2470113	1.1786	0.4627	0.1305551	1.9881	0.5808
0.0025	0.025	0.1149870	1.1031	1.0665	0.0266159	2.2943	2.1642
0.00125	0.0125	0.0541536	1.0863	3.0056	0.0071931	1.8876	8.2321
0.000625	0.00625	0.0249398	1.1186	9.4114	0.0018335	1.9720	32.1365
0.0003125	0.003125	0.0106227	1.2313	32.2939	0.0004413	2.0549	127.5357
0.00015625	0.0015625	0.0046647	1.1873	120.4340	0.0000886	2.3158	511.0992
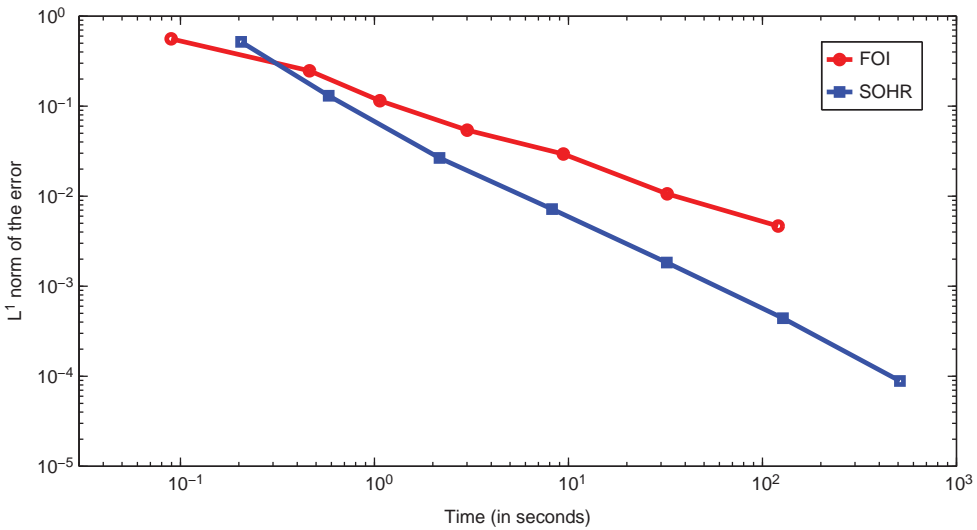
Figure 1.   The loglog plot of the L^1 norm of the errors for the FOI and the SOHR schemes against the computational time.

To better illustrate the order of accuracy in the SOHR scheme, we plot the L^1 norm of the errors in the FOI and SOHR schemes against the computation time using logarithmic scales on the horizontal and vertical axes. For less accurate approximations (errors greater than 0.5, in the L^1 norm), the FOI scheme is faster than the SOHR scheme. However, for improved accuracy (L^1 errors above 0.5), the SOHR scheme is much faster than the FOI scheme.

In our next example, we compute the solution for the total fish population using the SOHR scheme given in Equation (18) with $\Delta t = 0.005$ and $\Delta x = 0.05$. Then, we compute the solution for the total fish population using the FOI scheme from [8] using the same step sizes. We then halve the step sizes five times successively, with the final step sizes $\Delta t = 3.125 \times 10^{-4}$ and $\Delta x = 3.125 \times 10^{-3}$. In this example, we use five physiological classes, $m = 5$, the parameter values in Table 4, the function forms in Table 8, and the permutation-selection matrix given by

$$p_1 = \begin{bmatrix} 0.35 & 0.10 & 0.05 & 0.00 & 0.20 \\ 0.20 & 0.35 & 0.20 & 0.10 & 0.05 \\ 0.10 & 0.05 & 0.35 & 0.25 & 0.15 \\ 0.20 & 0.20 & 0.40 & 0.35 & 0.25 \\ 0.15 & 0.30 & 0.00 & 0.30 & 0.35 \end{bmatrix}. \tag{40}$$

Table 8. Forms of the rate functions for the multi-physiological example. Initial conditions are $S^i(0,x) = 10^6 \exp(-(5x-2)^2)$, $I^i(0,x) = 0$, for $i = 1, \ldots, 5$, and $B_a(0) = 10^4$, $B_u(0) = 10^4$, $M(0) = 10^4$.

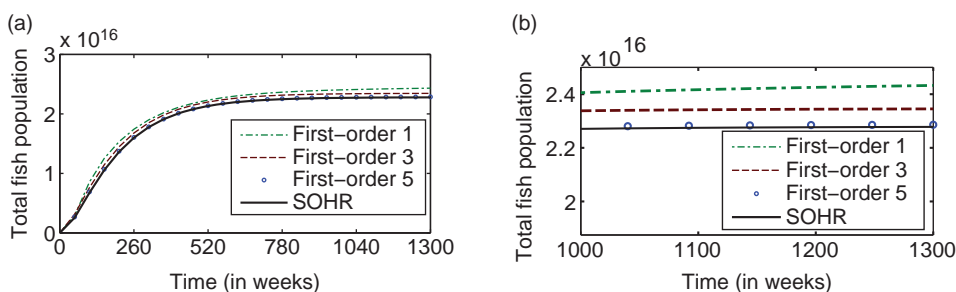| Function	Form	Function	Form
$g^1(P,x)$	$(x-1)\ln(0.34)/13$	$g^2(P,x)$	$-0.2398(x+0.01)(x-1)$
$g^3(P,x)$	$0.0829/(1+\exp(7(x-0.5))) - a_0$	$g^4(P,x)$	$(x-1)\ln(0.34)/13$
$g^5(P,x)$	$-0.2398(x+0.01)(x-1)$	$\tilde{g}^i(P,x)$	$0.5g^i(P,x)$, $i = 1,\ldots,5$
$\beta^i(P,x)$	$b^i x/(1+\nu P)$	$\tilde{\beta}^i(p,x)$	$0.15\beta^i(P,x)$, $i = 1,\ldots,5$
$\mu^i(P,x)$	$1/156$, $i = 1,\ldots,5$	$\tilde{\mu}(P,x)$	$2/156$, $i = 1,\ldots,5$
$c_1^i(x)$, $c_2^i(x)$	0.5, $i = 1,\ldots,5$	$\tilde{c}_1^i(x)$, $\tilde{c}_2^i(x)$	0.5, $i = 1,\ldots,5$
Parameter	Value	Parameter	Value
b^1	5×10^7	$b^2(P,x)$	6.3×10^7
b^3	7.6×10^7	$b^4(P,x)$	8.9×10^7
b^5	10.2×10^7	ν	5×10^{-5}
a_0	$0.0829/(1+\exp(7/2))$		

Figure 2. Comparison of first-order and second-order approximations of the total fish population. (a) Total fish population from 0 to 1300 weeks. (b) Total fish population from 1000 to 3000 weeks.

Figure 2(a) contains the plot of the second-order approximation over a 1300-week period along with the plots of the solutions from halving the step size one, three, and five times, so the step sizes are reduced by a factor of 1/4 in each successive plot. Figure 2(b) contains a zoomed in portion of Figure 2(a) over the last 300 weeks of the period so the convergence can clearly be seen.

We see that the step sizes must be approximately 16 times smaller in the first-order method to achieve a similar accuracy as found in the second-order method. Also, to achieve corresponding accuracy, the first-order method required over 61 min (3684 s) of run time, while the second-order method only required 10 min (617 s) of run time. We mention that while our initial conditions are continuous, we are not forcing compatibility at the boundary for each susceptible fish equation.

6.4. *An ecological example*

In our final numerical experiment, we explore the possible ecological implications of fish with different physiological (specifically, metabolic) characteristics, by examining the interplay of reproductive advantages conferred by growth and birth rates. Unless stated otherwise, the parameter values used here can be seen in Table 4, and the function forms in Table 9. In the interest of employing biologically tenable rate functions, we take a simple size-dependent form $\mu^i = x/312$ and $\tilde{\mu}^i(P,x) = x/156$ for $i = 1, 2, 3$, since it is likely that larger fish die at an increased rate than smaller fish, and we remind the reader that we are not considering predation here. Additionally, in previous simulation studies, we observed an exaggerated accumulation of fish at the largest

Table 9. Rate functions for the ecological examples. Initial conditions are $S^i(0,x) = 10^6$ $\exp(-(5x-2)^2)$, $I^i(0,x) = 0$, for $i = 1, \ldots, 3$, and $B_a(0) = 10^4$, $B_u(0) = 10^4$, $M(0) = 10^4$.

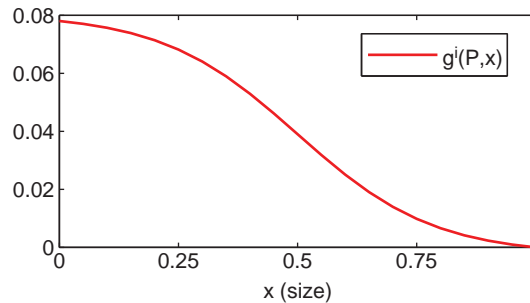| Function	Form	Function	Form
$g^i(P,x)$	$\gamma^i(0.0829/(1 + \exp(7(x - 0.5)))) - a_0$	$\tilde{g}^i(P,x)$	$0.5g^i(P,x)$, $i = 1,2,3$
$\beta^i(P,x)$	$b^i x/(1 + \nu P)$	$\tilde{\beta}^i(P,x)$	$0.5\beta^i(P,x)$, $i = 1,2,3$
$\mu(P,x)$	$x/312$	$\tilde{\mu}(P,x)$	$x/156$
$c_1^i(x)$, $c_2^i(x)$	0.5, $i = 1,2,3$	$\tilde{c}_1^i(x)$, $\tilde{c}_2^i(x)$	0.5, $i = 1,2,3$
a_0	$0.0829/(1 + \exp(7/2))$		

Figure 3. Growth function demonstrating loss of growth as an individual reaches sexual maturity.

sizes as they grew and remained there for long periods of time. Thus, this size-dependent death rate is incorporated with the intent of improving the biological integrity of the solutions studied. The growth function $g^i(P,x) = \gamma^i(0.0829/(1 + \exp(7(x - 0.5)))) - a_0)$ represents the idea from ecology that animals have finite energy and resources, and that there is a shift in energy expenditures from growth to reproduction as animals reach sexual maturity as seen in Figure 3.

We reiterate that the fecundity kernels will have the form $\beta^i(P,x) = b^i x/(1 + \nu P)$ to account for the possible impact of crowding on the ability of a fish of type i to reproduce at high population levels, and to implement the assumption that larger fish reproduce at a faster rate than smaller (juvenile) fish. The permutation-selection matrix p is taken to be the identity matrix in all solutions shown here, indicating that all fish beget fish of only the same physiological type. The growth and fecundity rates of infected fish are half that of their susceptible counterparts. To study the long-term effects of birth and growth in the context of size-dependent death, we examine solutions of varying values for parameters γ^i and b^i which accelerate and decelerate the speed of growth and birth, respectively.

The effect of varying growth rates is seen in Figure 4(a), with all other rates being the same. Initially, the fastest growing group has an advantage, and grows in subpopulation size due to higher reproduction rates of larger sized fish. This continues until all birth rates are substantially decreased (to less than the death rates) because of the large total population size. After this occurs, the birth rates for the faster growing class ($i = 3$) continue to be outweighed by the large death rates for fish of larger sizes. The slower growing fish ($i = 1$), on the other hand, enjoy an advantage after the initial growth and death period, as their population is less adversely affected by the higher death rates for fish of larger sizes. Therefore, it appears that higher metabolic activity (faster growth) does not provide an advantage in long term due to the crowding effect in the birth rate and size-dependent death rate. While this is understood in model terms, it is an example of a phenomenon that initially seems to disagree with one's intuition that faster growth would necessarily be advantageous.

In Figure 4(b), we clearly see that accelerated reproduction does indeed confer an edge in this model, as all other rates are constant amongst the physiological groups. This example does
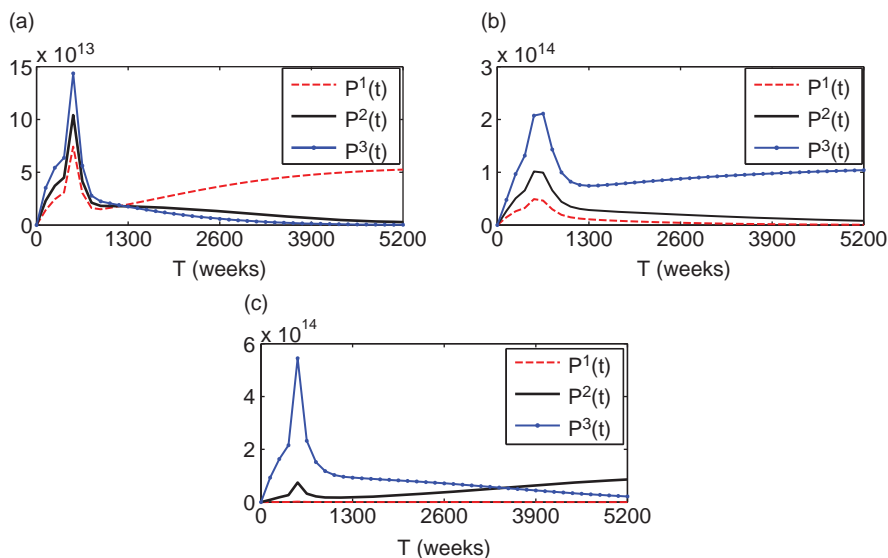
Figure 4. Total populations with death rates dependent on size. (a) Total fish populations with scaling factors $\gamma^1 = 0.8$, $\gamma^2 = 1$, $\gamma^3 = 1.2$, $b^1 = b^2 = b^3 = 5 \times 10^7$. (b) Total fish populations with scaling factors $\gamma^1 = \gamma^2 = \gamma^3 = 1$, $b^1 = 5 \times 10^7$, $b^2 = 5.3 \times 10^7$, $b^3 = 5.6 \times 10^7$. (c) Total fish populations with scaling factors $\gamma^1 = 0.25$, $\gamma^2 = 1$, $\gamma^3 = 2$, $b^1 = 4.5 \times 10^7$, $b^2 = 5.3 \times 10^7$, $b^3 = 5.6 \times 10^7$.

agree with what one would expect, and is included primarily for the sake of comparison of Figure 4(a) and (c). However, it is also interesting to note that the initial growth and decline period of all subpopulations is again observed, due to the crowding effect in the birth rate, which results in the populations having a time-dependent net reproductive rate. It also confirms that this phenomenon is not due to the differences in the growth rate in Figure 4(a). Taken together, this raises the question: is the long-term benefit due to a slower growth rate sufficient to overcome the advantage of a faster reproductive rate?

An initial investigation of that question is provided in Figure 4(c), in which group 1 has the smallest growth and birth rate, group 2 has moderate growth and birth rates, and group 3 has the largest growth and birth rates. As expected, initially the third group's population size increases the fastest. After the initial period of growth and subsequent decline, however, the second group enjoys an advantage, presumably due to the size-dependent death rate playing a dominant role during this interval and this group being of a smaller size. Its birth rate, however, is sufficiently higher than that of the second group, so that the lower death rate of this group is not enough to give it an edge over the moderately growing and reproducing class.

There are other scenarios possible, of course, depending on the choice of parameters taken, and there is considerable uncertainty in the parameter values used here. We present this example as an exploration of the model dynamics and ecological phenomena reproduced by the model. Also, we note that these are explorations only within the context of pure selection throughout generations since the identity matrix was used for the permutation-selection matrix. If we allow genetic spread, the results are potentially more rich; indeed, in studies not shown here we have observed that both competitive exclusion and coexistence are outcomes when the same permutation-selection matrix p is used, depending on the choice of birth, growth, and death rates. This suggests that this model is capable of providing insight into perhaps surprising or counterintuitive phenomena, that may be observed in populations exhibiting vital characteristics as represented in this model. Also, these examples further demonstrate the utility of this model to predict outcomes when several simultaneous processes, perhaps with conflicting effects, are at play.

7. Concluding remarks

We have developed a second-order high-resolution finite difference approximation for a mathematical model of Mm. This model is approximated using an implicit scheme. But due to sensible choices, it can be computed in an explicit fashion, which makes the scheme numerically efficient. We chose to take a finite difference approach because of the simplicity of implementation and the ability to prove existence and uniqueness properties of the method. Other possible choices for solving the model (2)–(4) (i.e. finite element methods, integration along the characteristics, etc.) do not lend themselves to proofs of convergence, or their complexities outweigh their benefit for this model.

The discretization of the model in Equation (9) is second-order accurate in space (except at the left boundary) and not in time. To achieve second-order accuracy in time, we implemented a Richardson extrapolation. Theorems 7 and 8 support the Richardson extrapolation iteration in Equation (39) converging to the unique weak solution of the system (2)–(4) in the sense given in Theorem 7.

We began our numerical results by showing that a simplified version of the method achieves the desired second-order accuracy when compared to an exact solution. Next, we demonstrated the fact that the full nonlinear version of our scheme converges with second-order accuracy when compared against a reference solution. The advantage of using a second-order method is achieve higher accuracy with faster computational time.

We concluded our investigations with an exploration of the potential long-term outcomes from using more biologically tenable rate functions. These included a crowding effect (which introduced a dependence on time) in the birth rate, and that the birth, growth, and death rates were dependent on size. Previous investigations had implemented only a constant death rate. We found that doing so can lead to outcomes that are not immediately obvious. That is, in some cases a lower or the lowest growth rate is actually favourable, which may be contrary to one's intuition. Further preliminary studies have suggested that there are several possible outcomes under different choices of these parameters and particularly, when genetic spread through generations is considered. Thus, there appears to be an interesting interplay between these metabolic and reproductive traits. These results can be understood within the context of the model mechanisms, demonstrating the potential use of the model as a tool to explain surprising ecological phenomena.

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