Numerical solution of Structured Population Models

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1 Introduction

Individuals in a structured population are distinguished by age, size, maturity or some other individual physical characteristic. The main assumption when modelling the evolution of such a population is that the structure of the population with respect to these individual physical characteristics at a given time, and posibly some enviromental input as time evolves, completely determines the dynamical behaviour of the population. Mathematical models describing this evolution are typically initial-boundary value problems for a partial differential equation or system of partial differential equations in which the independent variables are time t and these various structure variables $\mathbf{x} \in \mathcal{X} \subset I\!R^k$, and the dependent variables are the nonnegative density functions with respect to these independent variables $u_j(\mathbf{x}, t), j = 1, \ldots, m$, that completely describe the population state. The integral

$$\int_D u_j(\mathbf{x}, t) d\mathbf{x}, \quad j = 1, \ldots, m$$

gives therefore the number of individuals at time t of the j-th structured (sub)population with individual state variables in $D \subset \mathcal{X}$.

The governing equations in these models are generally nonlinear first-order hyperbolic partial differential equations stemming from the appropriate balance of individuals of the population inside a infinitesimally small box element before and after it has moved during infinitesimally small time intervals $(t, t+dt)$ along through $\mathcal{X}$ with the flow generated by the vector field of local speeds $g_i, i = 1, \ldots, k$, for each individual state variable x_i. A prototype of this class of PDE is given by

$$\frac{\partial u}{\partial t} + \frac{\partial (g(x, I_g(t), t) u)}{\partial x} = -\mu(x, I_\mu(t), t) u, \quad t > 0, \quad x_0 < x < \infty, \tag{1.1}$$

in which the nonnegative function $\mu(x, I_\mu(t), t)$ represents the mortality rate of the individuals of the population and $g(x, I_g(t), t)$ represents the growth rate of the magnitude x with the time. The mortality and growth rates are made to depend on some weighted averages, $I_\mu(t) = \int_{x_0}^{\infty} \gamma_\mu(x) u(x, t) dx$ and $I_g(t) = \int_{x_0}^{\infty} \gamma_g(x) u(x, t) dx$ respectively, of the density function u. The quantity $x_0 > 0$ is the initial magnitude of x at birth of the individuals. The boundary condition

$$g(x_0, I_g(t), t) u(x_0, t) = \int_{x_0}^{\infty} \beta(x, I_\beta(t), t) u(x, t) dx, \quad t \geq 0, \tag{1.2}$$

represents the birth law and $\beta(x, I_\beta(t), t)$ is the corresponding fertility rate for the individuals. Again it is assumed a dependence of β from some functional $I_\beta(t) = \int_{x_0}^{\infty} \gamma_\beta(x) u(x, t) dx$. Finally we must provide a initial x-specific distribution $\phi(x)$ for the individuals of the population; the initial condition

$$u(x, 0) = \phi(x), \quad x_0 \leq x \leq \infty, \tag{1.3}$$

for the evolutionary problem defined by (1.1) and (1.2). Age-structured population models are recovered when $g(x) \equiv 1$ and $x_0 = 0$. An extensive study of physiologically structured population dynamics, with discussion of the biological background of such models, can be found in [24].

Numerical methods for (1.1)-(1.3) are unavoidable for the most realistic cases in order to get some quantitative information from the model. Also inverse problems in which we must determine some estimations for the growth function or the fertility and mortality rates from the life story of the population requires intensive numerical computations with the model (1.1)-(1.3). On the other hand, qualitative behaviour of solutions of (1.1)-(1.3) requires also numerical methods to approximate essential parameters.

2 Numerical Solution of Age-Structured Population Models

In this section we shall concern with the numerical solution of the initial-boundary value problem for the nonlinear hyperbolic integro-differential equation

$$u_t + u_x = -\mu(x, I_\mu(t))u, \quad 0 \leq x \leq A, \quad 0 \leq t \leq T, \tag{2.1}$$

$$u(0,t) = \int_0^A \beta(x, I_\beta(t))u(x,t)dx, \quad 0 \leq t \leq T, \tag{2.2}$$

$$u(x,0) = \phi(x), \quad 0 \leq x \leq A, \tag{2.3}$$

where $I_\mu(t), I_\beta(t)$ denote

$$I_\mu(t) = \int_0^A \gamma_\mu(x)u(x,t)dx, \quad I_\beta(t) = \int_0^A \gamma_\beta(x)u(x,t)dx. \tag{2.4}$$

The independent variables x and t denote, respectively, age and time, and $u(x,t)$ represents the age-specific density of individuals of age x at time t. The nonnegative funcions μ and β represent the mortality and fertility rates, respectively, and is assumed they depend on the age x and on some weighted averages of the density function, $I_\mu(t)$ and $I_\beta(t)$, defined as in (2.4). The model (2.1)-(2.3) is more general than the well-known Gurtin-MacCamy model [14] where $\gamma_\mu \equiv \gamma_\beta \equiv 1$. An extensive study of linear and nonlinear age-dependent population dynamics can be found in the works of Webb [33] and Iannelli [15].

2.1 The upwind scheme

To begin with the numerical study, we consider a simple finite difference method.

2.1.1 A simple linear model equation

First, we consider some simple finite difference schemes for the following model equation

$$u_t + u_x = -\mu\, u, \quad x \geq 0, \quad t \geq 0, \tag{2.5}$$

in which we assume that the dependent variable u is a function of x (age) and t (time).

We choose this simple linear equation for convenience; at this stage in the discussion there is no advantage to be obtained by dealing more complex structured population equations. Here $\mu > 0$ can be seen as a constant mortality rate for the individuals of a single age-structured population described by the density function $u(x,t)$.

The most essential fact about (2.5) is that the partial differential equation has a single set of characteristic curves $x - t = c$, c constant, and that along a characteristic curve the solution $u(x,t)$ satisfies

$$\frac{du}{dt} = \frac{\partial u}{\partial t} + \frac{\partial u}{\partial x}\frac{dx}{dt} = -\mu u. \tag{2.6}$$

Thus from initial data

$$u(x,0) = \phi(x), \quad x \geq 0, \tag{2.7}$$

$\phi(x)$ a nonnegative function, and a boundary condition at $x = 0$ (the inflow boundary of the domain)

$$u(0,t) = B(t), \quad t \geq 0, \tag{2.8}$$

the solution $u(x,t)$ of (2.5),(2.7) and (2.8) is completely determined by integration of the ordinary differential equation (2.6) along each of the characteristic curves.

Now suppose we replace the time derivative in (2.5) with a forward difference, and the age derivative with a backward difference on a discrete mesh $x_j = j\Delta x, j = 0, 1, \dots$ and $t_n = n\Delta t, n = 0, 1, \dots$. The result is

$$\frac{U_j^{n+1} - U_j^n}{\Delta t} + \frac{U_j^n - U_{j-1}^n}{\Delta x} = -\mu U_j^n, \quad j = 0, 1, \dots \tag{2.9}$$

In equation (2.9), $U_j^n \approx u(x_j, t_n)$, and the index for time n appears, as usually in the finite differences method, as a superscript. The subscript j still denotes the grid points location.

The solution of (2.9) takes the form of a 'marching' solution in steps of time

$$U_j^{n+1} = U_j^n - \nu(U_j^n - U_{j-1}^n) - \Delta t \mu U_j^n, \quad j = 0, 1, \dots, \quad n = 0, 1, \dots \tag{2.10}$$

where $\nu := \dfrac{\Delta t}{\Delta x}$. Assume that we know the dependent variable at all x at some instant in time t, say from given initial conditions. Examining equation (2.10), we see that the dependent variable at time $(t + \Delta t)$ can be obtained explicitly from the known results at time t, i.e. U_j^{n+1} is obtained directly from the known values U_{j-1}^n, U_j^n, for $j = 1, \dots$. The boundary value $U_0^n, n \geq 0$, must be obtained from the boundary condition (2.8) at $x = 0$. This is the *upwind scheme* and it is the simplest example of an explicit finite-difference method for (2.5).

The *truncation error* τ_j^{n+1} of the scheme, at the grid point (x_j, t_{n+1}), is given by

$$\tau_j^{n+1} := \frac{u_j^{n+1} - u_j^n}{\Delta t} + \frac{u_j^n - u_{j-1}^n}{\Delta x} + \mu u_j^n.$$

As usual, an expansion about (x_j, t_n) gives, if u is sufficiently smooth,

$$\tau_j^{n+1} = \frac{\Delta t}{2} u_{tt}(x_j, t_n + \theta_1 \Delta t) - \frac{\Delta x}{2} u_{xx}(x_j - \theta_2 \Delta x, t_n).$$

Note that the truncation error for this scheme is $O(\Delta x)+O(\Delta t)$, if the derivatives u_{tt} and u_{xx} are bounded in the domain of the problem, and that the truncation error approaches to zero as $\Delta x \to 0$ and $\Delta t \to 0$. The scheme is said to be *consistent* of first order accurate in time and of first order accurate in age.

Suppose the difference scheme is applied for $j = 1, \ldots, J$, at the points $x_j = j\Delta x$, with $J\Delta x = X$, and the boundary values $U_0^n = B(t_n), n \geq 0$, as given by (2.8). Then for the error $e_j^n = U_j^n - u_j^n$ we have

$$e_j^{n+1} = (1-\nu)e_j^n + \nu e_{j-1}^n - \Delta t \mu e_j^n - \Delta t \tau_j^{n+1},$$

and $e_0^n = 0, 0 \leq n \leq N, (N\Delta t = T)$. Then, we deduce that if $0 < \nu \leq 1$, at all points

$$|e_j^{n+1}| \leq (1-\nu)|e_j^n| + \nu|e_{j-1}^n| + \Delta t\mu|e_j^n| + \Delta t|\tau_j^{n+1}|, \quad j = 1, \ldots, J.$$

and by introducing the maximum error at each time level, $E^n := \max_{j=1,\ldots,J} |e_j^n|$, we obtain

$$E^{n+1} \leq (1 + \Delta t\mu)E^n + \Delta t(\max_{j=1,\ldots,J} |\tau_j^{n+1}|).$$

If we suppose that the truncation error is bounded, so that $|\tau_j^n| \leq M_\tau$, for all j and n in the domain, a standard induction argument shows that

$$E^n \leq \exp(\mu n\Delta t)E^0 + \frac{1}{\mu}\exp(\mu n\Delta t)M_\tau, \quad 0 \leq n\Delta t \leq T. \tag{2.11}$$

Inequality (2.11) is sufficient to prove first order convergence of the upwind scheme if we make sucesssive refinements of the mesh while satisfying the *stability* condition

$$0 < \nu := \frac{\Delta t}{\Delta x} \leq 1, \tag{2.12}$$

and provided that the solution u has bounded second derivatives. From a practical point of view, condition (2.12) acts as a constraint for the Δt and it is typical of all explicit finite differences schemes for (2.5). In many cases, Δt must be very small; this can result in long computer running times to make calculations over a given interval $[0, T]$.

Condition (2.12) is also necessary for the convergence as shows the argument appeared at 1928 in a fundamental paper by Courant, Friedrichs and Lewy. For the numerical scheme (2.10), if condition (2.12) were violated, we could alter the data (initial or boundary) at the point where the characteristic curve passing through (x_j, t_{n+1}) crosses the initial line $t = 0$ or the boundary $x = 0$, without altering the computed numerical approximation U_j^{n+1}. The numerical solution therefore cannot converge to the exact solution $u(x_j, t_{n+1})$, that is altered by the changes in the data.

2.1.2 The nonlinear case

The upwind scheme for the nonlinear problem (2.1)-(2.3) takes the form

$$\frac{U_j^{n+1} - U_j^n}{\Delta t} + \frac{U_j^n - U_{j-1}^n}{\Delta x} = -\mu(x_j, I_\mu^h(\mathbf{U}^n))U_j^n, \tag{2.13}$$

for $1 \leq j \leq J$, $0 \leq n \leq N-1$, with the given initial condition

$$\mathbf{U}^0 = (U_1^0, U_2^0, \ldots, U_J^0)$$

and boundary condition

$$U_0^{n+1} = \sum_{j=1}^{J} h\beta(x_j, I_\beta^h(\mathbf{U}^{n+1}))U_j^{n+1}, \quad 0 \leq n \leq N-1. \tag{2.14}$$

Where we define approximations $I_\mu^h(\mathbf{U}^n) \approx I_\mu(t_n)$ and $I_\beta^h(\mathbf{U}^n) \approx I_\beta(t_n)$ based in the composite rectangle quadrature rule

$$I_\mu^h(\mathbf{U}^n) = \sum_{j=1}^{J} h\gamma_\mu(x_j)U_j^n, \quad I_\beta^h(\mathbf{U}^n) = \sum_{j=1}^{J} h\gamma_\beta(x_j)U_j^n.$$

The method as derived is explicit and very easy to implement. However, the convergence analysis is too much involved and is out of the scope of these lecture notes. In [23] convergence of first order in time and in age is proved through the use of a general analytic framework that uses a definition of stability with thresholds introduced in [22].

2.2 Second order Finite-Difference schemes: the box method.

The *box scheme* is a very compact implicit scheme. We introduce the notation

$$U_j^{n+1/2} := \frac{1}{2}(U_j^{n+1} + U_j^n), \quad U_{j-1/2}^n := \frac{1}{2}(U_{j-1}^n + U_j^n). \tag{2.15}$$

For the model problem (2.5) the box scheme then takes the form

$$\frac{\delta_t(U_j^{n+1/2} + U_{j-1}^{n+1/2})}{2\Delta t} + \frac{\delta_x(U_{j-1/2}^n + U_{j-1/2}^{n+1})}{2\Delta x} = \mu\frac{U_j^{n+1/2} + U_{j-1}^{n+1/2}}{2}, \tag{2.16}$$

for $1 \leq j \leq J, 0 \leq n \leq N-1$. If we expand all the terms in Taylor series about the central point $(x_{j-1/2}, t_{n+1/2})$ as origin, it is easy to see that the symmetry of the averaged differences will give an expansion in even powers of Δx or Δt, so that the scheme is second order accurate. The scheme is implicit as it involves two points on the new time level, but for the model problem (2.5) this requires no extra computation. We can write (2.16) in the form

$$U_j^{n+1} = U_{j-1}^n + (1+\nu-\frac{1}{2}\mu\Delta t)^{-1}\left[(1-\nu)(U_j^n - U_{j-1}^{n+1}) + \frac{\mu}{2}\Delta t(U_j^n + U_{j-1}^{n+1})\right], \tag{2.17}$$

where $\nu = \Delta t/\Delta x$. Therefore, if we define U_0^{n+1}, the first value of U on the new time level, from the boundary condition (2.8) then formula (2.17) will give directly the values $U_j^{n+1}, j = 1, \ldots,$ in succession from left to right.

In the nonlinear case, the box scheme for the problem (2.1)-(2.4) takes the form

$$\frac{\delta_t(U_j^{n+1/2}+U_{j-1}^{n+1/2})}{2\Delta t}+\frac{\delta_x(U_{j-1/2}^{n}+U_{j-1/2}^{n+1})}{2\Delta x}= \tag{2.18}$$
$$-\mu(x_{j-1/2},I_\mu^h(\mathbf{U}^{n+1/2}))\frac{U_j^{n+1/2}+U_{j-1}^{n+1/2}}{2},\quad 1\leq j\leq J, 0\leq n\leq N-1,$$

with the given initial condition

$$\mathbf{U}^0=(U_0^0,U_1^0,\ldots,U_J^0) \tag{2.19}$$

and the boundary condition

$$U_0^{n+1}=\sum_{j=0}^{J}{}''h\beta(x_j,I_\beta^h(\mathbf{U}^{n+1}))U_j^{n+1},\quad 0\leq n\leq N-1. \tag{2.20}$$

Where we define approximations $I_\mu^h(\mathbf{U}^{n+1/2})\approx I_\mu(t_{n+1/2})$ and $I_\beta^h(\mathbf{U}^n)\approx I_\beta(t_n)$ based in the composite trapezoidal rule

$$I_\mu^h(\mathbf{U}^{n+1/2})=\sum_{j=0}^{J}{}''h\gamma_\mu(x_j)U_j^{n+1/2},\quad I_\beta^h(\mathbf{U}^n)=\sum_{j=0}^{J}{}''h\gamma_\beta(x_j)U_j^n.$$

with notations introduced in (2.15).

The box scheme in the form given by (2.18)-(2.20) is truly implicit and at each time step the nonlinear equations must be solved by some fixed-point iteration procedure. The numerical method is second order accurate as Δx tends to zero assuming that the time step $\Delta t=\nu\Delta x$, with ν a fixed but arbitrary positive constant. The stability and convergence analysis can be found in [12].

The scheme (2.18)-(2.20) can be made explicit if at each time t_n, approximations to $I_\mu(t_{n+1/2})$ and $I_\beta(t_{n+1})$ are derived by extrapolation of the known approximations at earlier times, for example [13].

2.3 Finite-Difference methods along the characteristics

The most popular technique to integrate numerically problems like (2.1)-(2.3) is the characteristics method. The characteristic curves of equation (2.1) are the lines $x-t=c$, c constant, and along those characteristics the solution $u(x,t)$ satisfies

$$\frac{du}{dt}=-\mu(x,I_\mu(t))u.$$

If we integrate along characteristics, we obtain that solutions of the hyperbolic integro-differential equation (2.1) have the following property: For each x_0 with $0<x_0<A$, and such that $a+h<A$, then

$$u(x_0+h,t_0+h)=u(x_0,t_0)\exp\left(-\int_0^h\mu(x_0+\tau,I_\mu(t_0+\tau))d\tau\right), \tag{2.21}$$

where $t_0 > 0$. We are trying to obtain a numerical approximation to the values of the theoretical solution u of (2.1)-(2.3) in a time interval $[0,T]$ by discretizing the identity (2.21). Given a positive integer J, if $h = A/J$, and $N = [T/h]$, we introduce the grid points $x_j = jh, j = 0,\dots,J$ and time levels $t_n = nh, 0 \le n \le N$. Now as $(x_{j+1}, t_{n+1}) = (x_j + h, t_n + h), 0 \le j \le J-1, 0 \le n \le N-1$, we have that

$$u(x_{j+1}, t_{n+1}) = u(x_j, t_n) \exp\left(-\int_0^h \mu(x_j + \tau, I_\mu(t_n + \tau)) d\tau \right). \tag{2.22}$$

To derive a second order accurate numerical scheme, we form approximations $I_\mu^h(\mathbf{U}^n) \approx I_\mu(t_n)$ and $I_\beta^h(\mathbf{U}^n) \approx I_\beta^h(\mathbf{U}^n)$ using the composite trapezoidal rule. Also, let $R(z)$ denote a Padé (m,n)-rational approximation to the exponential $\exp(z)$ of at least second order; this means that $R(z) = P_m(z)/Q_n(z)$, $P_m(z), Q_n(z)$ polinomials of z of degrees m and n respectively, such that

$$|e^z - R(z)| = O(z^3), \quad (z \to 0).$$

For example the Padé (1,1), Padé (0,2), Padé (2,0), and Padé (2,2) rational approximations to the function e^z are given respectively by

$$\frac{2+z}{2-z}, \quad \frac{1}{1-z+\frac{1}{2}z^2}, \quad 1+z+\frac{1}{2}z^2, \quad \frac{12+6z+z^2}{12-6z+z^2}.$$

Then, we discretize (2.22) to obtain

$$U_{j+1}^{n+1} = U_j^n R\left(-\frac{h}{2}(\mu(x_j, I_\mu^h(\mathbf{U}^n)) + \mu(x_{j+1}, I_\mu^h(\mathbf{U}^{n+1}))) \right), \tag{2.23}$$

$0 \le j \le -1, 0 \le n \le N-1$, with given initial conditions $\mathbf{U}^0 = (U_0^0, \dots, U_J^0)$ and boundary condition

$$U_0^{n+1} = \sum_{j=0}^{J}{}'' h\beta(x_j, I_\beta^h(\mathbf{U}^{n+1}))U_j^{n+1}, \quad 0 \le n \le N-1. \tag{2.24}$$

Note that in (2.23) we have used the trapezoidal rule to approximate the integral inside the exponential in (2.21). This is mainly the cause of the implicitness of the formula (2.23). Also the composite trapezoidal rule make (2.24) implicit. The equations (2.23)-(2.24) are solved at each time step by a fixed-point iteration.

In [10] an explicit first-order accurate method was derived (and analyzed) with the same approach: the integral inside the exponential in (2.21) was approximated with the rectangle quadrature rule based at $\tau = 0$, $R(z) = \dfrac{1}{1-z}$, was the Padé $(0,1)$-rational approximation to the exponential and $I_\mu^h(\mathbf{U}^n)$, $I_\beta^h(\mathbf{U}^n)$ were based on the composite midpoint rule applied on coupled intervals $[x_{2j}, x_{2j+2}]$, $j = 0,\dots,J-1$.

It is posible to get a explicit second-order accurate method with a careful design of the quadratures, see for instance [1] .

2.4 Test problems

Numerical experiments will be reported on the following test problems. For the first one the exact solution is known and it is possible to take into account the convergence properties. In the second test we introduce a problem with more biological significant.

Problem 1. We choose the age-specific fertility and mortality moduli as

$$\begin{aligned} \mu(x,z,t) &= z\,, \\ \beta(x,z,t) &= \frac{4\,x\,z\,e^{-x}\,(2-2\,e^{-A}+e^{-t})^2}{(1+z)^2\,(1-e^{-A})\,(1-(1+2A)\,e^{-2A})\,(1-e^{-A}+e^{-t})}\,. \end{aligned}$$

Note the time dependence of the fertility and mortality rates. However this does not introduce aditional difficulties for the numerical methods studied. The weight functions are $\gamma_\mu \equiv \gamma_\beta \equiv 1$, and we consider as the initial age-specific density the function

$$u_0(x) = \frac{\exp(-x)}{2\,-\,\exp(-A)}\,.$$

The solution of the problem (2.1)–(2.3) is then given by

$$u(x,t) = \frac{\exp(-x)}{1\,-\,\exp(-A)\,+\,\exp(-t)}\,.$$

Problem 2. We study a model that describes the dynamics of the sexual phase of monogonont rotifers. The age-structured model consist on a system of PDEs,

$$\begin{aligned} v_t + v_a + \mu\,v &= -E\,H(t)\,v\,\kappa_{[0,T]}(a) \\ h_t + h_a + \delta\,h &= 0 \end{aligned}$$

with boundary conditions $v(0,t) = 1$, $h(0,t) = \int_1^\infty v(x,t)\,dx$. Where the state variables are v represents the density with respect to age of virgin mictic females at time t, h represents the density with respect to age of haploid males. The parameters are the following $\mu, \delta, E > 0$, $0 < T \le 1$ and the value of $H(t) = \int_0^\infty h(x,t)\,dx$ represents the number of haploid males.

3 Numerical Solution of Size-Structured Population Models

In this section we pay attention to the numerical integration of models describing the evolution of size-structured populations. We consider a minimum and a maximum possible size, and we establish the $[0,1]$ as the values of the size variable.

$$u_t + (g(x, I_g(t), t)\,u)_x = -\mu(x, I_\mu(t), t)\,u, \quad 0 < x < 1, \quad t > 0, \tag{3.1}$$

$$g(0, I_g(t), t)\,u(0,t) = \int_0^1 \alpha(x, I_\alpha(t), t)\,u(x,t)\;dx, \quad t > 0, \tag{3.2}$$

$$u(x,0) = u_0(x), \quad 0 \le x \le 1. \tag{3.3}$$

We assume that the size of any individual varies according to

$$\frac{dx}{dt} = g(x, I_g(t), t). \tag{3.4}$$

where $g(x, I_g(t), t)$ is the size-dependent growth rate with

$$g(1, \cdot, \cdot) = 0. \tag{3.5}$$

Size-structured population models were firstly proposed by Sinko and Streifer [29] and Bell and Anderson [7]. The basic assumption in the model (3.1)-(3.3) is that size characterizes the state of evolution of individuals in the population and therefore that the biological parameter size is strongly correlated to age. An extensive study of physiologically structured population dynamics, with discussion of the biological background of such models, can be found in [24].

3.1 Finite-Difference schemes: Lax-Wendroff method.

We are going to describe an explicit method that is very popular in fluid dynamics.

Let J be a positive integer, we introduce the grid points $x_j = j\,h$, $0 \le j \le J$, where $h = 1/J$ is the mesh size. The step length in time is denoted by k, and $t_n = n\,k$, $0 \le n \le N$, $N = [T/k]$ are the discrete time levels. A subscript j refers to the grid point x_j and a superscript n to the time level t_n.

Let U_j^n be the numerical approximations to the values $u(x_j, t_n)$, $0 \le j \le J$, $0 \le n \le N$.

The Lax-Wendroff method is defined by means of two stages as follows. First we define

$$U_{j+\frac{1}{2}}^{n+\frac{1}{2}} = U_{j+\frac{1}{2}}^{n} - \frac{k}{h}\,\left(g_{j+1}^n(\mathbf{U})\,U_{j+1}^n - g_j^n(\mathbf{U})\,U_j^n\right) - \frac{k}{2}\mu_{j+\frac{1}{2}}^n(\mathbf{U})\,U_{j+\frac{1}{2}}^n, \tag{3.6}$$

for $j = 0, \ldots, J-1$, where $g_j^n = g(x_j, I_g^h(\mathbf{U}^n), t_n)$, $U_{j+\frac{1}{2}}^n = \frac{1}{2}\,\left(U_{j+1}^n + U_j^n\right)$, $\mu_{j+\frac{1}{2}}^n(\mathbf{U}) = \mu(x_{j+\frac{1}{2}}, I_\mu^h(\mathbf{U}^n), t_n)$, $x_{j+\frac{1}{2}} = \frac{1}{2}\,(x_{j+1} + x_j)$ and

$$I_h^s(\mathbf{U}^n) = \sum_{j=0}^{J}{}'' h\,\gamma_s(x_j)\,U_j^n, \quad s = g, \mu.$$

Now, in the second stage, we update U_j^{n+1} for $j = 1, 2, \ldots, J-1$ using

$$U_j^{n+1} = U_j^n - \frac{k}{h}\,\left(g_{j+\frac{1}{2}}^{n+\frac{1}{2}}(\mathbf{U})\,U_{j+\frac{1}{2}}^{n+\frac{1}{2}} - g_{j-\frac{1}{2}}^{n+\frac{1}{2}}(\mathbf{U})\,U_{j-\frac{1}{2}}^{n+\frac{1}{2}}\right) - \frac{k}{2}\mu_j^{n+\frac{1}{2}}(\mathbf{U})\,U_j^{n+\frac{1}{2}}, \tag{3.7}$$

where $g_{j+\frac{1}{2}}^{n+\frac{1}{2}}(\mathbf{U}) = g(x_{j+\frac{1}{2}}, I_g^h(\mathbf{U}^{n+\frac{1}{2}}), t_n + \frac{k}{2})$, $U_j^{n+\frac{1}{2}} = \dfrac{1}{2}\,\left(U_{j+\frac{1}{2}}^{n+\frac{1}{2}} + U_{j-\frac{1}{2}}^{n+\frac{1}{2}}\right)$, $\mu_j^{n+\frac{1}{2}}(\mathbf{U}) = \mu(x_j, I_\mu^h(\mathbf{U}^{n+\frac{1}{2}}), t_n + \frac{k}{2})$, and

$$I_h^s(\mathbf{U}^{n+\frac{1}{2}}) = \sum_{j=1}^{J}\,h\,\gamma_s(x_{j-\frac{1}{2}})\,U_{j-\frac{1}{2}}^{n+\frac{1}{2}}, \quad s = g, \mu.$$

We use the property of the solution in $U_J^{n+1}=0$. And we get the value at the boundary node solving the next coupled nonlinear equations

$$I_\alpha^h(\mathbf{U}^{n+1}) = \sum_{j=0}^{J}{}'' h\, \gamma_\alpha(x_j)\, U_j^{n+1},$$

$$g_0^{n+1}\, U_0^{n+1} = \sum_{j=0}^{J}{}'' h\, \alpha(x_j, I_\alpha^h(\mathbf{U}^{n+1}), t_{n+1})\, U_j^{n+1}, 0 \le n \le N-1. \tag{3.8}$$

The method is completed with the given initial condition

$$\mathbf{U}^0 = (U_0^0, U_1^0, \ldots, U_J^0) \in \mathbb{R}^{J+1}. \tag{3.9}$$

3.2 Integration along characteristics curves

The next methods integrates the problem (3.1)-(3.3) along the characteristic curves. If we define $\mu^*(x, z_1, z_2, t) = \mu(x, z_1, t) + g_x(x, z_2, t)$, the equation (3.1) is written as

$$u_t + g(x, I_g(t), t)\, u_x = -\mu^*(x, I_\mu(t), I_g(t), t)\; u, 0 < x < 1, \quad t > 0. \tag{3.10}$$

When we use the characteristic curves, the numerical integration of the partial differential equation (3.1) has to solve two type of problems. First we integrate numerically

$$\begin{cases} x'(t; t_0, x_0) = g(x(t; t_0, x_0), I_g(t), t), \quad t \ge t_0, \\ x(t_0; t_0, x_0) = x_0, \end{cases} \tag{3.11}$$

that defines the characteristic curves $x(t; t_0, x_0)$ passing through (x_0, t_0), in order to get the grid of the scheme. Then we define, $w(t; t_0, x_0) = u(x(t; t_0, x_0), t)$, that verify

$$\begin{cases} \dfrac{d}{dt} w(t; t_0, x_0) = -\mu^*\left(x\left(t; t_0, x_0\right), I_\mu(t), I_g(t), t\right)\; w(t; t_0, x_0), \quad t \ge t_0, \\ w(t_0; t_0, x_0) = u(x_0, t_0), \end{cases} \tag{3.12}$$

that will be integrated using the representation formula of the solution

$$w(t; t_0, x_0) = u(x_0, t_0)\, \exp\left\{ -\int_{t_0}^{t} \mu^*\left(x\left(\tau; t_0, x_0\right), I_\mu(\tau), I_g(\tau), \tau\right)\; d\tau \right\}. \tag{3.13}$$

Both problems have to be solved in the complete model at the same time.

3.2.1 Autonomous model. Natural grid.

Given a positive integer N, we define $k = T/N$ and we introduce the discrete time levels $t_n = n\,k$, $0 \le n \le N$ and the natural grid

$$0 = x_0 < x_1 < \cdots < x_J < x_{J+1} = 1 \tag{3.14}$$

such that the points (x_j, t_n) and (x_{j+1}, t_{n+1}), $0 \le j \le J-1$, $0 \le n \le N-1$, belong to the same characteristic curve. In general, this is not possible because we are unable to solve (3.11) in an analytical form, so we integrate (3.11) numerically by means of the classical fourth-order Runge-Kutta method. Thus, we consider the grid points defined by the equations

$$\begin{aligned} x_0 &= 0, && (3.15)\\ x_{j+1} &= x_j + \frac{1}{6}(Y_1(x_j) + 2Y_2(x_j) + 2Y_3(x_j) + Y_4(x_j)), && (3.16)\end{aligned}$$

$$Y_1(x_j) = k\, g(x_j), \qquad Y_2(x_j) = k\, g(x_j + \frac{1}{2}Y_1(x_j)),$$

$$Y_3(x_j) = k\, g(x_j + \frac{1}{2}Y_2(x_j)), \qquad Y_4(x_j) = k\, g(x_j + Y_3(x_j)),$$

$0 \leq j \leq J-1$. Now, actually, the points (x_j, t_n) and (x_{j+1}, t_{n+1}), $0 \leq j \leq J-1$, $0 \leq n \leq N-1$, are not necessarily on the same characteristic. However, it is well-known that if g is sufficiently smooth then the local error satisfies, as $k \to 0$,

$$x_{j+1} - x(k; 0, x_j) = O(k^5), \quad 0 \leq j \leq J-1. \tag{3.17}$$

In addition, it was established in [4] that we can choose positive constants K_0 and K_1, which are independent of k, such that

$$K_0\, k < 1 - x_J \leq K_1\, k, \tag{3.18}$$

for k sufficiently small. We need this property of the grid point x_J to ensure appropiate properties of the quadrature rule used in the numerical scheme.

We refer to the grid point x_j by a subscript j and to the time level t_n by a superscript n. Let U_j^n be a numerical approximation to $u(x_j, t_n)$, $0 \leq j \leq J-1$, $0 \leq n \leq N-1$. The next stage in our method is to obtain an approximation U_{j+1}^{n+1} to $u(x_{j+1}, t_{n+1})$ for $0 \leq j \leq J-1$, $0 \leq n \leq N-1$. To this end, if we use the representation formula (3.13) with step size k, then

$$u(x(t_{n+1}; t_n, x_j), t_{n+1}) = u(x_j, t_n) \exp\left(-\int_{t_n}^{t_{n+1}} \mu^*(x(\tau; t_n, x_j), I_\mu(\tau), \tau)\, d\tau\right). \tag{3.19}$$

Then we discretize the identity (3.19) as follows

$$U_{j+1}^{n+1} = U_j^n \exp\left(-\frac{k}{2}\left(\mu^*(x_j, I_k^\mu(\mathbf{U}^n), t_n) + \mu^*(x_{j+1}, I_k^\mu(\mathbf{U}^{n+1}), t_{n+1})\right)\right), \tag{3.20}$$

$0 \leq j \leq J-1, \quad 0 \leq n \leq N-1$. In addition, we obtain an approximation to $u(0, t_{n+1})$ by means of the boundary condition (3.3)

$$g(0)\, U_0^{n+1} = \sum_{j=0}^{J} q_j^k\, \alpha(x_j, I_\alpha^k(\mathbf{U}^{n+1}), t_{n+1})\, U_j^{n+1}, \quad 0 \leq n \leq N-1. \tag{3.21}$$

To derive our numerical scheme we shall consider quadrature rules I_α^k and I_μ^k, with nodes at x_j, $0 \leq j \leq J+1$, to approximate the integral terms $I_\mu(t)$, $I_\alpha(t)$ and the boundary condition. Let us denote

$$I_s^k(\mathbf{U}^n) \;=\; \sum_{j=0}^{J} q_j^k\, \gamma_\alpha(x_j)\, U_j^n, \quad s = \alpha, \mu, \quad 0 \leq n \leq N.$$

The numerical scheme is completely defined if we assume that an approximation of the initial condition is known,

$$\mathbf{U}^0 = (U_0^0, U_1^0, \ldots, U_J^0). \tag{3.22}$$

and we define in our numerical method $U_{J+1}^n = 0$, $0 \le n \le N$.

We shall use a second order composite interpolation quadrature rule (I_μ^k and I_α^k) with the following properties such as done in [4]. Let f be a function defined on the interval $[0,1]$. The quadrature rule I_k has the form

$$I_k(f) = \sum_{j=0}^{J+1} q_j f(x_j) \,, \tag{3.23}$$

where the nodes x_j are those defined by (3.15)-(3.16), and such that, if f is sufficiently smooth, then we assume that, as $k \to 0$,

$$\int_0^1 f(x)\,dx = I_k(f) + O(k^2)\,, \tag{3.24}$$

with $s \ge 2$. Also, we shall assume that there exists a subset of indexes $\{j_l\}_{l=0}^{M+1}$, $0 \le j_l \le J+1$, such that

$$q_j = 0, \quad \text{for } j \notin \{j_l\}_{l=0}^{M+1}, \quad M = O(k^{-1}), \tag{3.25}$$

and

$$|q_{j_l}| \le q\,k\,, \quad 0 \le l \le M+1, \tag{3.26}$$

where q is a positive constant independent of k and j_l ($0 \le l \le M+1$).

The property (3.25) implies that the nodes actually considered by the quadrature rule are a suitable subgrid $\{x_{j_l}\}_{l=0}^{M+1}$ with $O(k^{-1})$ nodes of the grid defined by (3.15)-(3.16). It should be noted that the magnitude of J with respect to k is not determined. Also, there is an accumulation of the grid points $\{x_j\}_{j=0}^{J+1}$ close to 1 (recall that $\lim_{j\to\infty} x(j\,k; 0, 0) = 1$). So, the collection of grids defined by (3.15)-(3.16) is, in general, not quasiuniform and the coefficients of composite interpolation quadrature rules using all the nodes in such grids may not satisfy (3.26). The choice of a subgrid $\{x_{j_l}\}_{l=0}^{M+1}$ such that $x_{j_0} = 0$, $x_{j_{M+1}} = 1$, and

$$C_0\,k \le x_{j_{l+1}} - x_{j_l} \le C_1\,k, \quad 0 \le l \le M+1, \tag{3.27}$$

where C_0 and C_1 are positive constants independent of k, makes it possible to ensure (3.26). For more details we refer to [4].

3.2.2 Nonautonomous model.

Now we introduce the schemes that solve numerically the more difficult version of the problem (3.1)-(3.3). In this case, the two commented problems are coupled and we have to carry out the numerical integration at the same time.

Let J be a positive integer, $h = \dfrac{1}{J}$ an the initial grid nodes $X_j^0 = j\,h$, $0 \le j \le J$. We also know the approximation in $t = 0$, U_j^0, $0 \le j \le J$. We denote $\mathbf{X^0} = \left\{X_0^0 = 0, X_1^0, \ldots, X_{J-1}^0, X_J^0 = 1\right\}$ and $\mathbf{U^0} = \left\{U_0^0, U_1^0, \ldots, U_{J-1}^0, U_J^0 = 0\right\}$. The step in time is k and $t_n = n\,k$, $0 \le n \le N$, $N = \left[\dfrac{T}{k}\right]$, are the discrete time levels.

Both schemes are two step methods then we need the numerical approximation both for the grid nodes and for the solution at the level t_1. So we suppose that $\mathbf{X}^1 = \left\{X_0^1 = 0, X_1^1, \ldots, X_J^1, X_{J+1}^1 = 1\right\}$ and $\mathbf{U}^1 = \left\{U_0^1, U_1^1, \ldots, U_J^1, U_{J+1}^1 = 0\right\}$ are known.

Agregation Nodes Method The method we are going to introduce use a new node that flux from zero the boundary each time. Once we have got the initial aproximation we present the equations of the numerical approximations to the time level t_2, the grid nodes $\mathbf{X}^2 = \left\{X_0^2 = 0, X_1^2, \ldots, X_{J+1}^2, X_{J+2}^2 = 1\right\}$ by means of the explicit mid point rule and the first node with the modified Euler method,

$$X_1^2 = k\,g\left(\frac{k}{2}\,g(0, Q^1(\mathbf{X}^1, \boldsymbol{\gamma}_g^1\,\mathbf{U}^1), t_1), \frac{3\,Q^1(\mathbf{X}^1, \boldsymbol{\gamma}_g^1\,\mathbf{U}^1) - Q^0(\mathbf{X}^0, \boldsymbol{\gamma}_g^0\,\mathbf{U}^0)}{2}, t_1 + \frac{k}{2}\right), \tag{3.28}$$

$$X_j^2 = X_{j-2}^0 + 2\,k\,g(X_{j-1}^1, Q^1(\mathbf{X}^1, \boldsymbol{\gamma}_g^1\,\mathbf{U}^1), t_1), \quad 2 \le j \le J+1, \tag{3.29}$$

and $\mathbf{U}^2 = \left\{U_0^2, U_1^2, \ldots, U_{J+1}^2, U_{J+2}^2 = 0\right\}$, using the mid point rule in (3.13),

$$\begin{aligned} U_1^2 = {} & U_0^1 \exp\left(-k\,\mu^*\left(\frac{k}{2}\,g\left(0, Q^1(\mathbf{X}^1, \boldsymbol{\gamma}_g^1\,\mathbf{U}^1), t_1\right),\right.\right. \\ & \left.\left. \frac{3\,Q^1(\mathbf{X}^1, \boldsymbol{\gamma}_\mu^1\,\mathbf{U}^1) - Q^0(\mathbf{X}^0, \boldsymbol{\gamma}_\mu^0\,\mathbf{U})}{2}, \frac{3\,Q^1(\mathbf{X}^1, \boldsymbol{\gamma}_g^1\,\mathbf{U}^1) - Q^0(\mathbf{X}^0, \boldsymbol{\gamma}_g^0\,\mathbf{U}^0)}{2}, t_1 + \frac{k}{2}\right)\right), \end{aligned} \tag{3.30}$$

$$U_j^2 = U_{j-2}^0 \exp\left(-2\,k\,\mu^*\left(X_{j-1}^1, Q^1\left(\mathbf{X}^1, \boldsymbol{\gamma}_\mu^1\,\mathbf{U}^1\right), Q^1\left(\mathbf{X}^1, \boldsymbol{\gamma}_g^1\,\mathbf{U}^1\right), t_1\right)\right), \quad 2 \le j \le J+1, \tag{3.31}$$

finally, the discretization of the boundary condition (3.3) to get U_0^2 by means of an implicit equation

$$U_0^2 = \frac{Q^2(\mathbf{X}^2, \boldsymbol{\alpha}(\mathbf{X}^2, \mathbf{U}^2)\,\mathbf{U}^2)}{g(0, Q^2(\mathbf{X}^2, \boldsymbol{\gamma}_g^2\,\mathbf{U}^2), t_2)}. \tag{3.32}$$

Then we obtain the equations in t_{n+2} by means of the same equations using the approximations of the two previous time levels t_n y t_{n+1}

$$\mathbf{X}^n = \left\{X_0^n = 0, X_1^n, \ldots, X_{J+n-1}^n, X_{J+n}^n = 1\right\}, \quad \mathbf{U}^n = \left\{U_0^n, U_1^n, \ldots, U_{J+n-1}^n, U_{J+n}^n = 0\right\}$$

and

$$\mathbf{X}^{n+1} = \left\{X_0^{n+1} = 0, \ldots, X_{J+n}^{n+1}, X_{J+n+1}^{n+1} = 1\right\}, \quad \mathbf{U}^{n+1} = \left\{U_0^{n+1}, \ldots, U_{J+n}^{n+1}, U_{J+n+1}^{n+1} = 0\right\}.$$

Selection Nodes Method The scheme we are going to introduce modify the previous one. In this scheme we use a selection of the grid nodes to work every time with the same number of nodes. Then the computational cost diminish.

We get the values in the time level t_1, $\mathbf{X}^1 = \{X_0^1 = 0, X_1^1, \ldots, X_J^1, X_{J+1}^1 = 1\}$, $\mathbf{U}^1 = \{U_0^1, U_1^1, \ldots, U_J^1, U_{J+1}^1 = 0\}$, $Q^1(\mathbf{X}^1, \boldsymbol{\gamma}_g^1\,\mathbf{U}^1)$, $Q^1(\mathbf{X}^1, \boldsymbol{\gamma}_\mu^1\,\mathbf{U}^1)$ and in level t_2 $\mathbf{X}^2 = \{X_0^2 = 0, X_1^2, \ldots, X_{J+1}^2, X_{J+2}^2 = 1\}$, $\mathbf{U}^2 = \{U_0^2, U_1^2, \ldots, U_{J+1}^2, U_{J+2}^2 = 0\}$, $Q^2(\mathbf{X}^2, \boldsymbol{\gamma}_g^2\,\mathbf{U}^2)$, $Q^2(\mathbf{X}^2, \boldsymbol{\gamma}_\mu^2\,\mathbf{U}^2)$.

There is a new node that flux from the boundary in each time level, so in t_0 we work with $J+1$ nodes, in t_1 with $J+2$ and in t_2 with $J+3$. Then, to use the same structure in each time level, and the same formulae, we establish an strategy to select $J+2$ nodes in t_2 and $J+1$ in t_1 in order to calculate the values in t_3.

This selection strategy consist on select the node X_l^2 that verify

$$|X_{l+1}^2 - X_{l-1}^2| = \min_{1 \le j \le J+1} |X_{j+1}^2 - X_{j-1}^2| \tag{3.33}$$

and avoid it in the next time level, then we choose the node in the same characteristic curve in t_1, so we get X_{l-1}^1 out. Then we are ready to use the same formula we use in the time step t_2. This selection of nodes is made in each time level after we calculate the numerical approximations.

3.3 Test Problems

Numerical experiments will be reported on the following test problems. For the first one the exact solution is known and it is possible to take into account the convergence properties. In the second test we introduce a problem with more biological significant.

Problem 1. In this example, we choose the size-dependent growth, birth and mortality rate and the weight functions as

$$\begin{aligned}
g(x) &= 0.225\,(1-x^2),\\
\alpha(x,z,t) &= 47.25\,x^2(1-x)^2\frac{z}{(z+1)^2}\frac{(74+115\,e^{-0.45\,t})^2(1+e^{-0.45\,t})}{(73+115\,e^{-0.45\,t})(5+16\,e^{-0.45\,t})},\\
\mu(x,z,t) &= 0.45\,z\frac{1+2x}{73+115\,e^{-0.45\,t}},\\
\gamma_\alpha(x)=\gamma_\mu(x) &= \begin{cases} 252 & ,0 \le x \le 1/3\\ 252(2-3x)^3(54x^2-27x+4) & ,1/3 < x \le 2/3\\ 0 & ,2/3 < x \le 1 \end{cases}.
\end{aligned}$$

The solution of the related problem (3.1)-(3.3) is $u(x,t) = (1-x)^2 + e^{-0.45\,t}(1-x^2)$, which tends towards a *nontrivial equilibrium*.

Problem 2. We study the dynamics of a Gambussia affinis population. where $g(x,t,z) = g(x)\,T_g(t)$, $\mu(x,t,z) = \mu(x,z)\,T_\mu(t)$ and $\alpha(x,t,z) = \alpha(x)\,T_\alpha(t)$ will be defined in a suitable form taking into account the field data from [20, 8, 32] and the regularity requiered.

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