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Convergence of an Age-Physiology Dependent Population Model

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Abstract. We propose a method for partially discretizing a model of an age-dependent population dynamics with an additional structure whose growth rate is age-dependent. We give theoretical conditions under which a second order accuracy arises. A priori estimates are obtained. The main result indicates that the sum of these errors converges and is of second order accuracy.

1. Introduction

Age-dependent population dynamics are particularly of interest in population ecology, since they are closer to reality, and there is considerable literature on their analysis. Models of this type have been proposed in [5,6,12,14], and the references therein.

Because of their practical applications, numerical approaches to the problem of population dynamics is very important. We have considered a model equation with an additional structure, g, say, which may represent size, mass or any other attribute that affects the dynamics of individuals within a cohort, and we have *partially discretized* the age and time variables. A brief comment on previous works provides the context for this paper, which is an extension of the special case studied in [21].

There has been much investigation into numerical methods for solving age-structured models [1]. But Slobodkin [15] observed long ago that for many organisms or biological systems, a difference in age or size taken separately does not explain the differences in individual behaviour. This has led to physiologically structured population models [9].

Since there is an extensive description of numerical methods for the time integration of structured population models in the literature [9,10,], we discuss in brief some of the difficulties and technicalities involved. In full discretization schemes, time and state space are discretized simultaneously while in classical finite difference

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schemes (Richtmeyer and Morton, 1967), derivatives are replaced by differential quotients based on Taylor series expansion in grid points. Sulsky [16] used the classical Lax-Wendroff method for the non-linear density dependent age structured models and for size-structured models [17]. He also used a fixed grid and the resulting scheme is an adapted version of the classical Lax-Wendroff method.

Abia and Lopez-Marcos [1,2] considered the famous McKendrick Von Foerster equation and replaced the time derivative with a forward difference, the age derivative with a backward difference on a discrete mesh in the upwind scheme, and their solution takes the form of a marching solution in steps of time. The truncation error for this scheme relies heavily on the boundedness of the second order derivatives. Although the scheme is consistent of first order accuracy in time and age (if the stability condition $\frac{\Delta t}{\Delta a} \leqslant 1$ is satisfied), differential operators are in general not bounded. Iannelli *et al.,* [8] analyzed a scheme which has a special interest because it preserves for any time step of the discretization, many properties of the continuous system. They proved that without any restrictions on Δt, if the initial datum is between zero and one, the numerical solution (just as the real solution) stays between zero and one. The sum of errors is bounded provided the first order partial derivatives of the function are bounded as well as their second order counterparts. Our approach is simpler and does not rely on any of these stringent conditions.

A number of semi-discretization schemes (upwind and central difference schemes) are discussed in [7]. The resulting set of ordinary differential equations (ODEs) are further discretized in time and similar to the full discretization scheme, these methods work with a discrete representation of the density function. No single model considered the partial discretization scheme, and this motivated us to carry out this study.

The technique we employ transforms the model equation into a first order (ODE) and the obvious advantage is that the ODE obtained is dimensionally consistent and less complex, in the sense that the method of solution requires only basic notion of integration by parts. This approach is basically semi-discrete and the order of convergence is derived for the scheme. In a nutshell, this paper proposes a partial discretization scheme to solve a Partial Differential Equation model for an age-physiology dependent population dynamics. It presents a unique result which provides the estimate for the order of convergence. Therefore, though the method of proofs is simple and elegant, our result is robust compared to that in [6], and naturally extends the result in [21].

The theory and numerical aspects of population dynamics models are extensively analyzed in [22]. The difficulties associated to earlier scheme are enormous: boundedness of derivatives through second order, choice of sub-grids, use of Padé approximations which are not easy to calculate, etc... Our method, we do believe is simpler, and the analysis is robust enough because we need only assume that the vital rates are constants. Thus, there is no need to assume boundedness of derivatives as in [8,11]. Also, if the initial error is small enough, then the sum of all the errors committed in the successive iteration is of second order accuracy.

2. Model Framework and Algorithm

In this section, we derive a numerical scheme for an age-physiology dependent population model. The study of convergence properties is carried out in section 3. Since a typical idea to treat hyperbolic linear or quasi-linear age-dependent models is to discretize the age variable, we have extended this idea by formally discretizing age and time (and since the differential operators ∂_t and ∂_a below are of first order with constant coefficients, it is natural to discretize age and time with the same parameter). The method discussed is a semi-discrete type, appropriate for the study of a partial discretization of linear hyperbolic models of the form

$$u_t + u_a + G(a)u_g + \mu(a,g)u = 0. \tag{2.1}$$

The appropriate initial-boundary conditions are

$$u(0,a,g) = u_0(a,g) \quad , \quad u(t,0,g) = B(t,g),$$

respectively. $u(t,a,g)$ is the population density of individuals aged a, with physiological variable g at time t. $\mu(\cdot,\cdot) \geqslant 0$ is known as the mortality function, while $B(\cdot,\cdot)$ is the fertility function, sometimes referred to as renewal equation (this function is explicitly defined in section 3, $G(a)$ is the velocity of the physiology variable g. $t, a \in I\!R^{2+}, g \in \Omega \subset I\!R^{+}$. Equation (2.1) together with the initial conditions form a well-posed non local boundary-value problem, whose first integral solution in a scalar unknown function can be found in [19], though the context is different. B and μ are not allowed to depend on the total population size in this study, which is nonetheless not very practical in the real world. But, this non dependence makes (2.1) a quasi-linear equation, and thus rendering our model a modest case, which is mathematically tractable. The above equation may model the dynamical evolution of a population structured by age, with physiological variable g, which could represent mass, size or any other attribute that may affect the dynamics of individuals in the cohort.
In [19], equation (2.1) was used to model the dynamics of an inherited disease, with g representing the Haemoglobin F level of sickle cell patients. The complete derivation and analysis of (2.1) can be found in [14,18,], while the existence and uniqueness of the solution have been proved in [19]. It is therefore assumed here that the implicit solution of (2.1) exists and is smooth.

The algorithm derived below is a fully explicit scheme, where only function values at discretized points and simple arithmetic operations are needed at each step, so that the computational complexity of the algorithm is just of the order of the size of the discretization.

The constraint for the time step $\triangle t$ in the algorithm is simply $\triangle t = \triangle a$; $\triangle a$ being the mesh size of the age variable. Below we describe the finite difference method for the approximation of the solution of (2.1). The discretization is based on the standard finite-difference approximations, and the convergence (order) analysis is carried out along well-known lines.

Let T be the final time and $N \in I\!N$ the number of steps used to arrive at T, $t \in [0,T], a \in [0,A], g \in \Omega \subset I\!R^{+}$, A is the maximum attainable age.

Let $h = \triangle t = \triangle a = \frac{T}{N}$ be the age-time discretization parameter or mesh size. We now introduce a convenient notation.
Let $t_m = m\triangle t$, $a^n = n\triangle a = n\triangle t$, $m, n \geqslant 0$ $(\in \boldsymbol{Z})$.

We cover the specified domain by rectangular network with spacing h in the t and a directions respectively, and denote the nodal point by (m, n).

Let $u(t_m, a^n, g) = U_m^n(g)$, $\mu(a^n, g) = \mu^n(g)$ (for simplicity, we shall assume without loss of reality that $\mu^n(g)$ is independent of g), $G(a^n) = G^n$.

By substituting $t = t_m$, $a = a^n$ in equation (2.1), we obtain:

$$\begin{aligned} \frac{\partial}{\partial t}u(t_m, a^n, g) + \frac{\partial}{\partial a}u(t_m, a^n, g) + G(a^n)\frac{\partial}{\partial g}u(t_m, a^n, g), \\ = -\mu(a^n)u(t_m, a^n, g). \end{aligned} \tag{2.2}$$

$U_m^m(g)$ (see equation 2.6) is the exact solution, while $u_m^n(g)$ represents the approximate one (cf. equation 2.7). In what follows, we shall use the well-known divided forward difference.
Consider

$$u(\tau, g) := u(t_m + \tau, a^n + \tau, g),$$

$$u(0, g) = u_m^n,$$
$$u(-h, g) = u(t_m - h, a^n - h, g) = u(t_{m-1}, a^{n-1}, g).$$

By using a second order truncation scheme, Taylor series expansion gives

$$u(-h, g) = u(0, g) + u'(0, g)(-h) + u''(0, g)\frac{h^2}{2} + E,$$

$$\Longrightarrow \quad u'(0, g) = \frac{u(h, g) - u(0, g)}{h} + o(h), \tag{2.3}$$

where E denotes the error term.

It is evident that $u'(0, g) = \frac{\partial}{\partial t}u(t_m, a^n, g) + \frac{\partial}{\partial a}u(t_m, a^n, g)$, and this justifies why time and age derivative can be replaced by a divided forward difference, so that

$$\frac{\partial u}{\partial t}(t_m, a^n, g) + \frac{\partial}{\partial a}u(t_m, a^n, g) = \frac{U_m^n - U_{m-1}^{n-1}}{h} + o(h).$$

Now,

$$u_t + u_a + G(a)u_g = \frac{U_m^n - U_{m-1}^{n-1}}{h}G(a)u_g + o(h) = -\mu^n U_m^n,$$

$$\Longrightarrow U_m^n(\frac{1 + h\mu^n}{h}) + G^n\frac{dU_m^n}{dg} + o(h) = \frac{U_{m-1}^{n-1}}{h},$$

$$\Longrightarrow \frac{dU_m^n(g)}{dg} + \frac{1 + h\mu^n}{G^n h}U_m^n(g) = \frac{U_{m-1}^{n-1}(g)}{hG^n} + \frac{o(h)}{G^n}. \tag{2.4}$$

Equation (2.4) can readily be solved by making an entirely legitimate use of integration by parts, with the assumption that $\mu^n(g) := \mu^n$.
Let $\alpha = \frac{1+h\mu^n}{G^n h}$, and assume that g as well as α are scaled such that $\int_\Omega e^{\alpha g}dg \cong \frac{e^{\alpha g}}{\alpha}$.
Then,

$$U_m^n(g) = e^{-\alpha g}\left[\int_\Omega \frac{e^{\alpha g}}{hG^n}U_{m-1}^{n-1}(g)dg + \int_\Omega e^{\alpha g}\frac{o(h)}{G^n}dg\right]. \tag{2.5}$$

Recursion (2.5) is similar to a Markov process, because the present population depends only on the immediate preceding one, and does not have memory of the past. Equation (2.5) can be solved explicitly whenever the previous population density $U_{m-1}^{n-1}(g)$ is known. That is, in practice $U_{m-1}^{n-1}(g)$ must be a constant. In order to follow the argument set forth in [19], we assume the following approximate solution:

$$\begin{aligned} U_m^n(g) &\leqslant \frac{G^n h U_{m-1}^{n-1}(g)}{G^n(1+h\mu^n)h} + \frac{o(h^3)}{1+h\mu^n}, \\ &= \frac{U_{m-1}^{n-1}(g)}{1+h\mu^n} + \frac{o(h^3)}{1+h\mu^n}. \end{aligned} \tag{2.6}$$

Equation (2.1) thus takes the form

$$\frac{u_m^n(g) - u_{m-1}^{n-1}(g)}{h} + G^n \frac{du_m^n(g)}{dg} = -\mu^n u_m^n(g),$$

$$\Longrightarrow \quad \frac{du_m^n(g)}{dg} + \frac{(1+h\mu^n)}{G^n h} u_m^n(g) = u_{m-1}^{n-1}(g),$$

with solution given by

$$u_m^n(g) = \frac{u_{m-1}^{n-1}(g)}{1+h\mu^n}. \tag{2.7}$$

With these, we are now ready to consider the convergence of the algorithm.

3. Convergence of the Scheme

Following the explicit scheme introduced in [6] and extended in [3], we state and prove the following:

Theorem. Let the errors be denoted by $\xi_m^n(g) = u_m^n(g) - U_m^n(g)$, $\xi_m^0(g) = \xi_m^0$, $\int_\Omega |\xi_m^n(g)dg| = \xi_m^n$, with $\max|\beta_m^n(g)| \leqslant \bar{\beta} = 1$, if

$|\xi_m^0| = o(h^3)$, then $\sum_{n=1}^N |\xi_m^n| \leqslant 2\, o(h^2)$.

Proof. This proof does not assume boundedness of derivatives through second order in the characteristics direction $\tau = (\frac{\sqrt{2}}{2}, \frac{\sqrt{2}}{2})$ as in [8,11]. This assumption is somehow weakened here, and since $\xi_m^n(g)$ represents the error term, we have

$$\begin{aligned} \xi_m^n(g) &= \frac{u_{m-1}^{n-1}(g) - U_{m-1}^{n-1}(g)}{1+h\mu^n} + o(h^3), \\ &= \frac{\xi_{m-1}^{n-1}(g)}{1+\mu^n h} + o(h^3). \end{aligned} \tag{3.1}$$

For the sake of mathematical convenience, and without loss of reality, let $\beta(t,a,g)$ represents the birth rate, then we can formally write the renewal equation as follows:

$$u(t,0,g) = \int_\Omega \int_0^A \beta(t,a,g) u(t,a,g)\, da dg, \tag{3.2}$$

Now, we discretize the inner integral, which amounts to writing it as a Riemann sum. That is,

$$\begin{aligned} U_m^0(g) &= h\int_\Omega \sum_{n=0}^{N} \beta_m^n(g) U_m^n(g)dg + o(h^2), \\ &= h\int_\Omega \beta_m^0(g)U_m^0(g)dg + h\sum_{n=1}^{N}\int_\Omega \beta_m^n(g)U_m^n(g)dg + o(h^2). \end{aligned}$$

Now, let $U_m^0(g) := U_m^0$, then, after some algebraic manipulations and little rearrangement, we obtain

$$U_m^0 = \frac{h}{1-h\int_\Omega \beta_m^0(g)dg}\sum_{n=1}^{N}\int_\Omega \beta_m^n(g)U_m^n(g)dg + \frac{o(h^2)}{1-h\int_\Omega \beta_m^0(g)dg} = \xi_m^0. \tag{3.3}$$

Hence,

$$u_m^0 = \frac{h}{1-h\int_\Omega \beta_m^0(g)dg}\sum_{n=1}^{N}\int_\Omega \beta_m^n(g)U_m^n(g)dg. \tag{3.4}$$

From equation (3.1), the following inequality holds.

$$|\xi_m^n(g)| \leqslant |\xi_{m-1}^{n-1}(g) + o(h^3). \tag{3.5}$$

For brevity and without loss of generality, let $\max_{\substack{n\in[0,A]\\ m\in[0,T]}} |\beta_m^n(g)| = \bar{\beta} = 1$, and

$$\int_\Omega |\xi_m^n(g)dg| := \xi_m^n. \tag{3.6}$$

Then,

$$|\xi_m^0| \leqslant \frac{h}{1-hg}\sum_{n=1}^{N}|\xi_m^n| + \frac{o(h^2)}{1-hg}, \tag{3.7}$$

$$\begin{aligned} \Longrightarrow \sum_{n=1}^{N}|\xi_m^n| &\leqslant \frac{1-hg}{h}|\xi_m^0| + o(h), \\ &\leqslant \frac{1}{h}|\xi_m^0| + o(h). \end{aligned} \tag{3.8}$$

The order of accuracy will therefore depend on the order of truncation. For instance, if the initial error $|\xi_m^0|$ is of $o(h)$, then

$\sum_{n=1}^{N}|\xi_m^n| \leqslant O(h^2+1) \leqslant o(1)$.

which implies that the sum of errors is bounded.

Also, if $|\xi_m^0| = O(h^3)$, then

$\sum_{n=1}^{N}|\xi_m^n| \leqslant 2\ o(h^2)$.

which implies a second order accuracy for the sum of errors.

The above algorithm is rapidly converging compared to that in [6] which has a slow order of convergence (see equation (3.1)). Theoretically, we have attempted to provide a simple but robust method which is lest tasking mathematically; that is, the partial discretization herein seems simpler compared to the complex method provided by other authors whose approach are mathematically demanding. The above convergence result as well as its order are based on a partially discretized algorithm, initially developed in [19].

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