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A PARTIALLY DISCRETIZED AGE-DEPENDENT POPULATION MODEL WITH AN ADDITIONAL STRUCTURE

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Abstract

A semi-discretization method for solving an age-dependent population dynamics model with an additional structure is proposed. This method, unlike previous ones, considers the partial discretization which reduces the model equation into a first order ordinary differential equation. The latter is then solved explicitly and conditions under which second order accuracy arises are given. While the approach adopted is basically analytical, the main result shows that the sum of errors is bounded. An extension to the non-trivial case where growth depends on the additional parameter leads to a Riccati equation, and the existence and convergence of solutions are proved.

Key words: age structure, discrete scheme, population dynamics, physiology, convergence

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1. Introduction

Structured population models combine knowledge of individuals in the population – its basic unit – and the study of the higher organization level: the population (Abia et al. 2004). In other words, their purpose consists in reflecting the dependence on the individual physiological states of the dynamics of the whole population, usually conceived as a frequency distribution of individuals which evolves over time (Abia et al. 2004). This effect is introduced into the model by *structuring* the population, i.e. classifying the individuals by various continuous, internal variables which represent a particular physiological feature. Age-dependent population dynamics models are 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 by Sinko and Streifer (1967), Bell and Anderson (1967), Oster and Takahasi (1974), Chichia (1990) and the references therein).

Partial differential equations (PDEs) form the basis of very many mathematical models of physical, chemical and biological phenomena. Their use has spread more recently into economics, financial forecasting and other fields (Morton and Mayers, 1996). To investigate the predictions of these models, it is often necessary to approximate the solution of these PDEs numerically, combined with the analysis of simple special cases. Because of their practical applications, numerical approaches to the problem of population dynamics are very important and unavoidable for most realistic cases in order to get some quantitative information from the model. Also, knowledge of the qualitative behaviour of solutions requires numerical methods to approximate essential parameters. The motivation for this study comes from the fact that better methods that handle the Sinko-Streifer's equation would be of great value in modelling many biological systems. The following comments on related works provide the context for the present paper.

There has been much investigation into numerical methods for solving models with just age structure (Ayati, 2000). However, Slobodkin (1953) 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. The age variable alone has a limited practical value due to the fact that age is very difficult to measure experimentally in a large number of species (Abia, et al. 2004). This has led to physiologically structured population models (Kooi and Kelpin, 2003). An extensive study with discussion of the biological background of can be found in Metz and Diekmann (1986) and Zhao (2003).

Age and space structured models are applicable to problems in ecology, epidemiology, population genetics and cell growth. For models with both age and space structure, Milner (1990) developed a method for population that diffuse to avoid crowding. Kim (1996), Kim and Park (1995), and Lopez and Trigiante (1985) developed methods for random dispersal. All these methods involve uniform time and age discretizations, with age step chosen to equal the time step. Ayati (2000) allows for variable time steps and independent age and time discretizations with spatial diffusion. He argued that the use of moving age discretization that allows for a non uniform age and time preserves the important fact that age and time advance together, and the advantage of having variable time steps is the ability to adaptively choose the time steps to assure robustness and efficiency, while the advantages of independent age and time discretizations are fewer computations and less memory use when the dependence on age is weak relative to the dependence on time.

Extensive description of numerical methods for the time integration of structured population models are given in the literature (Kooi and Kelpin, 2003). In full discretization schemes, time and state space are discretized simultaneously while in classical finite difference schemes (Richtmeyer and Morton, 1967), derivatives are replaced by differential quotients based on Taylor series expansion in grid points. Sulsky (1993) used the classical Lax-Wendroff method (which is a very popular explicit method in fluid dynamics (Abia et al. 2000)) for the non-linear density dependent age structured models and later for size-structured models (Sulsky, 1994). He applied a fixed grid and the resulting scheme is an adapted version of the classical Lax-Wendroff method. For age-structured models, the support for the density distributions is known for the initial conditions and subsequently for all time in the admissible interval. For size-structured populations, the support of the size distribution is not known beforehand and several magnitudes in the size of the individuals within the population may occur. When this density function is zero in a large portion of the computational domain, this leads to wasted work over much of the grid at early times in the calculation (Kooi and Kelpin, 2003).

Abia and Lopez-Marcos (1997, 1999) 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 $\frac{\Delta t}{\Delta a} \leq 1$ is satisfied), the differential operator is in general not bounded. Iannelli et al. (1992) 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 data 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.

Fairweather and Lopez-Marcos (1991); Angulo and Lopez-Marcos (2002) consider the box method (which is a very compact implicit scheme), and their difference scheme is obtained by discretization of the integral terms obtained from the balance law. Ackleh and Ito (1997) proposed a different implicit scheme. A number of semi-discretization schemes (upwind and central difference schemes) are discussed in Gurney and Nisbet (1998). The resulting set of ordinary differential equations are further discretized in time and similar to the full discretization scheme, these methods work with a discrete representation of the density function. Ito, et al. (1991), Milner and Rabbiolo (1992), Angulo and Lopez-Marcos (2000, 2002) and Kostova (2002) proposed an approximation scheme for age-size structured PDE models in which the grid size in both age and time directions are taken equal. The procedure comprises three steps (see Kooi and Kelpin, 2003) and the method is equivalent to a time-integration along the characteristics with equidistant time-steps. Abia and Lopez-Marcos (1997) derived a second order accurate numerical scheme by forming some approximations using the composite trapezoidal rule and Padé (m, n) rational approximation to the exponential exp (z) of at least second order. Earlier on (in 1995), they used the Runge-Kutta methods for an age structured population model. In this case one needs to choose a sub-grid that makes it possible for the scheme to be bounded below and above. More details can be found in Angulo and Lopez-Marcos (1999). Ackleh and Deng (2000) developed a monotone approximation based on upper and lower solution techniques for non-autonomous size-structured model.

Kostova (2002) gives a short review of existing numerical methods with proven global error estimates and describe an explicit method of the third order. In Angulo and Lopez-Marcos (2002) the efficiency of three numerical methods: the box method, the Laz-Wendroff and a characteristics scheme is assessed. Their conclusion is that for an autonomous problem no best method exists and the box method proves more appropriate in non-autonomous problems. These schemes are related to Eulerian approach while the escalator boxcar train method (de Roos, 1998) uses Lagrangian approach, which can be used for a broad class of physiologically structured population models. Kelpin et al. (2000) used the simple forward Euler scheme for a model with pulsed reproduction, that is a model in which individuals are born in a specific period of the year or when a certain threshold for the mothers is satisfied.

Tchuenche (2003/4) analyzed the discretization of a simple age-dependent population dynamics model, which is a special case of the model considered herein. For a recent extensive analysis of the theory and numerical aspects of population dynamics models, see (Zhao, 2003). A review of the numerical methods for the solution of the size-structured population balance models is presented in Abia et al. (2004). By the middle of the last century some studies, which showed that age was not the principal physiological feature for determining the ability of an individual to survive, grow and reproduce in certain populations, began to appear. As an alternative, they took other physiological characteristics, which were not as difficult to measure as age, to model the dynamics of such species. These features could include, for example, length, weight, mass, biomass, maturity, energy reserves, amount of foliage, etc., which were grouped generically under the name of size (Abia et al. 2004).

From the aforementioned, no single model has so far considered a partial discretization scheme, which is the purpose of this paper. In this light, we consider a model with an additional structure, *g*, say, which may represents any attribute that can affect the dynamics of individuals within a population, and partially discretized it in the age and time domains. This technique transforms the model equation into a system of first order ordinary differential equations (ODEs). The obvious advantage is that the equation is dimensionally consistent (age and physiology variables do not have the same unit of measurement) and less complex, in the sense that the algorithm is simpler, and the method of solution requires only the basic notion of integration by parts. This method is basically semi-discrete and the model is a simplified version of the one presented by Sinko and Streifer (1967). The order of convergence is derived for this scheme and the main result shows that the sum of errors is bounded and is of second order accuracy. The analysis is extended to the non-trivial case where growth depends on the additional parameter, and this leads to a Riccati type equation. Existence and convergence of solutions are proved.

2. The Model and the Algorithm

We extend the idea of treating hyperbolic quasi-linear age-dependent models of discretizing the age variable by formally discretizing age and time, especially because they have the same unit of measurement. We are considering the following linear first order PDE which represents the evolution of a population with an age structure and a physiological variable *g*, say (for more details on this model equation, see Tchuenche, 2002, 2006):

$$u_t + u_a + G(a)u_g + R(a,g)u = 0 \qquad (2.1)$$

with the appropriate initial-boundary conditions.

$$u(0,a,g) = u_0(a,g);$$

$$u(t,0,g) = B(t,g) = \int_\Omega \int_0^A \beta(t,a,g)u(t,a,g)\,da\,dg\,. \qquad (2.2)$$

$u(t,a,g)$ represents the age-specific density of individuals of age a with physiological variable g at time t, $R(.,.)\geq 0$ is known as the mortality function while $B(.,.)$ is referred to as renewal equation or birth law, β is the fertility function or birth modulus, $G(a)$ is the velocity of g. The case where $G := G(a,g)$ is a function of age and size will be introduce briefly at the end for elaboration and will be fully treated elsewhere. A model with spatial diffusion can be found in Ayati (2000).

System (2.1) forms a well-posed non-local boundary-value problem whose first integral solution in a modified version can be found in Tchuenche (2002). For mathematical tractability and convenience, *B* and *R* are not allowed to depend on the total population size in this study. This is nonetheless not very realistic, though it makes equation $(2.1)_1$ to be of quasi-linear type and thus rendering our model a modest case. A complete derivation of equation (2.1) can be found in Sinko and Streifer (1969), Tchuenche (2005), the existence and uniqueness of the solution have been proved in Tchuenche (2002). Therefore, it is assumed that the implicit solution of (2.1) exists and is smooth. The scheme derived below is explicit and is such that only function values at discretized points and intuitive 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 truncation.

Since the age and time variables have the same dimension, they will be discretized together using constant steps along characteristics. Let T be the final time and $N\in\mathbb{N}$ the number of steps used to arrive at T, $t\in[0,T]$, a $\in[0,A]$, $g\in\Omega\subset\mathbb{R}^+$, where A is the maximum attainable age. Let $h=\Delta t=\Delta a=\dfrac{T}{N}$ be the age-time discretization parameter or mesh size. The following notations are used subsequently:
$t_m:=m\Delta t$, and $a_n:=n\Delta t=n\Delta t$, with $m,n\geq 0$ ($\in\mathbb{Z}$).

The population is approximated by piecewise constant functions of age, which are generally only first order correct. The function $u(t,a,g)$ which is the theoretical solution of (2.1) is assumed smooth enough for such approximations to hold. Thus, by covering the entire region with small rectangular networks with spacing h in the t and a directions respectively, and denoting by (m, n) the nodal points with u_m^n and U_m^n representing the approximate and the exact solutions (in a general sense) of the model equation (2.1), respectively, we have:
$U_m^n(g):=u(t_m,a^n,g)$, $R^n(g):=R(a^n,g)$, $G^n:=G(a^n)$ and by substituting $t=t_m$, $a=a^n$ into equation (2.1), we obtain

$$\frac{\partial}{\partial t}u(t_m,a^n,g)+\frac{\partial}{\partial a}u(t_m,a^n,g)+G(a^n)\frac{\partial}{\partial g}u(t_m,a^n,g)=-R(a^n,g)u(t_m,a^n,g)\ . \qquad (2.3)$$

The expression for $U_m^0(g):=u(t_m,0,g)$ will appear later. Now consider
$u(\tau,g):=u(t_m+\tau,a^n+\tau,g)$; $u(0,g)=u_m^n$ and
$u(-h,g):=u(t_m-h,a^n-h,g)=u(t_{m-1},a^{n-1},g)$.

By using a second order truncation scheme (where the prime symbol ' stands for derivative), Taylor series expansion with E as the error term or remainder gives

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

$$\Rightarrow u'(0,g)=\frac{u(0,g)-u(-h,g)}{h}+O(h). \qquad (2.4)$$

Since time and age derivatives can be replaced by a divided forward difference we have:

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

Now,

$$U_t+U_a+G(a)U_g+R(a,g)U=0\text{; that is, }\frac{U_m^n(g)-U_{m-1}^{n-1}(g)}{h}+G^nU_g+R^n(g)U_m^n+O(h)=0$$

$$\Rightarrow\frac{dU_m^n(g)}{dg}+\frac{1+hR^n(g)}{G^nh}U_m^n(g)=\frac{U_{m-1}^{n-1}(g)+O(h)}{G^nh} \qquad (2.5)$$

Equation (2.5) can readily be solved by making an entirely legitimate use of integration by parts, with the assumption that $R^n(g):=R^n$ (i.e., death is only age dependent. This can be justified in the case of Sickle-cell Anaemia where g represents the quantity of haemoglobin **F**, which is almost constant throughout individuals' life).

With due recourse to integration of first order ODE, after some little manipulations with $\alpha = \dfrac{1+hR^n}{G^n h}$ independent of *g*, a point such that $g_1 \le g \le g_2$, where $\Omega = (g_1, g_2)$, then from the first Mean-Value Theorem for integrals, we have $\int_\Omega e^{\alpha g} dg = \dfrac{1}{\alpha}(e^{\alpha g_2} - e^{\alpha g_1}) \le \dfrac{1}{\alpha} e^{\alpha g}$. This crude approximation helps to obtain a first integral solution of (2.5) as follows:

$$U_m^n(g) = e^{-\alpha g}[\int_\Omega \frac{e^{\alpha g}}{hG^n} U_{m-1}^{n-1}(g)dg + \int_\Omega \frac{O(h)}{G^n} dg \,, \tag{2.6}$$

and integration by parts yields the following approximate solution

$$\begin{aligned} U_m^n(g) &= e^{-\alpha g}[U_{m-1}^{'n-1}(g)\frac{e^{\alpha g}}{\alpha} - \frac{1}{\alpha}\int_\Omega e^{\alpha g} U_{m-1}^{n-1}(g)dg] + \frac{O(h^2)}{\alpha G^n} \\ &\le \frac{hG^n U_{m-1}^{n-1}(g)}{hG^n(1+hR^n)} + \frac{O(h^3)}{1+hR^n} \\ &= \frac{U_{m-1}^{n-1}(g)}{(1+hR^n)} + \frac{O(h^3)}{1+hR^n} \end{aligned} \tag{2.7}$$

Note that, R^n being independent of *g*, the solution should include an integral with $U_{m-1}^{n-1}(g)$, since equation (2.5) can be written in the form $z'(g)+\alpha z(g) = f(g)$, where $z(g) = U_m^n(g)$, $\alpha = \dfrac{1+hR^n}{hG^n}$, and $f(g) = \dfrac{U_{m-1}^{n-1}(g)}{hG^n} + \dfrac{O(h)}{G^n}$, but for mathematical convenience, the crude approximation in (2.7) is necessary for our analysis. Thus, since $u_m^n(g)$ is the approximate solution of (2.1), that is,

$$\frac{du_m^n(g)}{dg} + \frac{1+hR^n}{G^n h} u_m^n(g) = \frac{u_{m-1}^{n-1}(g)}{G^n h}, \tag{2.8}$$

we obtain from (2.7) the approximate solution of (2.8) as

$$u_m^n \le \frac{u_{m-1}^{n-1}(g)}{1+hR^n}. \tag{2.9}$$

Lemma 1: The above scheme converges if for $u \in C^1([0,T] \times [0,A] \times \Omega$ and $0 < |R^n| < \infty$, we can find a positive constant κ depending on the parameters of the equation such that, for sufficiently small *h*, $|u(t,a,g) - U_m^n(g)| \le \kappa h$.

Proof: The proof is based on the estimate of the following integral (cf. Tchuenche and Massawe (2006) for more details)

$$\exp\{-\int_0^h R(a+v,g)dv\} \cong \frac{1}{1+hR(a)}, \tag{2.10}$$

In Chichia (1990), the integral inside the exponential was approximated with the rectangle quadrature rule, and due to the explicitness of the exponential term above, we overlook the Padé for convenience. We adopt the above well-known estimate in order to obtain meaningful result in the next section. Then, from (2.10)

$$|u(t,a,g) - U_m^n(g)| \le \left| \frac{u(t-h,a-h,g) - U_m^n(g)}{1+hR^n} \right| \le \frac{h\kappa_{n-h}}{1+h|R^n|} \le \kappa h \tag{2.11}$$

where $\kappa = \kappa(h, R^n, \kappa_{n-h})$

3. Convergence of the Error Terms

If we set $\xi_m^n(g) = | u_m^n(g) - U_m^n(g) |$, $0 \le n \le A,\ m \ge 0$, then we have the following

Lemma 2: Let $\xi_m^n := \int_\Omega | \xi_m^n(g) dg |$ with $\max | \beta_m^n(g) | = 1$, then

(i) for $| \xi_m^0 | = O(h)$, the sum of errors is bounded (i.e., $\sum_{n=1}^{N} | \xi_m^n | \le O(1)$).

(ii) for $| \xi_m^0 | = O(h^3),\ \sum_{n=1}^{N} | \xi_m^n | \le 2O(h^2)$

Proof: Since $\xi_m^n(g)$ represents the error tem, from equation (2.7), we have

$$\begin{aligned}\xi_m^n(g) &= \frac{U_{m-1}^{n-1}(g) - u_{m-1}^{n-1}(g)}{1 + hR^n} + O(h^3) \\ &= \frac{\xi_{m-1}^{n-1}(g)}{1 + hR^n} + O(h^3) \qquad (3.1)\end{aligned}$$

This equation can also be written as

$$\frac{\xi_m^n(g) - \xi_{m-1}^{n-1}(g)}{h} + R^n \xi_m^n(g) = O(h^2) + R^n O(h^3), \qquad (3.2)$$

where for convenience, we shall omit the last term in the sequel. The convergence of the sum of errors depends on the order of the initial error as shown below. Discretizing the inner integral of the second equation in (2.2) amounts to writing it as a Riemann sum

$$\begin{aligned}U_m^0(g) &= h\int_\Omega \sum_{n=0}^{N} \beta_m^n(g) U_m^n(g) dg + O(h^2) \\ &= h\int_\Omega \beta_m^0(g) U_m^0(g) + h\sum_{n=1}^{N} \int_\Omega \beta_m^n(g) U_m^n(g) dg + O(h^2) \qquad (3.3)\end{aligned}$$

with the assumption that it is permissible to interchange the operations of integration and summation. If $U_m^0(g) := U_m^0$, then

$$U_m^0 = \frac{h}{1 - h\int_\Omega \beta_m^0(g) dg} \sum_{n=1}^{N} \int_\Omega \beta_m^n(g) U_m^n(g) dg + \frac{O(h^2)}{1 - h\int_\Omega \beta_m^0(g) dg} \qquad (3.4)$$

and hence,

$$u_m^0 = \frac{h}{1 - h\int_\Omega \beta_m^0(g) dg} \sum_{n=1}^{N} \int_\Omega \beta_m^n(g) u_m^n(g) dg \qquad (3.5)$$

From equation (3.1)

$$| \xi_m^n | \le | \xi_{m-1}^{n-1}(g) | + O(h^3). \qquad (3.6)$$

Since $\beta_m^n(g)$ is the birth rate, it is realistic to assume that $\max | \beta_m^n(g) | = 1$ (for $n \in [0, A]$, and $t \in [0, T]$), let $\xi_m^n := \int_\Omega | \xi_m^n(g) dg |$, then we have from (3.4)

$$| \xi_m^0 | \le \frac{h}{1 - h(g_2 - g_1)} \sum_{n=1}^{N} | \xi_m^n | + \frac{O(h^2)}{1 - h(g_2 - g_1)} \qquad (3.7)$$

By denoting $g_2 - g_1$ simply as $\overline{g}$, equation (3.7) can be rearranged to read

$$\sum_{n=1}^{N} |\xi_m^n| \le \frac{1-h\bar{g}}{h} |\xi_m^0| + O(h) = (\frac{1}{h} - \bar{g}) |\xi_m^0| + O(h) \tag{3.8}$$

Now two hypotheses present themselves, namely:

H$_1$: If the initial error $|\xi_m^0|$ is of $O(h)$, then $\sum_{n=1}^{N} |\xi_m^n| \le O(h+1) \le O(1)$. Hence the sum of errors is bounded.

H$_2$: If $|\xi_m^0| = O(h^3)$, then $\sum_{n=1} |\xi_m^n| \le 2O(h^2)$.

Hypothesis (H$_2$) above suggests that a third order truncation error will greatly minimize the sum of error terms and enhance its convergence.

4. Generalization

Body size is one of the most important attributes of an individual organism (Cushing, 1997) and is significant in determining the organism's energetic requirements and its interaction with its physical and biological environment. Few numerical methods of size-structured species exist when the growth function *G* depends on age and size. Nature is inherently not linear and non-homogeneous, thus this case is of great value in the modeling of biological systems.

If *G*:= *G*(*a*,*g*), then equation (2.4) now reads

$$\frac{d}{dg}[G^n(g)U_m^n(g)] + \frac{1+hR^n}{h} U_m^n(g) = \frac{U_{m-1}^{n-1}(g)}{h} + O(h) \tag{4.1}$$

which is a first order ODE of the form

$$\frac{d(vy)}{dg} + \alpha y = f(g) \tag{4.2}$$

where $v := G^n(g)$ is the velocity or rate of change of $y := U_m^n(g)$, α is as defined above and $f(g) := \frac{U_{m-1}^{n-1}(g)}{h} + O(h)$. This is a first order ODE which is challenging in its own right. A non trivial transformation of equation (4.2) leads to a non-homogeneous Riccati type equation with a singularity at *y*=0 and whose solution cannot be obtained by simple quadrature. The transformation is as follows:

From (4.2), we have

$$y\frac{dv}{dg} + v\frac{dy}{dg} + \alpha y = f(g). \tag{4.3}$$

Since $v = \frac{dy}{dt}$, equation (4.3) takes the form

$$y\frac{dv}{dg} + v^2 + \alpha y = f(g). \tag{4.4}$$

A further transformation of (4.4) with $\frac{dv}{dg} = \frac{d^2y}{dg^2}$ yields

$$y\frac{d^2y}{dg^2} + \left(\frac{dy}{dg}\right)^2 + \alpha y = f(g). \tag{4.5}$$

Equation (4.4) is a Riccati type equation which is not solvable by quadrature, and it defines a family of transcendental functions which are essentially distinct from the elementary transcendent (Roxin, 1972; Redheffer and Port, 1991). Since the closed-form solution is not certain, the problem of existence is of interest in order to ascertain the well-posedness of our problem. This is achieved by expressing (4.1) as an equation reducible to quadratures.

Lemma 3: *Existence*

Let v and y be continuous on their respective domains $\Omega = (g_1, g_2)$ and $\mathbb{R}^+$, then the initial-value problem (4.1) has a solution on the whole of $\mathbb{R}^+$.

Proof: First, we note that by the chain rule

$$\frac{d(vy)}{dg} = v\frac{d}{dy}(vy) = v(y\frac{dv}{dy} + v) = vy\frac{dv}{dy} + v^2 \tag{4.6}$$

Substituting (4.6) into (4.2) and after some little rearrangement, we obtain

$$\frac{dv}{dy} + \frac{v}{y} + \frac{\alpha}{v} = \frac{f(g)}{vy} \tag{4.7}$$

Since $f(g)$ is the previous iterate of y and therefore a known function, we can without loss of reality assume that its initial value is unity, then, rewriting equation (4.7) as

$$v\frac{dv}{dy} + \frac{v^2}{y} + \alpha = \frac{1}{y} \tag{4.8}$$

and using the transformation $S = v^2$, we obtain

$\frac{dS}{dy} + \frac{S}{2y} + \frac{\alpha}{2} = \frac{1}{2y}$. This equation can readily be solved by first multiplying through by $\sqrt{y}$.

That is, $\frac{d}{dy}(S\sqrt{y}) + \frac{\alpha}{2}\sqrt{y} = \frac{1}{2\sqrt{y}}$ and integration yields

$$S\sqrt{y} + \frac{\alpha}{3}y^{\frac{3}{2}} + K = \sqrt{y} \tag{4.9}$$

where K is the constant of integration. Substituting the value of S and taking into cognizance the fact that the integration above is performed with respect to y, the general family of solutions of (4.1) is given by

$$v^2 + \frac{\alpha}{3}y + \frac{K}{\sqrt{y}} = f(g) \tag{4.10}$$

Hence, a solution of (4.1) exists and this terminates the proof.

It is evident that the solution of (4.1) is not unique, but the following condition ensures uniqueness of a positive solution.

Lemma 4: *Uniqueness of a positive solution*

Equation (4.10) has a unique positive solution provided $y > \frac{3}{\alpha}[f(\text{g})\text{-}v^2]$.

Proof: The proof is elementary by simply rewriting equation (4.10) as

$K = \sqrt{y}\left(f(g) - v^2 - \frac{\alpha}{3}y\right) > 0$, and the result follows.

Since at least one biologically relevant solution denoted by $\Phi(\mathrm{g})$ exists, it is well-known that other solutions (of the Riccati equation) are of the form $\Phi(\mathrm{g})+\frac{1}{\Psi(\mathrm{g})}$, $\Psi(\mathrm{g})$ being a solution of an equation of the form (Ince, 1956) $\Psi^{'}(g)+\alpha\Psi(g)+d=0$.

Lemma 5: *Convergence*
The approximate solutions converges to the exact solution, provided $|\Psi(\mathrm{g})|\gg 1$.

Proof: Denote the exact solution of (4.1) by $\mathrm{U}_{\mathrm{m}}^{\mathrm{n}}(\mathrm{g})$, and assume that $\mathrm{U}_{\mathrm{m}}^{\mathrm{n}}(\mathrm{g})$ differs from $\Phi(\mathrm{g})$ by an infinitesimal constant ε, say. Then,
$||U_m^n(g)-\Phi(\mathrm{g})||=||\Phi(\mathrm{g})+\varepsilon-\Phi(\mathrm{g})||=\varepsilon$
Using the second solution, we have that
$||U_m^n(g)-\Phi(\mathrm{g})\text{-}\frac{1}{\Psi(\mathrm{g})}||=||\Phi(\mathrm{g})+\varepsilon-\Phi(\mathrm{g})\text{-}\frac{1}{\Psi(\mathrm{g})}||\rightarrow\varepsilon$, provided $|\Psi(\mathrm{g})|\gg 1$.
Using the definition of the L^1-norm (i.e., $||U(t,a,.)||=U(t,a):=\int_\Omega U(t,a,g)dg$), ε can be estimated. The exact solution of (4.1) is obtained by a direct crude integrating of (4.2) with respect to *g*, that is,

$$y+\frac{1}{v}\left(\int_\Omega[\alpha y-f]dg\right)=0. \tag{4.11}$$

Neglecting the order term appearing in *f*, we have,

$$U_m^n(g)+\frac{1}{v}(\alpha U_m^n-U_{m-1}^{n-1})=0 \tag{4.12}$$

where $U_m^n:=U(t,a)$. Equation (4.10) can be written as

$$v^2+\frac{\alpha}{3}U_m^n(g)+\frac{K}{\sqrt{U_m^n(g)}}-U_{m-1}^{n-1}(g)=0 \tag{4.13}$$

Let $||U_m^n(g)||\le\eta_1$, $||U_{m-1}^{n-1}(g)-\frac{U_{m-1}^{n-1}}{v}||\le\frac{\eta_2}{v}$, and $||U_m^n||\le\eta_3$, then subtracting equations (4.13) from (4.12) and taking the norm yields

$$\left\|U_m^n(g)+\frac{1}{v}(\alpha U_m^n-U_{m-1}^{n-1})-v^2-\frac{\alpha}{3}U_m^n(g)-\frac{K}{\sqrt{U_m^n(g)}}+U_{m-1}^{n-1}(g)\right\|$$

$$\le\left\|U_m^n(g)(1-\frac{\alpha}{3})+U_{m-1}^{n-1}(g)+\frac{\alpha}{v}U_m^n\right\|\le\eta_1(1-\frac{\alpha}{3})+\frac{\eta_2}{v}+\frac{\alpha}{v}\eta_3=\varepsilon \tag{4.14}$$

The quantity ε contains information on the cumulative effect of the errors.

Remark: Equation (4.2) can also be transformed into a matrix version of a scalar nonlinear, non homogeneous first order ODE, but the singularity makes it difficult to handle, and thus a challenging open problem. In (4.10), only positive values of *y* are relevant, since negative population values are biologically irrelevant.

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