Nonlinearity **22** (2009) 1983–1995 doi:10.1088/0951-7715/22/8/012

Mollified birth in natural-age-grid Galerkin methods for age-structured biological systems*

Bruce P Ayati[1] **and Todd F Dupont**[2]

[1] Department of Mathematics, University of Iowa, Iowa City, IA 52245, USA
[2] Department of Computer Science, University of Chicago, Chicago, IL 60637, USA

E-mail: ayati@math.uiowa.edu and dupont@cs.uchicago.edu

Received 19 December 2008, in final form 23 April 2009
Published 20 July 2009
Online at stacks.iop.org/Non/22/1983

Recommended by A L Bertozzi

Abstract
We present natural-age-grid Galerkin methods for a model of a biological population undergoing aging. We use a mollified birth term in the method and analysis. The error due to mollification is of arbitrary order, depending on the choice of mollifier.

The methods in this paper generalize the methods presented in [1], where the approximation space in age was taken to be a discontinuous piecewise polynomial subspace of L^2. We refer to these methods as 'natural-age-grid' Galerkin methods since transport in the age variable is computed through the smooth movement of the age grid at the natural dimensionless velocity of one. The time variable has been left continuous to emphasize this smooth motion, as well as the independence of the time and age discretizations. The methods are shown to be superconvergent in the age variable.

Mathematics Subject Classification: 65M15, 65M60, 35Q80, 92C15, 92C17, 92D25

(Some figures in this article are in colour only in the electronic version)

1. Introduction

We consider a model for a biological population $u(a, t)$ distributed in age a and time t,

$$\partial_t u + \partial_a u = -\mu(a, p)u, \qquad a \geqslant 0,\ t \geqslant 0, \tag{1a}$$

where $\mu(a, p) \geqslant 0$ is the death modulus. The total population, p, is given by

$$p(t) = \int_0^\infty u(a, t)\, \mathrm{d}a, \qquad t \geqslant 0. \tag{1b}$$

* This paper is published as part of a collection in honour of Todd Dupont's 65th birthday.

We have a birth condition

$$u(0,t) = b(u(\cdot,t)) = \int_0^\infty \beta(a,p)u(a,t)\,\mathrm{d}a, \qquad t \geqslant 0. \tag{1c}$$

We present natural-age-grid Galerkin methods for this system, with the addition that newborn individuals are distributed over a small interval around age zero, rather than born precisely at age zero. We refer to this as 'mollified birth'. To introduce the mollification process, we first rewrite (1*a*) and the birth condition (1*c*) as a single equation with a source term given by a Dirac delta function. Set $u(a,t)$ to zero for all $a < 0$ and extend μ to negative a by even reflection about $a = 0$. Then u satisfies

$$\partial_t u + \partial_a u + \mu(a,p)u = b(u)\delta(a), \qquad a \in \mathbb{R}, \quad t \geqslant 0, \tag{2}$$

The crux of the mollification process is replacing $\delta(a)$ with a bounded function $m(a)$ that is supported in $[-s, s]$.

The methods presented in this paper generalize the age discretization in [1], where the approximation space in age was taken to be a discontinuous piecewise polynomial subspace of L^2. We refer to the class of methods presented in this paper and in [1, 2] as 'natural-age-grid' Galerkin methods since transport in the age variable is computed through the smooth movement of the grid at the natural dimensionless velocity of one—rather than through an approximation of the age derivative. This generally leaves polynomial approximation error as the only source of error in the age variable, which in turn underlies our superconvergence results.

Although spatial structure is not treated in this paper, the motivation for the natural-age-grid Galerkin methods is the need for computationally efficient and robust methods so that age structure can be added to models of populations distributed in space. The natural-age-grid Galerkin methods differ qualitatively from previous methods that also solve such systems along age-time characteristics [3–6]. These methods 'shift' the age nodes in a manner that results in a grid with nodes that are effectively in fixed positions—every node is shifted onto the previous location of another node. A major consequence of using an effectively fixed grid along characteristics is the often crippling constraint that the age and time steps must remain equal and constant in magnitude. This restriction is not mitigated in practice with the use of high-order methods, even though once we rewrite the age-structured system with a total derivative in age and time the number of suitable integrations methods becomes very large.

The natural-age-grid Galerkin methods, since they decouple the age and time discretizations, provide two major benefits over these fixed-grid methods. First they allow, in general, larger age intervals than ones restricted to be the same as the time steps. This was the case in several applications: *Proteus mirabilis* swarm-colony development [7], biofilm growth [8] and tumor invasion [9]. Second, relaxing the requirement of having constant time steps allows adaptive time stepping.

The use of standard continuous and discontinuous finite element methods on partitions of the age-time plane results in methods that also allow different age and time discretizations, and the use of adaptive time stepping. However, the current state-of-the-art versions of these methods have orders of convergence that are below those normally associated with the degree of the approximating polynomials, demonstrated both in theory and in example systems [10–12]. This contrasts with the superconvergence properties of the natural-age-grid Galerkin methods that were proven and illustrated with simple computational examples in [1, 2], and implemented in applications in [7–9].

Further discussions on the history of age- and space-structured models and the numerical methods for solving them can be found in [1, 2].

In the methods presented in this paper, we keep time continuous to emphasize two things: the qualitative difference between the smooth movement of the natural-age-grid Galerkin methods and the shifting movement between fixed nodal locations in methods such as [3–6]; and the independence of the natural age grid from any suitable time discretization. We note that the choice of time discretizations is largely left to the user in the natural-age-grid Galerkin methods, whereas in the previous methods it was embedded by necessity into the definition of the methods. The only constraints that occur in practice are that the time step must not be larger than the age step (this has yet to be an issue for our problems of interest), and that a time step must end when a new age interval is introduced (this results in no meaningful loss in efficiency).

Leaving time continuous also simplifies the presentation and analysis of the methods. The methods and analysis when the approximation space in age is restricted to piecewise constants in age were presented in [2]. In this case, time was discretized using a backward Euler method, illustrating the integration of the methods and analysis in age with a specific time discretization.

One particularly effective and simple method for adaptive time stepping is step-doubling with local extrapolation (see [13] and references therein). Step-doubling with local extrapolation consists of taking one step of backward Euler over a time step, and then taking two half steps of backward Euler over the same time interval. This results in two things. First, we can compare the two late-time solutions for the error control needed for the adaptivity in time. Second, we can extrapolate the two solutions to get a likely second-order accurate solution in time.

In some situations we have found that for step-doubling with local extrapolation to work more smoothly in conjunction with the natural-age-grid Galerkin methods, we need to mollify the birth term over several intervals. For example, this was the case for some *Proteus* computations [14], whereas the computational example in [2] (see figure 9.3 in [2]) would not benefit from mollification of the birth term, since the time steps are relatively even.

To understand the nature of the problem, if all the birthing is done in the first age interval, the introduction of a new first interval due to the movement of the grid may result in a sudden increase in the difficulty of the problem, prompting an adaptive method to drastically cut the time step. This may be the case, for example, if the second derivative in the previous first age interval becomes large with the sudden removal of birth, indicating to some adaptive time-stepping methods that the problem has become much harder. Thus, without mollification, the age discretization can, in certain situations, unduly influence the time discretization in an undesirable manner.

The aim of mollification is to smooth the time-stepping process for greater efficiency and robustness, but it is a source of additional error in the computation. This error will, in general, be tolerable and offset by the benefits of mollification if the death modulus does not change much near birth and the birth term is not heavily dependent on very young individuals. For many problems, one can choose the mollification interval $[-s, s]$ so that these issues are reduced (see section 3).

Although mollifying the birth term is not needed in all applications of our natural-age-grid Galerkin methods, the situations where it is of benefit are sufficiently general to warrant a numerical analysis of the effects of mollifying the birth term in an age-structured model. We find that the error due to mollification is of arbitrary order, depending on the choice of mollifier. The need for mollification in specific applications is currently determined by computational experiment.

This paper is organized as follows. We present, in order, conditions on the model equations, the natural-age-grid Galerkin methods with mollified birth, the stability and error analyses for these methods and a computational example.

2. Conditions on the continuous model

We assume existence and uniqueness of smooth, non-negative solutions. Existence results generally allow conditions that are less restrictive than what one assumes for the kind of stability and control we seek. Existence and uniqueness results, including an extensive bibliography, can be found in [15].

We make several assumptions:

Condition 2.1. *The function* $\beta(a, p)$ *is smooth as a function of* a *and* $\|\beta(\cdot, p)\| \leqslant C_\beta$ *for all* p.

Condition 2.2. *There exist constants* C_0 *and* C_1 *such that for* $p \in \mathbb{R}$, μ *satisfies* $\mu(a, p) \leqslant C_1$ *for all* a *and* $0 < C_0 \leqslant \mu(a, p)$ *for* $a > a_c$, *where* a_c *is some critical age.*

Condition 2.3. *The function* $\mu(a, p)$ *is smooth as a function of* a *and is uniformly Lipschitz continuous with respect to* p *with Lipschitz constant* K_μ. *The derivative* $\partial_a \mu(a, p)$ *exists, is uniformly bounded by* C_1 *as a function of all its arguments, and* $\|\partial_a \mu(\cdot, p)\|_{L^2(\mathbb{R}^+)} \leqslant C_1$ *uniformly as a function of* p.

We choose a mollifier, $m(a)$, that is smooth, has compact support on $[-s, s]$, and satisfies, for some integer $\lambda > 0$,

$$\int_{-\infty}^{\infty} m(a) a^l \, \mathrm{d}a = \begin{cases} 1, & l = 0, \\ 0, & l = 1, \ldots, \lambda. \end{cases} \tag{3}$$

Mollification is appropriate only when the death modulus does not change much near birth and the birth term is not heavily dependent on very young individuals. Consequently, we assume the following condition.

Condition 2.4. *The death modulus* $\mu(a, p)$ *is constant for* $a \in [0, s)$. *We extend* μ *to be this constant for* $a \in (-\infty, 0)$.

3. An age discrete method with mollified birth term

We let $\tilde{u} = m * u$, where '$*$' denotes convolution in the age variable. Let $\delta(a)$ denote the Dirac delta function centered at $a = 0$. Assume u is sufficiently smooth and that $\int_{-\infty}^{\infty} |m(a)| \, \mathrm{d}a$ is bounded by some constant. For $a \in (-\infty, -s) \cup (s, \infty)$, the error between the true solution, u, and the mollified true solution, $\tilde{u}$, is

$$\begin{aligned} u(a, t) - \tilde{u}(a, t) &= u(a, t) - \int_{-\infty}^{\infty} m(a - \alpha) \bigg(u(a) + \partial_a u(a)(\alpha - a) \\ &\quad + \frac{\partial_a^2 u(a)}{2} (\alpha - a)^2 + \cdots \bigg) \mathrm{d}\alpha \\ &= - \int_{-\infty}^{\infty} m(a - \alpha) \left(\frac{\partial_a^{\lambda+1} u(a)}{(\lambda + 1)!} (\alpha - a)^{\lambda+1} + \frac{\partial_a^{\lambda+2} u(a)}{(\lambda + 2)!} (\alpha - a)^{\lambda+2} + \cdots \right) \mathrm{d}\alpha \\ &= \mathcal{O}(s^{\lambda+1}). \end{aligned} \tag{4}$$

Let $D = \partial_t + \partial_a$. We rewrite (1$a$) as

$$Du = b(u)\delta(a) - \mu(a, p)u, \qquad a \in \mathbb{R}, \quad t \geqslant 0, \tag{5}$$

so that

$$D\tilde{u} = m(a)b(u) - \mu(a, p)\tilde{u} + r, \qquad a \in \mathbb{R}, \quad t \geqslant 0, \tag{6}$$

where, if $a > s$,

$$
\begin{aligned}
r(a,t) &= \mu\tilde{u} - m * (\mu u) \\
&= \int_{-\infty}^{\infty} m(a-\alpha)(\mu(a) - \mu(\alpha))u(\alpha)\,\mathrm{d}\alpha \\
&= \int_{-\infty}^{\infty} m(a-\alpha)(u(a) + \partial_a u(a)(\alpha - a) + \cdots) \\
&\cdot \left(-\partial_a \mu(a)(\alpha - a) - \frac{\partial_a^2 \mu(a)}{2}(\alpha - a)^2 + \cdots\right) \mathrm{d}\alpha \\
&= \mathcal{O}(s^{\lambda+1}).
\end{aligned} \tag{7}
$$

Note also that the population defined by $\tilde{u}$, $\int_{\mathbb{R}} \tilde{u}(a,t)\,\mathrm{d}a$ is just the $p(t)$ defined by u.

Assume that $\beta(a, p)$ is extended to $\mathbb{R} \times \mathbb{R}^{+}$ as a nonnegative function that has $\lambda + 1$ continuous derivatives in a which are bounded independently of a and p. The smoothness of the extension of β is related to the order of accuracy that we can get in the mollification.

Let $\{a_i\}_{i=0}^{-\infty}$ be a sequence such that $a_0 = \tilde{a}_{\max}$, $0 < a_{i+1} - a_i = \Delta a_i \leqslant \Delta a \leqslant s$, and $a_i \to -\infty$ as $i \to -\infty$. Let $\mathcal{J}$ be the set of a_is. For a fixed nonnegative integer q, let $\mathcal{C}$ denote the space of all piecewise continuous functions over the partition of $(-\infty, \tilde{a}_{\max}]$ defined by $\mathcal{J}$ such that $\varphi \in \mathcal{C}$ has the property that φ restricted to $[a_i, a_{i+1})$ is a polynomial of degree at most q. We think of the functions in $\mathcal{C}$ as being zero on $(\tilde{a}_{\max}, \infty)$. For nonnegative t let $I_i(t) = [a_i + t, a_{i+1} + t)$ and let $i_{\min}(t)$ be the value of i such that $-s \in I_{i_{\min}(t)}$. We suppose that there is a k such that at most k intervals $I_i(t)$ have nonvoid intersection with $[-s, s]$. We define a finite dimensional space in age that moves along the characteristic curves, $\mathrm{d}a/\mathrm{d}t = 1$:

$$
\mathcal{A}(t) = \{\varphi : \varphi(\cdot - t) \in \mathcal{C}, \varphi(a) = 0, a < a_{i_{\min}(t)} + t\}. \tag{8}
$$

The dimension of $\mathcal{A}(t)$ is $(q+1)|i_{\min}(t)|$. We take $U \in \mathcal{A}(t)$. For $t \notin \mathcal{J}$, we have the method with mollified birth term,

$$
\int_{I_i(t)} (DU)v\,\mathrm{d}a = \int_{I_i(t)} b(U(\cdot,t))m(a)v(a) - \mu(a,P)U(a,t)v(a)\,\mathrm{d}a, \tag{9}
$$

for every $v \in \mathcal{A}(t)$. For $t \in \mathcal{J}$, new variables added to (9) are set to zero, and the others are continuous. The total population density is approximated by

$$
P(t) = \int_{-\infty}^{\infty} U(a,t)\,\mathrm{d}a. \tag{10}
$$

4. Stability and error analyses

Let $\|\cdot\|_i$ denote the L^2 norm on the interval $I_i(t)$ and $\|\cdot\|$ the L^2 norm over $\mathbb{R}$.

Theorem 4.1 (Stability of mollified birth method). *Assume conditions 2.1 and 2.2 hold and that $|m(a)| < m_0/s$ for some fixed constant m_0. Let k denote the maximum number of age intervals for which $m(a)$ is nonzero. Let $P_i = \int_{I_i} U\,\mathrm{d}a$. Then*

$$
\|U\|^2(T) \leqslant \check{C}\|U\|^2(0), \tag{11}
$$

$$
|P(T)| \leqslant \sum_i |P_i(0)| + \tilde{C}, \tag{12}
$$

where $\check{C}$ depends on C_β, T and k, and $\tilde{C}$ depends on $\check{C}$, C_1, $\|U\|(0)$, C_β, T and k.

Proof. Let $v = U$ in (9) to obtain

$$\frac{1}{2}\frac{\mathrm{d}}{\mathrm{d}t}\|U\|_i^2 = b(U)\int_{I_i(t)} m(a)U\,\mathrm{d}a - \int_{I_i(t)} \mu U^2\,\mathrm{d}a \tag{13}$$

$$\leqslant b(U)\|m(a)\|_i\|U\|_i. \tag{14}$$

The birth term satisfies

$$|b(U)| = \left|\int_{-\infty}^{\infty} \beta(a,P)U(a,t)\,\mathrm{d}a\right| \leqslant \|\beta(\cdot,P)\|\|U\| \leqslant C_\beta\|U\|. \tag{15}$$

Then

$$\frac{1}{2}\frac{\mathrm{d}}{\mathrm{d}t}\|U\|_i^2 \leqslant C_\beta\|U\|\|m\|_i\|U\|_i. \tag{16}$$

Recall that $|m(a)| < m_0/s$ for some fixed constant m_0. Then

$$\|m\|_i = \left(\int_{I_i(t)} m^2(a)\,\mathrm{d}a\right)^{\frac{1}{2}} \leqslant \frac{m_0\sqrt{\Delta a_i}}{s} \leqslant \frac{m_0\sqrt{\Delta a}}{s} \tag{17}$$

when $I_i(t) \cap [-s,s] \neq \emptyset$, and $\|m\|_i = 0$ otherwise. Moreover, $m(a)$ is nonzero on at most an interval of length $2s$. Apply lemma 4.1, given below, with $w(t) = 0$ and $h_i(t) = \|U\|_i(t)$, to get (11).

Let $\bar{\mu}_i$ and $\bar{U}_i$ be the average of μ and U, respectively, on I_i. Then

$$\frac{\mathrm{d}}{\mathrm{d}t}P_i = b(U)\int_{I_i} m(a)\,\mathrm{d}a - \bar{\mu}_i P_i + \int_{I_i}(\mu-\bar{\mu}_i)(U-\bar{U}_i)\,\mathrm{d}a. \tag{18}$$

Multiply by P_i and drop the $-\bar{\mu}_i P_i^2$ term to get

$$|P_i|\frac{\mathrm{d}}{\mathrm{d}t}|P_i| \leqslant |P_i|\left(b(U)\int_{I_i}|m(a)|\,\mathrm{d}a + \left|\int_{I_i}(\mu-\bar{\mu}_i)(U-\bar{U}_i)\,\mathrm{d}a\right|\right). \tag{19}$$

Since $\bar{U}_i$ is the L^2-projection into constant functions of U on I_i, we have that $\|U-\bar{U}_i\|_i \leqslant \|U\|_i$. Using $\|\mu-\bar{\mu}_i\|_i \leqslant \|\partial_a\mu(\cdot,P)\|_i\Delta a_i$ we get

$$\int_{I_i}(\mu-\bar{\mu}_i)(U-\bar{U}_i)\,\mathrm{d}a \leqslant \|U-\bar{U}_i\|_i\|\mu-\bar{\mu}_i\|_i \leqslant \|\partial_a\mu(\cdot,P)\|_i\|U\|_i\Delta a_i. \tag{20}$$

Then

$$\frac{\mathrm{d}}{\mathrm{d}t}|P_i| \leqslant \left(b(U)\int_{I_i}|m(a)|\,\mathrm{d}a + \|\partial_a\mu(\cdot,P)\|_i\|U\|_i\Delta a_i\right). \tag{21}$$

Integrating gives

$$|P_i(T)| \leqslant |P_i(0)| + C_\beta\|U\|(T)\int_{I_i}|m(a)|\,\mathrm{d}a + \int_0^T \|\partial_a\mu(\cdot,P)\|_i\|U\|_i\Delta a_i\,\mathrm{d}t. \tag{22}$$

Using the arithmetic–geometric mean inequality on the last term and summing gives

$$|P(T)| \leqslant \sum_i |P_i(T)| \tag{23}$$

$$\leqslant \left(\sum_i |P_i(0)|\right) + C_\beta\|U\|(T)\frac{2m_0(s+\Delta a)}{s} \tag{24}$$

$$+ \frac{\Delta a}{2}\left(\|\partial_a\mu(\cdot,P)\|^2 T + \int_0^T \|U\|^2\,\mathrm{d}t\right). \tag{25}$$

Applying (11) to bound $\|U\|$ and using $\|\partial_a\mu(\cdot,P)\| \leqslant C_1$ gives (12). □

We denote by $\mathsf{A}(t)$ the L^2-projection into $\mathcal{A}(t)$. We choose $X(t) \in \mathcal{A}(t)$ such that $X(t) = \mathsf{A}(t)(\tilde{u}(\cdot, t))$ and set $Y(t) = \int_{-\infty}^{\infty} X(t)\,\mathrm{d}a$. We set

$$\vartheta = U - X, \qquad \eta = \tilde{u} - X, \qquad \varpi = P - Y, \qquad \sigma = p - Y.$$

Note that σ is identically zero because $A(t)$ preserves the integral. For definiteness, we will take $U(a, 0) = X(a, 0)$; this gives that $\vartheta(a, 0) = 0$ and $\varpi(0) = 0$.

Theorem 4.2 (Convergence of mollified birth method). *Assume conditions 2.1–2.4 hold, that $|m(a)| < m_0/s$ for some fixed constant m_0, and that $\|\partial_p b(\cdot, \rho)\|$, $\|\beta(\cdot, \rho)\|_{H^{q+1}(\mathbb{R})}$, and $\|U(\cdot, t)\|$ are bounded. Let k denote the maximum number of age intervals for which $m(a)$ is nonzero. Then*

$$|\varpi|^2 + \sum_i \|\vartheta\|_i^2 \leqslant \hat{C} \int_0^T \left(\|\eta\|_{H^{-q-1}(\mathbb{R})}(t) + s^{\lambda+1}\right)^2 \mathrm{d}t, \tag{26}$$

where $\hat{C}$ depends on C_0, C_1, K_μ, $\|\tilde{u}(\cdot, t)\|_{L^\infty(\mathbb{R})}$, $\|u(\cdot, t)\|_{L^\infty(\mathbb{R})}$, k, $\|\partial_p b(\cdot, \rho)\|$, $\|\beta(\cdot, \rho)\|_{H^{q+1}(\mathbb{R})}$, and $\|U(\cdot, t)\|$.

Remark. If there are at most k intervals $I_i(t)$ that intersect $[-s, s]$, $q = 1$ (discontinuous piecewise linears in a), and $m(a)$ is chosen so that $\lambda = 2$, we get a uniform bound on $\|\vartheta\|$ of $C(k)(\Delta a)^3$, i.e. superconvergence with one extra power of Δa. Moreover, $U - \tilde{u} = \mathcal{O}((\Delta a)^3)$ at the two Gauss points in each interval.

Proof. We take the inner product of (6) with $v \in \mathcal{A}(t)$ and integrate over age to get

$$\int_{I_i(t)} (D\tilde{u})v\,\mathrm{d}a = \int_{I_i(t)} mb(u)v - \mu(a, p)uv + rv\,\mathrm{d}a, \tag{27}$$

for $a \in \mathbb{R}$, $t \geqslant 0$.

We subtract (27) from (9), and let $v = \vartheta$, to get

$$\int_{I_i(t)} (D(\vartheta - \eta))\vartheta\,\mathrm{d}a$$
$$= \int_{I_i(t)} (b(U) - b(u))m(a)\,\vartheta - (\mu(a, P)U - \mu(a, p)\tilde{u})\vartheta + r\vartheta\,\mathrm{d}a. \tag{28}$$

By orthogonality,

$$\int_{I_i(t)} \eta\,\vartheta\,\mathrm{d}a = 0. \tag{29}$$

For $t \notin \mathcal{J}$, let $\varepsilon > 0$ be such that $(t - \varepsilon, t + \varepsilon) \cap \mathcal{J} = \emptyset$. For a given $v \in \mathcal{A}(t)$ extend it to $(t - \varepsilon, t + \varepsilon)$, by taking it to be constant along characteristics. By (29) we have, for $0 < \Delta t < \varepsilon$,

$$0 = \frac{1}{\Delta t} \int_{I_i(t)} \eta(a, t + \Delta t)v(a, t + \Delta t) - \eta(a, t)v(a, t)\,\mathrm{d}a$$
$$= \frac{1}{\Delta t} \int_{I_i(t)} \big(\eta(a + \Delta t, t + \Delta t) - \eta(a, t)\big)v(a, t)\,\mathrm{d}a. \tag{30}$$

Taking limits we see that for $v \in \mathcal{A}(t)$,

$$\int_{I_i(t)} \big(D\eta(a, t)\big)v(a, t)\,\mathrm{d}a = 0. \tag{31}$$

For the death term we have

$$\int_{I_i(t)} (\mu(a, P)U - \mu(a, p)\tilde{u})\vartheta \, da$$
$$= \int_{I_i(t)} (\mu(a, P) - \mu(a, p))\tilde{u}\vartheta \, da + \int_{I_i(t)} \mu(a, P)(\vartheta - \eta)\vartheta \, da$$
$$\leqslant K_\mu |P - p| \|\tilde{u}\|_i \|\vartheta\|_i + C_1 \|\vartheta\|_i^2 - \int_{I_i(t)} \mu(a, P)\eta\,\vartheta \, da. \tag{32}$$

Let $\bar{\mu}$ denote the average of μ in age over each $I_i(t)$. Then

$$\int_{I_i(t)} \mu(a, P)\eta\,\vartheta \, da = \int_{I_i(t)} (\mu(a, P) - \bar{\mu}(P))\eta\,\vartheta \, da$$
$$\leqslant \|\mu(a, P) - \bar{\mu}(P)\|_{L^\infty(\mathbb{R})} \|\eta\|_i \|\vartheta\|_i$$
$$\leqslant \frac{C_1}{2} \Delta a \|\eta\|_i \|\vartheta\|_i. \tag{33}$$

Recall that

$$\|m\|_i = \left(\int_{I_i(t)} m^2(a) \, da\right)^{\frac{1}{2}} \leqslant \frac{m_0\sqrt{\Delta a_i}}{s} \leqslant \frac{m_0\sqrt{\Delta a}}{s} \tag{34}$$

when $I_i(t) \cap [-s, s] \neq \emptyset$, and $\|m\|_i = 0$ otherwise, and that $m(a)$ is nonzero on at most an interval of length $2s$. For each age interval in our partition we have

$$\int_{I_i(t)} (b(U) - b(u))\,\vartheta\, m(a) \, da \leqslant |b(U) - b(u)| \|m(a)\|_i \|\vartheta\|_i, \tag{35}$$

We now need some bound on $|b(U) - b(u)|$. Note that

$$|b(\tilde{u}) - b(u)| = \left| \int_{\mathbb{R}} \beta(a, p)(\tilde{u} - u)(a, t) \, da \right|$$
$$= \left| \int_{\mathbb{R}} (\tilde{\beta}(a, p) - \beta(a, p))u(a, t) \, da \right|, \tag{36}$$

where $\tilde{\beta}$ is the convolution in age of β with $\check{m}(a) = m(-a)$. Because β is smooth in a this term is bounded by $Cs^{\lambda+1}p(t)$. Next

$$|b(U) - b(\tilde{u})| = \left| \int_{\mathbb{R}} \beta(a, P)U(a, t) - \beta(a, p)\tilde{u}(a, t) \, da \right|$$
$$= \left| \int_{\mathbb{R}} (\beta(a, P) - \beta(a, p))U(a, t) - \beta(a, p)(U - \tilde{u})(a, t) \, da \right|$$
$$\leqslant C(|P - p| + \|\vartheta - \eta\|_{H^{-q-1}(\mathbb{R})})$$
$$\leqslant C(|\varpi| + \|\vartheta\|_{H^{-q-1}(\mathbb{R})} + \|\eta\|_{H^{-q-1}(\mathbb{R})}). \tag{37}$$

Here we used a bound on $\|\partial_p b(\cdot, \rho)\|$ and a bound on $\|\beta(\cdot, \rho)\|_{H^{q+1}(\mathbb{R})}$, in addition to a bound on $\|U(\cdot, t)\|$. We summarize these two results as

$$|b(U) - b(u)| \leqslant C(|\varpi| + \|\vartheta\|_{H^{-q-1}(\mathbb{R})} + \|\eta\|_{H^{-q-1}(\mathbb{R})} + s^{\lambda+1}). \tag{38}$$

From (28), (31), (32), (33) and (38), we get

$$\frac{d}{dt}\|\vartheta\|_i^2 \leqslant K_\mu |P - p| \|\tilde{u}\|_i \|\vartheta\|_i + C_1 \|\vartheta\|_i^2 + \frac{C_1}{2}\Delta a \|\eta\|_i \|\vartheta\|_i + \|r\|_i \|\vartheta\|_i$$
$$+ C(|\varpi| + \|\vartheta\|_{H^{-q-1}(\mathbb{R})} + \|\eta\|_{H^{-q-1}(\mathbb{R})} + s^{\lambda+1})\|m(a)\|_i \|\vartheta\|_i. \tag{39}$$

We now need a bound on $|p - P|$. To bound the error in the total population density, we integrate (1a) over a to obtain

$$\partial_t p = b(u) - \int_{-\infty}^{\infty} \mu(a, p)u \, \mathrm{d}a. \tag{40}$$

For the approximate total population density we have

$$\partial_t P = b(U) - \int_{-\infty}^{\infty} \mu(a, P)U \, \mathrm{d}a. \tag{41}$$

We subtract (40) from (41) and multiply by $v = \varpi$ to get

$$\begin{aligned}
\frac{1}{2}\partial_t|\varpi|^2 &= (b(U) - b(u))\varpi - \int_{-\infty}^{\infty} \mu(a, p)u - \mu(a, P)U \, \mathrm{d}a \\
&\leqslant |b(U) - b(u)||\varpi| + \left| \int_{-\infty}^{\infty} (\mu(a, P) - \mu(a, p))u + \mu(a, P)(u - U) \, \mathrm{d}a \right| \\
&\leqslant C(|\varpi| + \|\vartheta\|_{H^{-q-1}(\mathbb{R})} + \|\eta\|_{H^{-q-1}(\mathbb{R})} + s^{\lambda+1})|\varpi| \\
&\quad + (C_1 + K_\mu \|u\|_{L^\infty(\mathbb{R})})|\varpi|.
\end{aligned} \tag{42}$$

To deal with this complex set of evolution inequalities we need a variation on Gronwall's inequality, lemma 4.1, given below. To apply the lemma to our situation let $h_0(t) = |\varpi(t)|$ and $f_0(t) = g_0(t) = 1/2$. For $i < 0$ let $h_i(t) = \|\vartheta\|_i$, $f_i(t) = K_\mu|P - p|\|\tilde{u}\|_i + (C_1/2)\Delta a\|\eta\|_i + \|r\|_i$, and $g_i(t) = \|m\|_i$. The function $w(t)$ is just $\|\eta\|_{H^{-q-1}(\mathbb{R})}(t) + s^{\lambda+1}$. Recall $\vartheta(a, 0) = 0$ and $\varpi(0) = 0$. Then (39) and (42) give the convergence result

$$|\varpi|^2 + \sum_i \|\vartheta\|_i^2 \leqslant \hat{C} \int_0^T \left(\|\eta\|_{H^{-q-1}(\mathbb{R})}(t) + s^{\lambda+1}\right)^2 \, \mathrm{d}t. \tag{43}$$

□

Lemma 4.1 (A Gronwall-like Inequality). *Let T be positive and suppose that q and g_i and h_i, for $i \in \mathcal{I}$, are nonnegative continuous functions on $[0, T]$, where $\mathcal{I}$ is some finite set. Assume that the h_is are differentiable, that $q^2(t) = \sum_i f_i^2(t)$, and that there is a C_0 such that $\int_0^T g_i^2(t)\,\mathrm{d}t \leqslant C_0$ and $\int_0^T q^2(t)\,\mathrm{d}t \leqslant C_0$. In addition we assume that at most k of the g_i's are nonzero at any value of t. If on $[0, T]$ we have*

$$\frac{\mathrm{d}}{\mathrm{d}t}h_i^2(t) \leqslant C_1 \left(w^2(t) + \sum_j h_j^2(t) \right)^{\frac{1}{2}} (g_i(t) + f_i(t))\, h_i(t) \tag{44}$$

then there is a $C_2 = C_2(C_0, C_1, T, k)$ such that for $t \in [0, T]$

$$\sum_i h_i^2(t) \leqslant C_2 \left(\sum_i h_i^2(0) + \int_0^T w^2(t)\,\mathrm{d}t \right).$$

Proof. Without loss of generality we can assume that $C_1 = 1$ since we can replace g_i and q by $C_1 g_i$ and $C_1 q$, and this replaces C_0 by $C_0 C_1^2$. Let $G_i(t) = \int_0^t g_i^2(\tau) + q^2(\tau)\,\mathrm{d}\tau$. From (44) we get that

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t}(h_i^2(t)\exp(-G_i(t))) &= \exp(-G_i(t)) \left(\left(\frac{\mathrm{d}h_i}{\mathrm{d}t} \right)^2 - g_i^2 h_i^2 - q^2 h_i^2 \right) \\
&\leqslant \exp(-G_i(t)) \left(\left(w^2(t) + \sum_j h_j^2(t) \right)^{\frac{1}{2}} (g_i + f_i)\, h_i - g_i^2 h_i - q^2 h_i^2 \right).
\end{aligned} \tag{45}$$

Let $\omega_i = \exp(-G_i/2)h_i$ and note that $\exp((G_j - G_i)/2) \leqslant \exp(G_j/2) \leqslant \exp(C_0)$. Then

$$\frac{\mathrm{d}}{\mathrm{d}t}\omega_i^2 \leqslant \exp(C_0)\left(w^2 + \sum_j \omega_j^2\right)^{\frac{1}{2}} (g_i + f_i)\omega_i - g_i^2\omega_i^2 - q^2\omega_i^2. \tag{46}$$

Hence

$$\frac{\mathrm{d}}{\mathrm{d}t}\sum_i \omega_i^2 \leqslant \exp(C_0)\left(w^2 + \sum_j \omega_j^2\right)^{\frac{1}{2}} \sum_i (g_i + f_i)\omega_i - \sum_i \left(g_i^2\omega_i^2 + q^2\omega_i^2\right). \tag{47}$$

Note

$$\left(\sum_i 1\cdot(g_i\omega_i)\right)^2 \leqslant \left(\left(\sum_i 1\right)^{\frac{1}{2}}\left(\sum_i g_i\omega_i\right)^{\frac{1}{2}}\right)^2 \leqslant k\sum_i (g_i\omega_i)^2. \tag{48}$$

The sum is only taken on the i values such that $g_i \neq 0$. We make the bound

$$\begin{aligned}
\exp(C_0))&\left(w^2 + \sum_j \omega_j^2\right)^{\frac{1}{2}} \sum_i g_i\omega_i \\
&\leqslant \frac{k}{4}\exp(2C_0)\left(w^2 + \sum_j \omega_j^2\right) + \frac{1}{k}\left(\sum_i g_i\omega_i\right)^2 \\
&\leqslant \frac{k}{4}\exp(2C_0)\left(w^2 + \sum_j \omega_j^2\right) + \sum_i g_i^2\omega_i^2.
\end{aligned} \tag{49}$$

Thus

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t}\sum_i \omega_i^2 &\leqslant \frac{k}{4}\exp(2C_0)\left(w^2 + \sum_i \omega_i^2\right) \\
&\quad + \exp(C_0)\left(w^2 + \sum_i \omega_i^2\right)^{\frac{1}{2}} \sum_i g_i\omega_i - \sum_i q^2\omega_i^2 \\
&\leqslant \frac{k}{4}\exp(2C_0)\left(w^2 + \sum_i \omega_i^2\right) \\
&\quad + \exp(C_0)\left(w^2 + \sum_i \omega_i^2\right)^{\frac{1}{2}}\left(\sum_i g_i^2\right)^{\frac{1}{2}} (\omega_i^2)^{\frac{1}{2}} - \sum_i q^2\omega_i^2 \\
&\leqslant \left(\frac{k}{4} + \frac{1}{4}\right)\exp(2C_0)\left(w^2 + \sum_i \omega_i^2\right) + q^2\sum_i \omega_i^2 - \sum_i q^2\omega_i^2 \\
&\leqslant \frac{k+1}{4}\exp(2C_0)\left(w^2 + \sum_i \omega_i^2\right)
\end{aligned} \tag{50}$$

Gronwall's inequality then gives that $\sum_i(\omega_i^2)$ is bounded on $[0, T]$ by a multiple of the sum of its initial value and the integral of w^2. Another factor of $\exp(2C_0)$ allows us to remove the exponentials from the bound, and that proves the claim. □

5. Computational example

We consider system (1*a*)–(1*c*) with birth term

$$b(u(\cdot, t)) = \int_0^\infty \beta_0\, a\, u\, \mathrm{d}a, \tag{51}$$

so that fecundity increases linearly in age with slope β_0. For the death modulus, we use

$$\mu(a, p) = \mu(a) = \frac{10\mathrm{e}^{10(a-0.8)}}{\mathrm{e}^{10(a-0.8)} + \mathrm{e}^{-10(a-0.8)}} + \frac{1}{2}. \tag{52}$$

This represents a situation where mortality remains low until around a certain age, at which point it increases dramatically.

For the initial condition, we use a population of older organisms,

$$u_0(a) = 128|a - 0.5|^3 - 48(a - 0.5)^2 + 1, \tag{53}$$

if $|a - 0.5| < 0.25$, and $u_0(a) = 0$, otherwise.

Our numerical treatment is as follows. For the birth mollifier, we use a piecewise C^1 cubic with compact support on $[-s, s]$,

$$m(a) = \begin{cases} \dfrac{1}{s}\left(2\left(\dfrac{|a|}{s}\right)^3 - 3\left(\dfrac{|a|}{s}\right)^2 + 1\right), & -s \leqslant a \leqslant s, \\ 0, & \text{otherwise.} \end{cases} \tag{54}$$

This satisfies equation (3) with $\lambda = 1$, giving us $\mathcal{O}(s^2)$ error according to equation (4). We build our natural-age-grid finite element space in age, equation (8), by using a partition, $\mathcal{J}$, of $(-\infty, \tilde{a}_{\max}]$ with intervals of equal length Δa, and use piecewise constants over $\mathcal{J}$ as the approximation space ($q = 0$). In the computations using mollified birth presented here, we set $s = \Delta a$. Thus, the errors due to discretizing the age distributions and mollifying birth are both $\mathcal{O}((\Delta a)^2)$. We take $\Delta a = 0.0375$

We take the temporal domain to be [0, 3]. We find that truncating the age domain for sharp birth to [0, 2], and to [−0.0375, 2] for mollified birth, is sufficient for an accurate solution.

We consider two cases, $\beta_0 = 30$ and $\beta_0 = 40$, that differ in the benefit of using mollified birth. The two cases are shown in figures 1 and 2. In the first case, the exponential growth of the total population p, and consequently the number of newborns, is sufficiently small so that mollification provides no benefit, and even some loss of efficiency. In the second case, the exponential growth is sufficiently large to induce sufficiently rapid change in the number of newborns so that mollification is necessary to prevent the the time step from diving down to the minimum allowed time step.

These are due to rapid changes in the birth terms in the first two age intervals when a new age interval is introduced. Moreover, the density increase or decrease triggering the error controls is not well-mitigated by cutting the time steps because much of the density increase or decrease, (newborn production rate $\times \Delta t)/\Delta t$, does not change significantly with changes in the time step. Under mollification, the new, small, first age interval only receives a small portion of all newborns, which solves the problem.

A kludge is to turn off error control in the first two age intervals. This is inadvisable in situations where rapid changes in newborn production may require some adaptivity to get the correct timing of rapid changes in the population as a whole. Mollification is important to ensure we are avoiding large errors at critical junctions in a system's evolution—rather than hoping our minimum allowed time step will do the job.

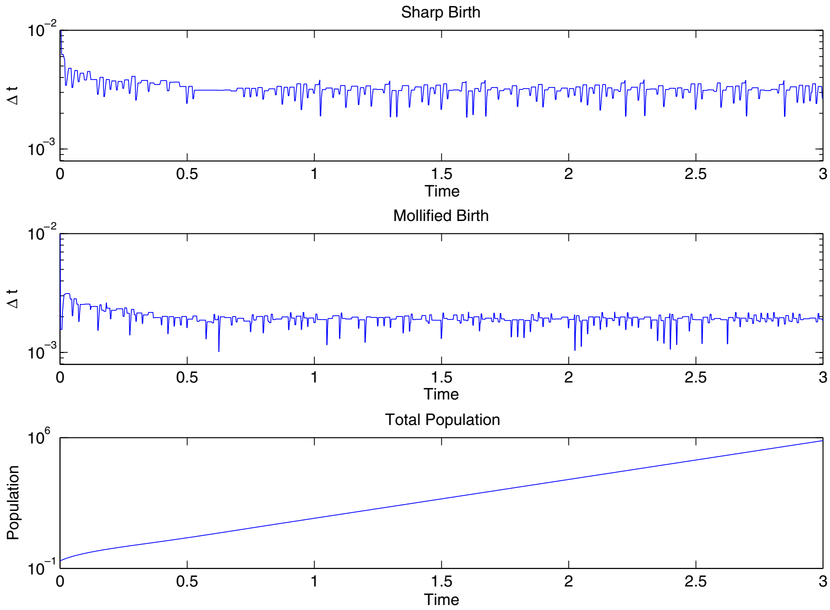

Figure 1. Time steps taken with sharp and mollified birth for $\beta_0 = 30$. The bottom figure shows the base-10 logarithm of the associated total population p.

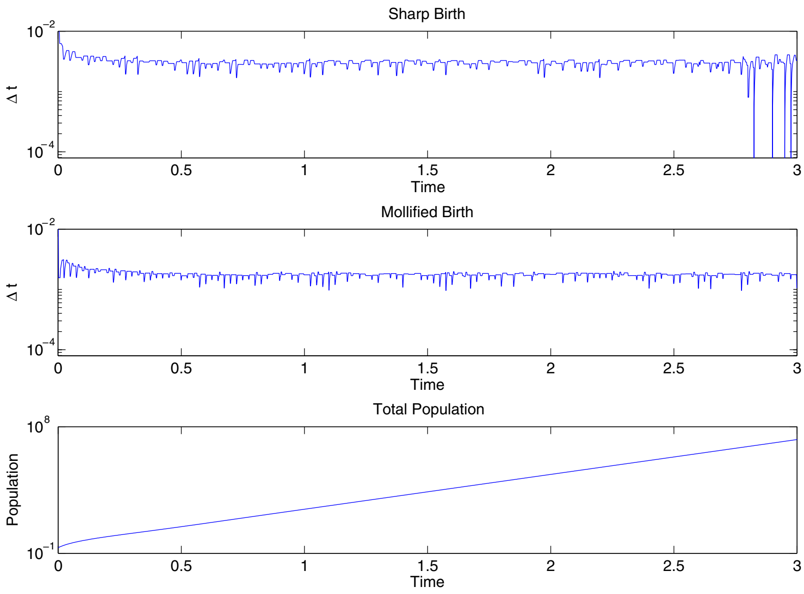

Figure 2. Time steps taken with sharp and mollified birth for $\beta_0 = 40$. The bottom figure shows the base-10 logarithm of the associated total population p. The time-step dives seen in the top figure descend to an imposed minimum time step of 10^{-6}.

Acknowledgments

This material is based upon the work supported by the National Science Foundation under Grant No. DMS-0802609.

References

[1] Ayati B P and Dupont T F 2002 Galerkin methods in age and space for a population model with nonlinear diffusion *SIAM J. Numer. Anal.* **40** 1064–76

[2] Ayati B P 2000 A variable time step method for an age-dependent population model with nonlinear diffusion *SIAM J. Numer. Anal.* **37** 1571–89

[3] Douglas J Jr and Milner F A 1987 Numerical methods for a model of population dynamics *Calcolo* **24** 247–54

[4] Kim M-Y 1996 Galerkin methods for a model of population dynamics with nonlinear diffusion *Numer. Methods Partial Diff. Eqns.* **12** 59–73

[5] Kwon Y and Cho C-K 1993 Second-order accurate difference methods for a one-sex model of population dynamics *SIAM J. Numer. Anal.* **30** 1385–99

[6] Lopez L and Trigiante D 1985 A finite difference scheme for a stiff problem arising in the numerical solution of a population dynamic model with spatial diffusion *Nonlinear. Anal. Theory Methods Appl.* **9** 1–12

[7] Ayati B P 2006 A structured-population model of *Proteus mirabilis* swarm-colony development *J. Math. Biol.* **52** 93–114

[8] Ayati B P and Klapper I 2007 A multiscale model of biofilm as a senescence-structured fluid *Multiscale Modelling Simul.* **6** 347–65

[9] Ayati B P, Webb G F and Anderson A R A 2006 Computational methods and results for structured multiscale models of tumor invasion *Multiscale Modelling Simul.* **5** 1–20

[10] Kim M-Y 2006 Discontinuous Galerkin methods for a model of population dynamics with unbounded mortality *SIAM J. Sci. Comput.* **27** 1371–93

[11] Kim M-Y 2008 Discontinuous-continuous Galerkin methods for a structured model of a biological system *SIAM J. Sci. Comput.* **31** 913–38

[12] Milner F A 1988 A finite element method for a two-sex model of population dynamics *Numer. Methods Partial Diff. Eqns.* **4** 329–45

[13] Ayati B P and Dupont T F 2005 Convergence of a step-doubling Galerkin method for parabolic problems. *Math. Comput.* **74** 1053–65

[14] Ayati B P 2007 Modeling the role of the cell cycle in regulating *Proteus mirabilis* swarm-colony development *Appl. Math. Lett.* **20** 913–8

[15] Webb G F 2008 Population models structured by age, size, and spatial position *Structured Population Models in Biology and Epidemiology* (Berlin: Springer)