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Parameter Estimation in a Size-Structured Population Model with Distributed States-at-Birth

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Abstract: A least-squares method is developed for estimating parameters in a size-structured population model with distributed states-at-birth from field data. First and second order finite difference schemes for approximating the nonlinear-nonlocal partial differential equation model are utilized in the least-squares problem. Convergence results for the computed parameters are established. Numerical results demonstrating the efficiency of the technique are provided.

1 Introduction

It is often the case that direct observations of vital rates of individual organisms are not accessible and our knowledge of the vital rates is incomplete. Therefore, the inverse problem approach often plays an important role in deducing such information at the individual level from observation at the population level. In recent years substantial attention has been given to inverse problems governed by age/stage/size structured population models [1,2,3,6,7,8,9,12,13]. Methodologies applied to solve such inverse problems include the least-squares approach [1,3,9] and the fixed point iterative technique [17]. The least-squares approach has been often used in inverse problems governed by size-structured models. For example, in [8,9] the authors used least-squares method to estimate the growth rate distribution in a linear size-structured population model. A similar technique was applied to a semi-linear size-structured model in [14] where the mortality rate depends on the total population due to competition between individuals. Furthermore, such least-squares methodology has been applied for estimating parameters in general conservation laws [13]. Therein the author utilizes monotone finite-difference schemes to numerically solve the conservation law and present numerical results for estimation the flux function from numerically generated data. And in [3], the authors solved an inverse problem governed by structured juvenile-adult model. Therein, the least-squares approach was used to estimate growth, mortality and reproduction rates in the adult stage from field data on an urban green tree frog population. The estimated parameters

were then utilized to understand the long-term dynamics of this green tree frog population.

In this paper we consider the following nonlinear Gurtin-MacCamy type model with distributed states-at-birth:

$$\begin{aligned} \frac{\partial}{\partial t} p(x, t; \theta) + \frac{\partial}{\partial x} (g(x, t, Q(t; \theta)) p(x, t; \theta)) &= -\mu(x, t, Q(t; \theta)) p(x, t; \theta) \\ &+ \int_{x_{min}}^{x_{max}} \beta(x, y, t, Q(t; \theta)) p(y, t; \theta) dy, \quad (x, t) \in (x_{min}, x_{max}) \times (0, T), \\ g(x_{min}, t, Q(t; \theta)) p(x_{min}, t; \theta) &= 0, \quad t \in [0, T], \\ p(x, 0; \theta) &= p^0(x), \quad x \in [x_{min}, x_{max}]. \end{aligned} \tag{1}$$

Here, $\theta = (g, \mu, \beta)$ is the vector of parameters to be identified. The function $p(x, t; \theta)$ is the parameter-dependent density of individuals of size x at time t .

Therefore, $Q(t; \theta) = \int_{x_{min}}^{x_{max}} p(x, t; \theta) dx$ provides the total population at time t

which depends on the vector of parameters $\theta = (g, \mu, \beta)$. The functions g and μ represent the individual growth and mortality rates, respectively. It is assumed that individuals may be recruited into the population at different sizes with $\beta(x, y, t, Q)$ representing the rate at which an individual of size y gives birth to an individual of size x . Henceforth, we will call the model (1) Distributed Size Structured Model and abbreviate it as DSSM.

The main goal of this paper is to develop a least-squares approach for estimating the parameter θ from population data and to provide convergence results for the parameter estimates. The paper is organized as follows. In Section 2, we set up a least-squares problem and present finite difference schemes for computing an approximate solution to this least-squares problem. In Section 3 we provide convergence results for the computed parameters. In Section 4, numerical examples showing the performance of the least-squares technique and an application to a set of field data on green tree frogs are presented.

2 The Least-Squares Problem and Approximation Schemes

Let $\mathbb{D}_1 = [x_{min}, x_{max}] \times [0, T] \times [0, \infty)$ and $\mathbb{D}_2 = [x_{min}, x_{max}] \times [x_{min}, x_{max}] \times [0, T] \times [0, \infty)$ throughout the discussion. Let $\mathbf{B} = C_b^1(\mathbb{D}_1) \times C_b(\mathbb{D}_1) \times C_b(\mathbb{D}_2)$, where $C_b(\Omega)$ denotes the Banach space of bounded continuous functions on Ω endowed with the usual supremum norm and $C_b^1(\Omega)$ is the Banach space of bounded continuous functions with bounded continuous derivatives on Ω and endowed with the usual supremum norm. Clearly, \mathbf{B} is a Banach space when endowed with the natural product topology. Let c be a sufficiently large positive constant and assume that the admissible parameter space Θ is any compact subset of \mathbf{B} (endowed with the topology of \mathbf{B}) such that every $\theta = (g, \mu, \beta) \in \Theta$ satisfies (H1)-(H4) below.

- (H1) $g \in C_b^1(\mathbb{D}_1)$ with $g_x(x, t, Q)$ and $g_Q(x, t, Q)$ being Lipschitz continuous in x with Lipschitz constant c , uniformly in t and Q . Moreover, $0 < g(x, t, Q) \leq c$ for $x \in [x_{min}, x_{max}]$ and $g(x_{max}, t, Q) = 0$.
- (H2) $\mu \in C_b(\mathbb{D}_1)$ is Lipschitz continuous in x and Q with Lipschitz constant c , uniformly in t . Also, $0 \leq \mu(x, t, Q) \leq c$.
- (H3) $\beta \in C_b(\mathbb{D}_2)$ is Lipschitz continuous in Q with Lipschitz constant c , uniformly in x, y and t . Also, $0 \leq \beta(x, y, t, Q) \leq c$ and for every partition $\{x_i\}_{i=1}^N$ of $[x_{min}, x_{max}]$, we have

$$\sup_{(y,t,Q) \in [x_{min}, x_{max}] \times [0, T] \times [0, \infty)} \sum_{i=1}^N |\beta(x_i, y, t, Q) - \beta(x_{i-1}, y, t, Q)| \leq c.$$

- (H4) $p^0 \in BV([x_{min}, x_{max}])$, the space of functions with bounded total variation on $[x_{min}, x_{max}]$, and $p^0(x) \geq 0$.

We now define a weak solution to the model (1).

Definition 21 Given $\theta \in \Theta$, by a weak solution to problem (1) we mean a function $p(\cdot, \cdot; \theta) \in L^\infty([x_{min}, x_{max}] \times [0, T])$, $p(\cdot, t; \theta) \in BV([x_{min}, x_{max}])$ for $t \in [0, T]$, and satisfies

$$\begin{aligned} & \int_{x_{min}}^{x_{max}} p(x, t; \theta) \phi(x, t) dx - \int_{x_{min}}^{x_{max}} p^0(x) \phi(x, 0) dx \\ &= \int_0^t \int_{x_{min}}^{x_{max}} p(x, \tau; \theta) [\phi_\tau(x, \tau) + g(x, \tau, Q(\tau; \theta)) \phi_x(x, \tau) - \mu(x, \tau, Q(\tau; \theta)) \phi(x, \tau)] dx d\tau \\ &+ \int_0^t \int_{x_{min}}^{x_{max}} \int_{x_{min}}^{x_{max}} \beta(x, y, \tau, Q(\tau; \theta)) p(y, \tau; \theta) \phi(x, \tau) dy dx d\tau. \end{aligned} \tag{2}$$

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

We are interested in the following least-squares problem: given data X_s which corresponds to the number of individuals at time t_s , $s = 1, 2, \dots, S$, find a parameter $\theta = (g, \mu, \beta) \in \Theta$ such that the weighted least-squares cost functional $F(\theta) = \sum_{s=1}^S |W(Q(t_s; \theta)) - W(X_s)|^2$ is minimized over the admissible parameter space Θ , i.e., find θ^* such that

$$\theta^* = \arg \min_{\theta \in \Theta} F(\theta) = \arg \min_{\theta \in \Theta} \sum_{s=1}^S |W(Q(t_s; \theta)) - W(X_s)|^2, \tag{3}$$

where $W \in C([0, \infty))$ is a weight function.

In order to numerically approximate the solution to the minimization problem (3), we first need to approximate the solution of model (1). To this end, we utilize similar finite-difference approximation schemes as those developed in [5]. Suppose that the intervals $[x_{min}, x_{max}]$ and $[0, T]$ are divided into N and L subintervals, respectively. The following notations will be used throughout the

parameter: $\Delta x = (x_{max} - x_{min})/N$ and $\Delta t = T/L$. The discrete mesh points are given by $x_i = x_{min} + i\Delta x$, $t_k = k\Delta t$ for $i = 0, 1, \dots, N$, $k = 0, 1, \dots, L$. For ease of notation, we take a uniform mesh with constant sizes Δx and Δt . More general nonuniform meshes can be similarly considered. We shall denote by $p_i^k(\theta)$ and $Q^k(\theta)$ the finite difference approximation of $p(x_i, t_k; \theta)$ and $Q(t_k; \theta)$, respectively. For convenience we will also use the notation p_i^k and Q^k without explicitly stating their dependence on θ . We also let $g_i^k = g(x_i, t_k, Q^k)$, $\mu_i^k = \mu(x_i, t_k, Q^k)$, $\beta_{i,j}^k = \beta(x_i, y_j, t_k, Q^k)$. Here, $Q^k = \sum_{i=1}^N p_i^k \Delta x$.

We define the ℓ^1 , ℓ^∞ norms and TV (total variation) seminorm of the grid functions p^k by

$$\|p^k\|_1 = \sum_{i=1}^N |p_i^k| \Delta x, \quad \|p^k\|_\infty = \max_{0 \leq i \leq N} |p_i^k|, \quad TV(p^k) = \sum_{i=0}^{N-1} |p_{i+1}^k - p_i^k|,$$

and the finite difference operators by

$$\Delta_+ p_i^k = p_{i+1}^k - p_i^k, \quad 0 \leq i \leq N-1, \quad \Delta_- p_i^k = p_i^k - p_{i-1}^k, \quad 1 \leq i \leq N.$$

Throughout the discussion, we impose the following CFL condition concerning Δx and Δt :

$$(H5) \quad \frac{\Delta t}{\Delta x} + \Delta t \leq \frac{1}{c}.$$

We discretize model (1) using the following first order explicit upwind finite difference scheme (FOEU):

$$\begin{aligned} \frac{p_i^{k+1} - p_i^k}{\Delta t} + \frac{g_i^k p_i^k - g_{i-1}^k p_{i-1}^k}{\Delta x} &= -\mu_i^k p_i^k + \sum_{j=1}^N \beta_{i,j}^k p_j^k \Delta x, \quad 1 \leq i \leq N, \quad 0 \leq k \leq M-1, \\ g_0^k p_0^k &= 0, \quad 0 \leq k \leq M, \\ p_i^0 &= p^0(x_i), \quad 0 \leq i \leq N. \end{aligned} \tag{4}$$

We could write the first equation in (4) equivalently as

$$p_i^{k+1} = \frac{\Delta t}{\Delta x} g_{i-1}^k p_{i-1}^k + \left(1 - \frac{\Delta t}{\Delta x} g_i^k - \mu_i^k \Delta t\right) p_i^k + \left(\sum_{j=1}^N \beta_{i,j}^k p_j^k \Delta x\right) \Delta t, \quad 1 \leq i \leq N, \quad 0 \leq k \leq M-1. \tag{5}$$

It is easy to check that under assumptions (H1)-(H4) FOEU scheme converges to a unique weak solution of system (1) as proved in [5]. The above approximation can be extended to a family of functions $\{p_{\Delta x, \Delta t}(x, t; \theta)\}$ defined by $p_{\Delta x, \Delta t}(x, t; \theta) = p_i^k(\theta)$ for $(x, t) \in [x_{i-1}, x_i) \times [t_{k-1}, t_k)$, $i = 1, 2, \dots, N$, $k = 1, 2, \dots, M$.

Since the parameter set is infinite dimensional, a finite-dimensional approximation of the parameter space is necessary for computing minimizers. Thus, we consider the following finite-dimensional approximations of (3): Let $Q_{\Delta x, \Delta t}(t; \theta) =$

$\int_{x_{min}}^{x_{max}} p_{\Delta x, \Delta t}(x, t; \theta) dx$ denote the finite difference approximation of the total population and consider the finite dimensional minimization problem

$$\arg \min_{\theta \in \Theta_m} F_{\Delta x, \Delta t}(\theta) = \arg \min_{\theta \in \Theta_m} \sum_{s=1}^S |W(Q_{\Delta x, \Delta t}(t_s; \theta)) - W(X_s)|^2. \quad (6)$$

Here, $\Theta_m \subseteq \Theta$ is a sequence of compact finite-dimensional subsets that approximate the parameter space Θ , i.e., for each $\theta \in \Theta$, there exist a sequence of $\theta_m \in \Theta_m$ such that $\theta_m \rightarrow \theta$ in the topology of \mathbf{B} as $m \rightarrow \infty$.

Remark 22 *If the compact parameter space Θ is chosen to be finite dimensional, then the approximation space sequence can be taken to be $\Theta_m = \Theta$.*

Since the FOEU (4) scheme is first order it would require a large number of grid points to achieve high accuracy. Thus, we next propose a second order minmod finite difference scheme based on MUSCL schemes [5,15,18] to approximate the solutions of the DSSM model (1) in the least-squares problem. We begin by using the following second order approximations for the integrals:

$$Q^k = \sum_{i=0}^N \star p_i^k \Delta x = \frac{1}{2} p_0^k \Delta x + \sum_{i=1}^{N-1} p_i^k \Delta x + \frac{1}{2} p_N^k \Delta x$$

and

$$\sum_{j=0}^N \star \beta_{i,j}^k p_j^k \Delta x = \frac{1}{2} \beta_{i,0}^k p_0^k \Delta x + \sum_{j=1}^{N-1} \beta_{i,j}^k p_j^k \Delta x + \frac{1}{2} \beta_{i,N}^k p_N^k \Delta x.$$

Then we approximate the model (1) by

$$\begin{aligned} \frac{p_i^{k+1} - p_i^k}{\Delta t} + \frac{\hat{f}_{i+\frac{1}{2}}^k - \hat{f}_{i-\frac{1}{2}}^k}{\Delta x} &= -\mu_i^k p_i^k + \sum_{j=0}^N \star \beta_{i,j}^k p_j^k \Delta x, \quad i = 1, 2, \dots, N, \quad k = 0, 1, \dots, L-1, \\ g_0^k p_0^k &= 0, \quad k = 0, 1, \dots, L, \\ p_i^0 &= p^0(x_i), \quad i = 0, 1, \dots, N. \end{aligned} \quad (7)$$

Here, the limiter is defined as

$$\hat{f}_{i+\frac{1}{2}}^k = \begin{cases} g_i^k p_i^k + \frac{1}{2}(g_{i+1}^k - g_i^k)p_i^k + \frac{1}{2}g_i^k mm(\Delta_+ p_i^k, \Delta_- p_i^k), & i = 2, \dots, N-2, \\ g_i^k p_i^k, & i = 0, 1, N-1, N, \end{cases} \quad (8)$$

where $mm(a, b) = \frac{sign(a) + sign(b)}{2} \min(|a|, |b|)$.

3 Convergence Theory for the Parameter Estimation Problem Using FOEU

The results in this section pertain to the case when (1) is approximated by the FOEU scheme (4). Our future efforts will focus on extending these theoretical

results to case when the model (1) is approximated by the higher order SOEM scheme (7). We establish the convergence results for the parameter estimation problem using an approach based on the abstract theory in [8]. To this end, we have the following theorem:

Theorem 31 *Let $\theta^r = (g^r, \mu^r, \beta^r) \in \Theta$. Suppose that $\theta^r \rightarrow \theta$ in Θ and $\Delta x_r, \Delta t_r \rightarrow 0$ as $r \rightarrow \infty$. Let $p_{\Delta x_r, \Delta t_r}(x, t; \theta^r)$ denote the solution of the finite difference scheme with parameter θ^r and initial condition p^0 , and let $p(x, t; \theta)$ be the unique weak solution of the problem with initial condition $p^0(x)$ and parameter θ . Then $p_{\Delta x_r, \Delta t_r}(\cdot, t; \theta^r) \rightarrow p(\cdot, t; \theta)$ in $L^1(x_{min}, x_{max})$, uniformly in $t \in [0, T]$.*

Proof. Define $p_i^{k,r} = p_i^k(\theta^r)$. From the fact that Θ is compact and using similar arguments as in [5], there exist positive constants c_1, c_2, c_3 and c_4 such that $\|p^{k,r}\|_1 \leq c_1$, $\|p^{k,r}\|_\infty \leq c_2$, $TV(p^{k,r}) \leq c_3$ and

$$\sum_{i=1}^N \left| \frac{p_i^{m,r} - p_i^{n,r}}{\Delta t_r} \right| \Delta x_r \leq c_4(m - n),$$

where $m > n$. Thus, there exist $\hat{p} \in BV([x_{min}, x_{max}])$ such that $p_{\Delta x_r, \Delta t_r}(\cdot, t; \theta^r) \rightarrow \hat{p}(\cdot, t)$ in $L^1(x_{min}, x_{max})$ uniformly in t . Hence, from the uniqueness of bounded variation weak solutions which can be established using similar techniques as in [5], we just need to show that $\hat{p}(x, t)$ is the weak solution corresponding to the parameter θ .

In order to prove this, let $\phi \in C^1([x_{min}, x_{max}] \times [0, T])$ and denote the value of $\phi(x_i, t_k)$ by ϕ_i^k . Multiplying equation (5) by ϕ_i^{k+1} and rearranging some terms we have

$$\begin{aligned} p_i^{k+1,r} \phi_i^{k+1} - p_i^{k,r} \phi_i^k &= p_i^{k,r} (\phi_i^{k+1} - \phi_i^k) + \frac{\Delta t}{\Delta x} [g_{i-1}^{k,r} p_{i-1}^{k,r} (\phi_i^{k+1} - \phi_{i-1}^{k+1}) - (g_{i-1}^{k,r} p_{i-1}^{k,r} \phi_{i-1}^{k+1} - g_i^{k,r} p_i^{k,r} \phi_i^{k+1})] \\ &\quad - \mu_i^{k,r} p_i^{k,r} \phi_i^{k+1} \Delta t + \sum_{j=1} \beta_{i,j}^{k,r} p_j^{k,r} \phi_i^{k+1} \Delta x \Delta t. \end{aligned} \tag{9}$$

Multiplying the above equation by Δx , summing over $i = 1, 2, \dots, N$, $k = 0, 1, \dots, M-1$, and applying $p_0^k = 0$ and $g_N^k = 0$ we obtain,

$$\begin{aligned} \sum_{i=1}^N (p_i^{L,r} \phi_i^L - p_i^{0,r} \phi_i^0) \Delta x &= \sum_{k=0}^{M-1} \sum_{i=1}^N p_i^{k,r} \frac{\phi_i^{k+1} - \phi_i^k}{\Delta t} \Delta x \Delta t + \sum_{k=0}^{M-1} \sum_{i=0}^{N-1} g_{i-1}^{k,r} p_{i-1}^{k,r} \frac{\phi_i^{k+1} - \phi_{i-1}^{k+1}}{\Delta x} \Delta x \Delta t \\ &\quad - \sum_{k=0}^{M-1} \sum_{i=1}^N \mu_i^{k,r} p_i^{k,r} \phi_i^{k+1} \Delta x \Delta t + \sum_{k=1}^{M-1} \sum_{i=1}^N \sum_{j=1}^N \beta_{i,j}^{k,r} p_j^{k,r} \phi_i^{k+1} \Delta x \Delta t \Delta x. \end{aligned} \tag{10}$$

Using the fact that $\theta^r \rightarrow \theta$ as $r \rightarrow \infty$ in Θ , passing to the limit in (10) we find that $\hat{p}(x, t)$ is the weak solution corresponding to the parameter θ .

Since W is a continuous on $[0, \infty)$, as an immediate consequence of Theorem 31, we obtain the following.

Corollary 32 Let $p_{\Delta x_r, \Delta t_r}(x, t; \theta^r)$ denote the numerical solution of the finite difference scheme with parameter $\theta^r \rightarrow \theta$ in Θ and $\Delta x_r, \Delta t_r \rightarrow 0$ as $r \rightarrow \infty$. Then

$$F_{\Delta x_r, \Delta t_r}(\theta^r) \rightarrow F(\theta), \text{ as } r \rightarrow \infty.$$

In the next theorem, we establish the continuity of the approximate cost functional in the parameter $\theta \in \Theta$ (a compact set), so that the computational problem of finding an approximate minimizer has a solution.

Theorem 33 Let Δx and Δt be fixed. For each $\theta \in \Theta$, let $p_{\Delta x, \Delta t}(x, t; \theta)$ denote the solution of the finite difference scheme and $\theta^r \rightarrow \theta$ as $r \rightarrow \infty$ in Θ ; then $p_{\Delta x, \Delta t}(\cdot, t; \theta^r) \rightarrow p_{\Delta x, \Delta t}(\cdot, t; \theta)$ as $r \rightarrow \infty$ in $L^1(x_{\min}, x_{\max})$ uniformly in $t \in [0, T]$.

Proof. Fix Δx and Δt . Define p_i^{k, θ^r} and $p_i^{k, \theta}$ to be the solution of the finite difference scheme with parameter θ^r and θ , respectively. Let $v_i^{k, \theta} = p_i^{k, \theta^r} - p_i^{k, \theta}$. Then $v_i^{k, \theta}$ satisfy the following

$$\begin{aligned} v_i^{k+1, \theta} &= \frac{\Delta t}{\Delta x} \left(g_{i-1}^{k, \theta^r} p_{i-1}^{k, \theta^r} - g_{i-1}^{k, \theta} p_{i-1}^{k, \theta} \right) + (p_i^{k, \theta^r} - p_i^{k, \theta}) - \frac{\Delta t}{\Delta x} \left(g_i^{k, \theta^r} p_i^{k, \theta^r} - g_i^{k, \theta} p_i^{k, \theta} \right) \\ &\quad - \Delta t (\mu_i^{k, \theta^r} p_i^{k, \theta^r} - \mu_i^{k, \theta} p_i^{k, \theta}) + \sum_{j=1}^N \left(\beta_{i,j}^{k, \theta^r} p_j^{k, \theta^r} - \beta_{i,j}^{k, \theta} p_j^{k, \theta} \right) \Delta x \Delta t, \quad 1 \leq i \leq N, \quad 0 \leq k \leq M-1, \\ v_0^{k+1, \theta} &= p_0^{k+1, \theta^r} - p_0^{k+1, \theta} = 0, \quad 0 \leq k \leq M-1. \end{aligned} \tag{11}$$

Here, $Q^{k, \theta^r} = \sum_{i=1}^N p_i^{k, \theta^r} \Delta x$, $g_i^{k, \theta^r} = g^{\theta^r}(x_i, t_k, Q^{k, \theta^r})$ and similar notations are used for μ_i^{k, θ^r} and $\beta_{i,j}^{k, \theta^r}$. Using the first equation in (11) and assumption (H5) we obtain

$$\begin{aligned} \sum_{i=1}^N |v_i^{k+1, \theta}| \Delta x &\leq \sum_{i=1}^N \left[1 - \Delta t \mu_i^{k, \theta^r} + \left(\sum_{j=1}^N \beta_{i,j}^{k, \theta^r} \Delta x \right) \Delta t \right] |v_i^{k, \theta}| \Delta x - \Delta t \sum_{i=1}^N \left(g_i^{k, \theta^r} |v_i^{k, \theta}| \right. \\ &\quad \left. - g_{i-1}^{k, \theta^r} |v_{i-1}^{k, \theta}| \right) + \Delta t \sum_{i=1}^N \left| \left(g_{i-1}^{k, \theta^r} - g_{i-1}^{k, \theta} \right) p_{i-1}^{k, \theta} - \left(g_i^{k, \theta^r} - g_i^{k, \theta} \right) p_i^{k, \theta} \right| \\ &\quad + \Delta t \sum_{i=1}^N \left| \mu_i^{k, \theta^r} - \mu_i^{k, \theta} \right| p_i^{k, \theta} \Delta x + \Delta t \sum_{i=1}^N \sum_{j=1}^N \left| \beta_{i,j}^{k, \theta^r} - \beta_{i,j}^{k, \theta} \right| p_j^{k, \theta} \Delta x \Delta x. \end{aligned} \tag{12}$$

By assumption (H1), and (11)

$$\sum_{i=1}^N \left(g_i^{k, \theta^r} |v_i^{k, \theta}| - g_{i-1}^{k, \theta^r} |v_{i-1}^{k, \theta}| \right) = \left(g_N^{k, \theta^r} |v_N^{k, \theta}| - g_0^{k, \theta^r} |v_0^{k, \theta}| \right) = 0. \tag{13}$$

By assumptions (H2) and (H3) we have

$$\sum_{i=1}^N \left[1 - \mu_i^{k,\theta^r} \Delta t + \left(\sum_{j=1}^N \beta_{i,j}^{k,\theta^r} \Delta x \right) \Delta t \right] |u_i^{k,\theta}| \Delta x \leq (1 + c(x_{\max} - x_{\min}) \Delta t) \|v^{k,\theta}\|_1. \quad (14)$$

By assumption (H1),

$$\begin{aligned} & \sum_{i=1}^N | (g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}) p_{i-1}^{k,\theta} - (g_i^{k,\theta^r} - g_i^{k,\theta}) p_i^{k,\theta} | \\ & \leq \sup_i |g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}| \sum_{i=1}^N |p_i^{k,\theta} - p_{i-1}^{k,\theta}| + \sum_{i=1}^N \left| \frac{(g_i^{k,\theta^r} - g_{i-1}^{k,\theta^r}) - (g_i^{k,\theta} - g_{i-1}^{k,\theta})}{\Delta x} \right| p_i^{k,\theta} \Delta x. \end{aligned} \quad (15)$$

$$\begin{aligned} \left| \frac{(g_i^{k,\theta^r} - g_{i-1}^{k,\theta^r}) - (g_i^{k,\theta} - g_{i-1}^{k,\theta})}{\Delta x} \right| & \leq \int_0^1 \left| g_x^{\theta^r}(\tau x_{i-1} + (1-\tau)x_i, t_k, Q^{k,\theta^r}) - g_x^{\theta^r}(\tau x_{i-1} + (1-\tau)x_i, t_k, Q^{k,\theta}) \right| \\ & \quad + \int_0^1 \left| g_x^{\theta^r}(\tau x_{i-1} + (1-\tau)x_i, t_k, Q^{k,\theta}) - g_x^{\theta}(\tau x_{i-1} + (1-\tau)x_i, t_k, Q^{k,\theta}) \right| d\tau. \end{aligned} \quad (16)$$

Assumption (H1), (15) and (16) yield

$$\begin{aligned} \sum_{i=1}^N | (g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}) p_{i-1}^{k,\theta} - (g_i^{k,\theta^r} - g_i^{k,\theta}) p_i^{k,\theta} | & \leq \sup_i |g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}| \sum_{i=1}^N |p_i^{k,\theta} - p_{i-1}^{k,\theta}| \\ & \quad + \sum_{i=1}^N \left[\int_0^1 \left| g_x^{\theta^r}(\tau x_{i-1} + (1-\tau)x_i, t_k, Q^{k,\theta^r}) - g_x^{\theta^r}(\tau x_{i-1} + (1-\tau)x_i, t_k, Q^{k,\theta}) \right| d\tau \right. \\ & \quad \left. + \int_0^1 \left| g_x^{\theta^r}(\tau x_{i-1} + (1-\tau)x_i, t_k, Q^{k,\theta}) - g_x^{\theta}(\tau x_{i-1} + (1-\tau)x_i, t_k, Q^{k,\theta}) \right| d\tau \right] p_i^{k,\theta} \Delta x. \end{aligned} \quad (17)$$

Note that

$$|Q^{k,\theta^r} - Q^{k,\theta}| = \left| \sum_{i=1}^N (p_j^{k,\theta^r} - p_j^{k,\theta}) \Delta x \right| \leq \sum_{i=1}^N |v_i^{k,\theta}| \Delta x = \|v^{k,\theta}\|_1. \quad (18)$$

By the assumption (H1) and the equation above, (17) yields

$$\begin{aligned} & \sum_{i=1}^N | (g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}) p_{i-1}^{k,\theta} - (g_i^{k,\theta^r} - g_i^{k,\theta}) p_i^{k,\theta} | \\ & \leq \sup_i |g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}| TV(p^{k,\theta}) + \left(c \|v^{k,\theta}\|_1 + \sup_i \int_0^1 \left| g_x^{\theta^r}(\bar{x}_i, t_k, Q^{k,\theta}) - g_x^{\theta}(\bar{x}_i, t_k, Q^{k,\theta}) \right| dx \right) \|p^{k,\theta}\|_1, \end{aligned} \quad (19)$$

where $\bar{x}_i = \tau x_{i-1} + (1-\tau)x_i$. By assumption (H2)

$$\sum_{i=1}^N |\mu_i^{k,\theta^r} - \mu_i^{k,\theta}| p_i^{k,\theta} \Delta x \leq \sup_i |\mu_i^{k,\theta^r} - \mu_i^{k,\theta}| \|p^{k,\theta}\|_1. \quad (20)$$

And from assumption (H3) we obtain

$$\sum_{i=1}^N \sum_{j=1}^N |\beta_{i,j}^{k,\theta^r} - \beta_{i,j}^{k,\theta}| p_j^{k,\theta} \Delta x \Delta x \leq \sup_{i,j} |\beta_{i,j}^{k,\theta^r} - \beta_{i,j}^{k,\theta}| \|p^{k,\theta}\|_1. \quad (21)$$

Using (13)- (21) we arrive at

$$\begin{aligned} \|v^{k+1,\theta}\|_1 &\leq (1 + c(x_{\max} - x_{\min})\Delta t) \|v^{k,\theta}\|_1 + \Delta t \left[\sup_i |\mu_i^{k,\theta^r} - \mu_i^{k,\theta}| \|p^{k,\theta}\|_1 + \sup_{i,j} |\beta_{i,j}^{k,\theta^r} - \beta_{i,j}^{k,\theta}| \|p^{k,\theta}\|_1 \right. \\ &\quad \left. + \sup_i |g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}| TV(p^{k,\theta}) + \left(c \|v^{k,\theta}\|_1 + \sup_i \int_0^1 |g_x^{\theta^r}(\bar{x}_i, t_k, Q^{k,\theta}) \right. \right. \\ &\quad \left. \left. - g_x^{\theta}(\bar{x}_i, t_k, Q^{k,\theta})| dx \right) \|p^{k,\theta}\|_1 \right]. \end{aligned} \quad (22)$$

Note that

$$\begin{aligned} |\mu_i^{k,\theta^r} - \mu_i^{k,\theta}| &\leq |\mu^{\theta^r}(x_i, t_k, Q^{k,\theta^r}) - \mu^{\theta^r}(x_i, t_k, Q^{k,\theta})| + |\mu^{\theta^r}(x_i, t_k, Q^{k,\theta}) - \mu^{\theta}(x_i, t_k, Q^{k,\theta})|, \\ |g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}| &\leq |g^{\theta^r}(x_{i-1}, t_k, Q^{k,\theta^r}) - g^{\theta^r}(x_{i-1}, t_k, Q^{k,\theta})| + |g^{\theta^r}(x_{i-1}, t_k, Q^{k,\theta}) - g^{\theta}(x_{i-1}, t_k, Q^{k,\theta})|, \\ |\beta_{i,j}^{k,\theta^r} - \beta_{i,j}^{k,\theta}| &\leq |\beta^{\theta^r}(x_i, y_j, t_k, Q^{k,\theta^r}) - \beta^{\theta^r}(x_i, y_j, t_k, Q^{k,\theta})| + |\beta^{\theta^r}(x_i, y_j, t_k, Q^{k,\theta}) - \beta^{\theta}(x_i, y_j, t_k, Q^{k,\theta})|. \end{aligned} \quad (23)$$

Thus, by assumptions (H1)-(H4) and the equations (23) (18), we have

$$\begin{aligned} \sup_i |\mu_i^{k,\theta^r} - \mu_i^{k,\theta}| &\leq c \|v^{k,\theta}\|_1 + \sup_i |\mu^{\theta^r}(x_i, t_k, Q^{k,\theta}) - \mu^{\theta}(x_i, t_k, Q^{k,\theta})|, \\ \sup_i |g_{i-1}^{k,\theta^r} - g_{i-1}^{k,\theta}| &\leq c \|v^{k,\theta}\|_1 + \sup_i |g^{\theta^r}(x_{i-1}, t_k, Q^{k,\theta}) - g^{\theta}(x_{i-1}, t_k, Q^{k,\theta})|, \\ \sup_{i,j} |\beta_{i,j}^{k,\theta^r} - \beta_{i,j}^{k,\theta}| &\leq c \|v^{k,\theta}\|_1 + \sup_{i,j} |\beta^{\theta^r}(x_i, y_j, t_k, Q^{k,\theta}) - \beta^{\theta}(x_i, y_j, t_k, Q^{k,\theta})|. \end{aligned}$$

Set $\delta_k = 3c \|p^{k,\theta}\|_1 + c TV(p^{k,\theta})$ and

$$\begin{aligned} \rho_k^r &= \|p^{k,\theta}\|_1 \left(\sup_i |\mu^{\theta^r}(x_i, t_k, Q^{k,\theta}) - \mu^{\theta}(x_i, t_k, Q^{k,\theta})| + \sup_{i,j} |\beta^{\theta^r}(x_i, y_j, t_k, Q^{k,\theta}) - \beta^{\theta}(x_i, y_j, t_k, Q^{k,\theta})| \right. \\ &\quad \left. + \sup_i \int_0^1 |g_x^{\theta^r}(\bar{x}_i, t_k, Q^{k,\theta}) - g_x^{\theta}(\bar{x}_i, t_k, Q^{k,\theta})| dx \right) + \sup_i |g^{\theta^r}(x_{i-1}, t_k, Q^{k,\theta}) - g^{\theta}(x_{i-1}, t_k, Q^{k,\theta})| TV(p^{k,\theta}) \end{aligned}$$

Then we have

$$\|v^{k+1,\theta}\|_1 \leq (1 + c(x_{\max} - x_{\min})\Delta t) \|v^{k,\theta}\|_1 + \Delta t (\rho_k^r + \delta_k) \|v^{k,\theta}\|_1. \quad (24)$$

Since for each k , $\rho_k^r \rightarrow 0$ as $r \rightarrow \infty$, the result follows from (24).

Next, we establish subsequential convergence of minimizers of the finite dimensional problem (6) to a minimizer of the infinite dimensional problem (3).

Theorem 34 *Suppose that Θ_m is a sequence of compact subsets of Θ . Moreover, assume that for each $\theta \in \Theta$, there exist a sequence of $\theta_m \in \Theta_m$ such that $\theta_m \rightarrow \theta$ as $m \rightarrow \infty$. Then the function $F_{\Delta x, \Delta t}$ has a minimizer over Θ_m . Furthermore, if θ_m^r denotes a minimizer of $F_{\Delta x_r, \Delta t_r}$ over Θ_m and $\Delta x_r, \Delta t_r \rightarrow 0$, then any subsequence of θ_m^r has a further subsequence which convergence to a minimizer of F .*

Proof. The proof here is a direct application of the abstract theory in [10], based on the convergence of $F_{\Delta x_r, \Delta t_r}(\theta^r) \rightarrow F(\theta)$.

4 Numerical Results

In this section we present several numerical simulations to demonstrate the performance of the parameter estimation methodology. Although the theory presented here applies for the case of infinite dimensional parameter space Θ , for simplicity we restrict the unknown parameter space to finite-dimensional in the examples below.

4.1 Convergence of parameter estimates computed by FOEU and SOEM in the least-squares problem

In this example, we test the performance of the parameter-estimation technique using both FOEU and SOEM approximation schemes. As a first step in generating data, we choose $\Delta x = 0.0100$, $\Delta t = 0.0025$, $x_{min} = 0$, $x_{max} = 1$, $T = 1.0$, $g(x, t, Q) = (1-x)/2$, $\beta(x, y, t, Q) = 10 \sin(4t) + 10$, $\mu(x, t, Q) = 1/4 \exp(Q)$, and the initial condition

$$p^0(x) = \begin{cases} 0.8, & 0.25 \leq x \leq 0.45, \\ 2.5, & 0.45 < x \leq 0.65, \\ 0.7, & 0.65 < x < 0.8, \\ 0, & \text{else.} \end{cases}$$

We then solve system (1) with this choice of parameters in MATLAB using SOEM discretization and collect the resulting total population $Q(t^k) = \int_0^1 p(x, t^k) dx$ for $t^k = k/20$, $k = 1, \dots, 20$. Observe that while $p(x, t)$ is discontinuous because $p^0(x)$ is, $Q(t)$ is a smooth function.

Assume all parameters are known except for $\mu = b \exp(Q)$ with b being an unknown parameter to be estimated. In our parameter estimation simulations, we fixed $\Delta x = 0.005$, $\Delta t = 0.0025$ for FOEU scheme. As for the SOEM scheme, the mesh sizes were chosen to be four times larger, that is, $\Delta x = 0.020$ and $\Delta t = 0.010$. We began with the above-mentioned data without noise in the least-squares problem described in Section 2. We then modified the data by adding normally distributed noise with mean zero and standard deviation $\sigma = 0.05, 0.10$, and 0.15 , respectively, to the data. To solve the least-squares minimization problem we set $\theta = b$ and use the goal function

$$F(\theta) = \sum_{s=1}^S |Q(t_s; \theta) - X_s|^2,$$

i.e., $W = 1$. For each data set the least-squares minimization process was performed to estimate b using both numerical schemes. Our simulation results corroborate the convergence results of computed parameters. Figure 1 demonstrates

the agreement of best fit model solutions obtained using FOEU and SOEM schemes in solving DSSM with the corresponding data sets with no noise as well as with different noise levels. A comparison of the two finite difference methods performing in the least-squares parameter estimation process was provided in Table 1. It can be seen that using the SOEM scheme for approximating DSSM in the least-squares problem one could obtain a similar estimated value b (where the least-squares errors are at the same scale) with less than 10% of the CPU time compared to that using the FOEU scheme.

Table 1. Performance comparisons of FOEU and SOEM schemes in least-squares parameter estimates process

	Without noise		With noise					
	FOEU	SOEM	$\sigma = 0.05$		$\sigma = 0.10$		$\sigma = 0.15$	
			FOEU	SOEM	FOEU	SOEM	FOEU	SOEM
Estimated value of b	0.2507	0.2503	0.2674	0.2768	0.2853	0.2837	0.3033	0.3028
Least-squares error	6.33-04	3.85e-04	0.0838	0.1871	0.3112	0.2857	0.6583	0.6473
CPU time (in minutes)	285.48	20.67	264.59	16.45	367.49	22.47	368.71	15.33

4.2 Fitting DSSM model to green tree frog population estimates from field data

In this example, we fit DSSM to a set of green tree frog population estimates obtained from capture-mark-recapture (CMR) field data during years 2004-2009 (as shown in Figure 2 (Left) [3]). The purpose is to estimate individual level vital rates for adult green tree frogs, and then use these parameter estimates to gain understanding of the dynamics of this population. In [3,4] the authors developed a model (referred to as JA model hereafter) to describe the dynamics of green tree frog population by dividing individuals into two stages, juveniles and adults, and set a least-squares problem to obtain the best fitted parameters to the CMR field data. With those estimated parameter values, they obtained the adult frog population curve (see Figure 2 (Left)). Due to the relative short duration for the tadpole stage and the lack of other information regarding tadpoles, the authors in [3] simply assumed constant vital rates for tadpole stage. To circumvent this issue, we consider the short duration of juvenile stage as part of the reproduction process and adopt the DSSM to describe the adult frog dynamics. Here, $\beta(x, y, t, Q)$ in DSSM represents the rate at which an adult frog of size y gives birth to tadpoles that survive to metamorphose into frogs of size x .

As in [3], we take $t = 0$ to be the first week in January 2004. We chose $\Delta t = 1/52$. Since there are 52 weeks every year Δt represents one week. Let X_s , $s = 1, 2, \dots, 136$, denote the observed number of frogs which was estimated statistically from CMR experiment data for 136 weeks during the breeding seasons in this six year experiment. The growth rate and mortality rates are assumed to

take the same forms as in [3]:

$$g(x, t, Q) = \alpha_1(6 - x),$$

and

$$\mu(x, t, Q) = \begin{cases} \left(\alpha_2(1 - \frac{t}{2}) + \alpha_3 \frac{t}{2} \right) (1 + 0.00343Q) \exp(\alpha_5 x), & 0 \leq t \leq 2, \\ \left(\alpha_3(2 - \frac{t}{2}) + \alpha_4(\frac{t}{2} - 1) \right) (1 + 0.00343Q) \exp(\alpha_5 x), & 2 \leq t \leq 4, \\ \left(\alpha_4(3 - \frac{t}{2}) + 3.093(\frac{t}{2} - 2) \right) (1 + 0.00343Q) \exp(\alpha_5 x), & 4 \leq t \leq 6. \end{cases}$$

Here, the mortality rate was assumed to depend linearly on density as well as time since frogs hibernate during winter time. By monitoring program [16] the breeding season begins around the middle of April and ends in early August. Thus, similar to [3] the birth rate function was assumed to be

$$\beta(x, y, t, Q) = \begin{cases} \frac{\alpha_6}{0.3 + \varepsilon} \gamma(x, \alpha_7, \alpha_8), & 0.3 \leq t \leq 0.6, 3 \leq y \leq 6, \\ \frac{\alpha_6(y - 3 + \varepsilon)}{\varepsilon(0.3 + \varepsilon)} \gamma(x, \alpha_7, \alpha_8), & 0.3 - \varepsilon \leq t < 0.3, 2.7 + t < y < 6, \\ \frac{\alpha_6(y - 3 + \varepsilon)}{\varepsilon(0.3 + \varepsilon)} \gamma(x, \alpha_7, \alpha_8), & y - 2.7 < t < 3.6 - y, 0.3 - \varepsilon < y < 0.3, \\ \frac{\alpha_6(0.6 + \varepsilon - t)}{\varepsilon(0.3 + \varepsilon)} \gamma(x, \alpha_7, \alpha_8), & 0.6 < t < 0.6 + \varepsilon, 3.6 - t \leq y \leq 6, \\ 0, & \text{else.} \end{cases}$$

Here, the gamma distribution density function with the shape parameter α_7 and scale parameter α_8 , $\gamma(x, \alpha_7, \alpha_8)$, was chosen to model the size distribution of newly metamorphosed frogs. The constant ε is a positive small number that allows β to be extended to $(x, y, t) \in [1.5, 6] \times [1.5, 6] \times [0, 1]$ and to satisfy the smoothness properties in (H4). We then also extend β periodically over one year intervals $[t, t + 1]$, $t = 1, 2, \dots, 5$.

We have $\alpha_1, \dots, \alpha_8$ as unknown constants to be estimated (i.e., $\theta = (\alpha_1, \dots, \alpha_8)$). We chose the initial condition in DSSM to be $p(x, 0) = 615.96 \exp(-0.75x)$ which implies $Q(0) = 257.2$ (cf. [3]). To solve the least-squares minimization problem, similar to [3], we set the goal function to be

$$F(\theta) = \sum_{s=1}^S |\log(Q(t_s; \theta) + 1) - \log(X_s + 1)|^2.$$

To guarantee that the estimated parameter values are biologically relevant, we set appropriate upper and lower bounds for each α_i . That is, $\underline{\alpha}_i \leq \alpha_i \leq \bar{\alpha}_i$, $i = 1, \dots, 8$. Using the vital rates determined by estimated α_i , $i = 1, \dots, 8$ given in Table 2, we simulated DSSM and compared the resulting adult frog population approximations to the data as well as the population estimates from the JA model in [3]. The comparison results are demonstrated in Figure 2 (Left).

It shows clearly that DSSM model output agrees with the population estimates resulting from field observations better than the JA model. Specifically, DSSM is more accurate in capturing the population dynamics when adult frog numbers are relatively low. Also, the DSSM fitting bears a smaller least-squares error of 33.5 compared to the JA model fitting which yielded an error of 37.8. Furthermore, the γ distribution that provided the best fit as presented in Figure 2 (Right) indicates that the newly metamorphosed frogs have body length between 1.5 cm and 2 cm and approximately 99.6% of adult frogs give birth to tadpoles that eventually metamorphose into frogs of size between 1.5 cm and 2.0 cm.

Table 2. Parameter estimation values and corresponding standard deviation

	α_1	α_2	α_3	α_4	α_5	α_6	α_7	α_8
Estimated value	0.486	2.973	0.0085	2.376	0.000	47.061	6.740	1.849
Standard deviation	0.0183	0.7044	0.1164	1.6373	0.125	2.8295	0.8000	1.4763

We also applied a statistically based method to compute the variance in the estimated model parameters $\theta = (\alpha_1, \dots, \alpha_8)$ similar to the work in [3] using standard regression formulations [12]. Table 2 provides the standard deviation for α_i 's estimated above.

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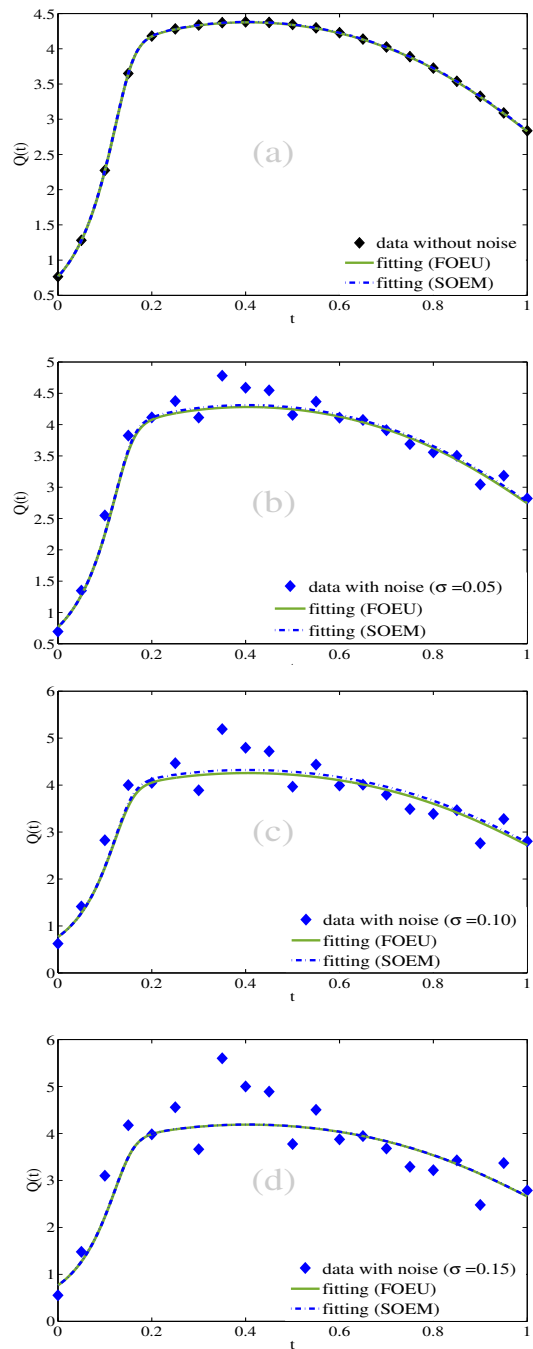


Fig. 1. (a) Comparison of data sets without noise and the corresponding best fit model solution using FOEU and SOEM schemes in solving DSSM. (b) (c) (d) Comparison of data at different noise levels ($\sigma = 0.05, 0.10, 0.15$) and the corresponding best fit model solutions using FOEU and SOEM schemes in solving DSSM.

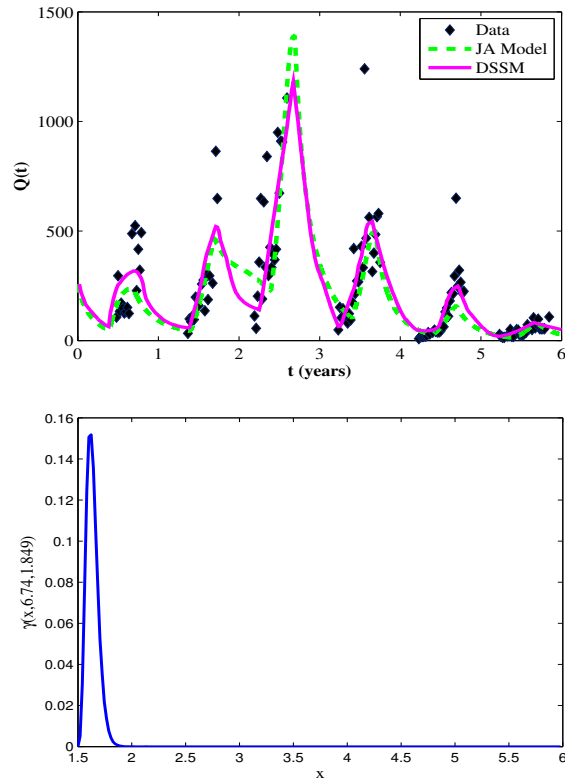


Fig. 2. Left: A comparison of the total population resulting from CMR field data to the total population resulting from model (1) and the JA model in [3]. Right: The probability density function that an adult frog gives birth to tadpoles that eventually metamorphose into frogs of size x .