Finite Difference Schemes for the McKendrick Von Foerster Equation

Luke Sheard

March 16, 2016

Abstract

This is my Abstract

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Introduction

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Characteristic Based Population Models

In this chapter we consider the models in M'Kendrick (1925) and Foerster (1959) who describe a system indexed by age. We then consider of the advances in Silvert and Platt (1978) who describe new equations indexed by weight and the derive the standard McKendrick-von Foerster Equation for weight indexed systems.

This work serves as the basis for Datta et al. (2010), who constructs a stochastic model for the dynamics of population, which they call the deterministic jump-growth equation. We consider the relevance of this equation in relation to the McKendrick-von Foerster Equation drawing further on the work of Datta et al. (2010).

2.1 Age Indexed Models

M'Kendrick (1925) first posed the idea of modeling biological processed for medicinal science by a single characteristic. In a process of individuals meet they transfer information within the system, and if one considers these as individuals as particles in a system moving according to a dimension indexed by this single characteristic then their movement becomes a study in kinetics.

Foerster (1959) extended the principle equations derived in M'Kendrick (1925) with extensions. Trucco gives a full rigorous discussion of the advancements made in Foerster (1959). It's discussion involve considering the steady state solutions of what he calls "The Von Foerster Equation", which we discuss further in section 4.1.

2.1.1 The Von Foerster Equation

$$\frac{\partial n}{\partial t} + \frac{\partial n}{\partial a} = -m(a)n \tag{2.1}$$

Following the work of Trucco we now describe Von Foerster's reasoning to determine Equation 2.1. Suppose that $n(t,a)$ represents the density of individuals at time t in the age category $(a, a + \Delta a)$. Then we have that

$$
\begin{aligned}
\frac{\partial}{\partial t}(n(a,t)\Delta a) &= + \text{ rate of entry of } a \\
&= - \text{ rate of departure at } (a + \Delta a) \\
&= - \text{ deaths in } (a, a + \Delta a).
\end{aligned}
\tag{2.2}
$$

We can express which in mathematical terms for some *flux*, $J(t,a)$, which describes that rate of movement of individuals in $(a, a + \Delta a)$ as

$$
\frac{\partial n}{\partial t} = \frac{J(t,a) - J(t, a + \Delta a)}{\Delta a} - m(a)n(a,t).
\tag{2.3}
$$

for some per capita mortality rate m. When dealing with the flux J we consider that this represents the movement of individuals in age. As individuals become older the flux can be assumed the be proportional to the density of individuals with some velocity $v(t,a)$. If the aging corresponds to the parsing of time then we have that

$$
v = \frac{\partial a}{\partial t} = 1
$$

and so $J(t,a) = n(t,a)$. Substituting this in it is clear that, in the limit as as $\Delta a \to 0$, Equation 2.3 becomes the von Foerster Equation (Equation 2.1).

2.2 Weight Indexed Models

2.2.1 McKendrick-von Foerster Equation

Silvert and Platt (1978) introduced a more general construction of the McKendrick-von Foerster Equation, notwithstanding a change from age indexed population to sized based population, in a model which allowed growth and mortality to be functions of body mass. Their changes are widely used in mathematical biology and a full derivation can be found in Silvert and Platt (1978), however a simple argument is that the *flux* described in Equation 2.3 is changed for a flux that depends on the growth of individuals

$$
J(t,w) = g(t,w)n(t,w)
$$

and $m(a)$ becomes a mortality function in weight and age $\mu(w)$. Thus the McKendrick-von Foerster Equation reads

$$
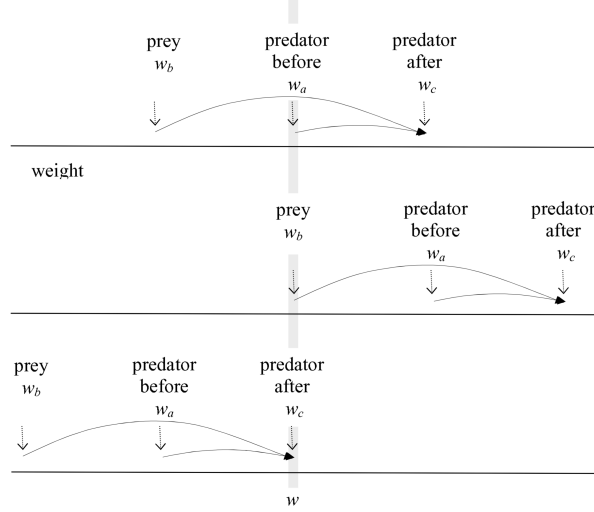\frac{\partial n}{\partial t} + \frac{\partial}{\partial w}(g \cdot n) = -\mu \cdot n.
\tag{2.4}
$$

Figure 2.1: Figure 1 from Datta et al. (2010). The death of an individual with weight w_b is attributed to the growth of another individual weight w_a, who consequently dies to yield a new individual with weight $w_c = w_a + Kw_b$ for some predation efficiency K that could be a function of weight.

2.2.2 Jump Growth Equation

While the mathematical framework presented in Silvert and Platt (1978), Datta et al. (2010) presents a different method of describing weight indexed population under a the assumption that predation is a Markov process. The predation event extends the ideas of Silvert and Platt (1980) where predation is modeled the coupled death at one size to the growth of another. This is illustrated in Figure 2.1 where we see there are three types of predation to yield news individuals weight w_c.

$$\frac{\partial \phi(w)}{\partial t} = \int \big(-k(w, w')\phi(w)\phi(w') \\ - k(w, w')\phi(w')\phi(w) \\ + k(w - Kw', w')\phi(w - Kw')\phi(w')\big)\, \mathrm{d}w'. \tag{2.5}$$

The research in Datta et al. (2010) yields the "Deterministic Jump-Growth Equation", an analytic partial differential equation derived from the macroscopic stochastic models. Equation 2.5 represents this model, where K is the predation efficiency and $k(w, w')$ is the feeding rate for individuals weight w feeding on individuals weight w'.

2.2.3 Relation of the Jump Growth Equation and McKendrick-von Foerster Equation

Law et al. (2009) shows that under the assumption of stochastic predation that Equation 2.4 is a suitable model for population dynamics under the assumption that the growth rate of an individual with weight w from feeding on smaller organizations can be expressed as

$$g(w) = \int K w' k(w, w') \phi(w') \, \mathrm{d}w', \tag{2.6}$$

and similarly the per capita mortality rate at weight w is modelled as

$$\mu(w) = \int k(w', w) \phi(w') \, \mathrm{d}w'. \tag{2.7}$$

Datta et al. (2010), Chapter 2.5, shows that this model can be shown as an approximation to Equation 2.5. By expanding the Taylor series of the last term of Equation 2.5 we see that

$$
\begin{aligned}
\frac{\partial \phi(w)}{\partial t} &= \int k(w', w) \phi(w) \phi(w') \, \mathrm{d}w' \\
&\quad - \frac{\partial}{\partial w} \int K w' k(w, w') \phi(w') \phi(w) \, \mathrm{d}w' \\
&\quad + \frac{1}{2} \frac{\partial}{\partial w} \int (K w')^2 k(w, w') \phi(w') \phi(w) \, \mathrm{d}w' \\
&\quad + R,
\end{aligned}
\tag{2.8}
$$

for a remainder term R. Clearly the first two terms correspond the McKendrick-von Foerster Equation. Therefore in our method for constructing a numerical scheme for the Jump Growth Equation we will focus on Equation 2.8, which we call the Growth-Diffusion Equation, since it is numerically easier to compute.

2.3 McKendrick-von Foerster Equation with Diffusion

When we consider Equation 2.8 later in this paper we need to consider concrete equations. Here we derive a representation of Equation 2.8 to have similar form to a transport equation, where

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial w}(g \cdot u) - \mu \cdot u + \frac{\partial}{\partial w^2}\left(\frac{1}{2} D \cdot u\right) \tag{2.9}$$

If we first restrict the study to Equation 2.8 without the remainder term, to keep our study to second order accurary, then we can make the analogy from Equation 2.8 to Equation 2.9 by taking

$$D(w) = \int (K w')^2 k(w, w') u(w) \, \mathrm{d}w' \tag{2.10}$$

and G, μ from Equation 2.6, Equation 2.7 for some feeding kernel $k(w, w')$. As described in Benoıt and Rochet (2004) we assume that the feeding rate takes the form

$$k(w, w') = w^\alpha S\left(\frac{w}{w'}\right) \tag{2.11}$$

for some α, and further we take S to be a local Gaussian of the the form

$$S\left(\mathrm{e}^z\right) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(z-\beta)^2}{2\sigma^2}\right) \tag{2.12}$$

for some β, σ to be determined experimentally.

Chapter 3

Finite Difference Equations

Unfortunately the equations that are derived in chapter 2 do not have well formed analytics solutions. In fact, generally, most partial differential equations do not have explicit analytic solutions. Consequently we must find accurate numerical approximations and methods for solving these problems.

In this chapter we introduce the required mathematics for understanding the numerical methods used in chapter 4. We introduce the idea of a finite difference equation, and the finite difference method for numerically solving partial differential equations. As well as the required knowledge to understand the stability of the methods described.

3.1 Relation to Differential Calculus

As Gorge Boole writes in Boole and Moulton (1880), "Differential Calculus is occupied about the limits to which such ratios approach as the increments are indefinitely diminished." However, "The Calculus of Finite Differences may be strictly defined as the science which is occupied about the ratios of the simultaneous increments of quantities mutually dependent." In simple terms the calculus of finite differences is only concerned about ratios of infinitesimals, in line with the ideas of Newtonian calculus.

To understand this, consider the simple *ordinary* differential equation:

$$\frac{\mathrm{d}y}{\mathrm{d}x} = y. \tag{3.1}$$

In differential calculus we can represent the left hand of Equation 3.1 by

$$\frac{\mathrm{d}y}{\mathrm{d}x} = \frac{\mathrm{d}}{\mathrm{d}x}(y) = \lim_{h \to 0} \frac{y(x+h) - y(x)}{h}, \tag{3.2}$$

but what instead if we represented it with respect to some infinitesimal Δx and in terms of some ratio Δ, prefixed to any function of x, which increments the value of that function by

Δx. This would give that

$$\Delta y = y(x + \Delta x) - y(x) \tag{3.3}$$

and then introduce the the quotient

$$\frac{\Delta y}{\Delta x} = \frac{y(x + \Delta x) - y(x)}{\Delta x} \tag{3.4}$$

which we can see is the foundation of the operator $\dfrac{d}{dx}$. Thus, if we can say that $\dfrac{d}{dx}$ is the fundamental operator in differential calculus; then $\dfrac{\Delta}{\Delta x}$ is the fundamental operator in finite difference calculus. From undergraduate know that

$$
\begin{aligned}
\lim_{\Delta x \to 0} \frac{\Delta y}{\Delta x} = \lim_{\Delta x \to 0} \frac{y_{x + \Delta x} - y_x}{\Delta x} &= \lim_{h \to 0} \frac{y(x + h) - y(x)}{h} \\
&= \frac{dy}{dx}.
\end{aligned} \tag{3.5}
$$

However $\dfrac{dy}{dx}$ is not a true fraction, dy and dx do not have any intrinsic value where as Δy and Δx have exact value. As Boole and Moulton (1880) notes in the opening remarks: "In consequence of the fundamental difference above noted between the Differential Calculus and the Calculus of Finite Differences, the term Finite ceases to be necessary as a mark of distinction. The former is a calculus of limits, not of differences."

3.2   Difference Quotients

In section we begin to construct the frameworks needed to numerically model and solve partial differential equations in the discrete space of finite difference equations. We begin by introducing a deeper model of differences using a directional differences, and then using this to construct approximations to partial derivatives of any order.

3.2.1   Difference Notation

In this section we assume that our fractional $\Delta x > 0$ is fixed throughout.

In section 3.1 we introduced the definition of a difference as

$$\Delta u = u(x + \Delta x) - u(x). \tag{3.6}$$

Following the notation of Milne-Thomson (1933) we define this as the first forward difference of u, and generalize this to a function $u : \mathbb{R}^n \to \mathbb{R}$.

Definition 3.1 (First Forward Difference). Let $f : \mathbb{R}^n \to \mathbb{R}$ then the forward difference of f, is defined by

$$\Delta[f](x) = f(x_1, ..., x_i + \Delta x, ...) - f(x_1, ..., x_i, ...) \tag{3.7}$$

Remark 3.1 (Properties of the Difference Operator). Just as with the differential operator we have that it is linear and satisfies the Leibniz rule. The proof of this is left to the reader, but follows exactly the same method as for derivatives.

Following this principle it is easy to construct the nth forward difference $(\Delta^n[f](x))$ by simply considering $\Delta[\Delta^{n-1}[f]](x)$.

The forward difference is just one way of taking a difference. We can define a difference to be either *forwards*, *backwards*, or *central*. A backwards difference can be defined by simply considering a fractional of $-\Delta x$ and is denoted by $\nabla[f](x)$, and can be useful in different situations.

Definition 3.2 (First Central Difference). Let $f : \mathbb{R}^n \to \mathbb{R}$ then the forward difference of f, is defined by

$$\delta[f](x) = f(x_1, ..., x_i + \Delta x/2, ...) - f(x_1, ..., x_i - \Delta x/2, ...) \tag{3.8}$$

3.2.2 Relation to Derivatives

Now that we have the definitions of differences we can study their relation to derivatives in more detail. Consider the first forward difference of some function $u : \mathbb{R} \to \mathbb{R}$. Then from section 3.1 we know that

$$u'(x) = \lim_{\Delta x \to 0} \frac{\Delta[u](x)}{\mathrm{d}x}. \tag{3.9}$$

Hence we can see that

$$\frac{\Delta[u](x)}{\mathrm{d}x} - u'(x) = O(\Delta x) \to 0 \tag{3.10}$$

as $\Delta x \to 0$ and this is derived in Hildebrand (1987) using Taylor's Theorem. Now we ask the question: "How, in general, do we approximate the nth derivative of u by a difference?".

Theorem 3.1. *Suppose that $u \in \mathcal{C}^n([a, b])$. Then for any fractional Δx there exists a finite difference equation to represent $u^{(k)}(x)$ for all $k \leq n$ and all $x \in [a, b]$.*

Proof. The explicit details of this proof are left for the reader, but can be found in Fornberg (1988). A proof for the first derivative goes as follows.

Suppose that $u \in \mathcal{C}^1([a, b])$ then we have that

$$u(x + \Delta x) = u(x) + \Delta x \frac{\mathrm{d}u}{\mathrm{d}x} + E_1 \tag{3.11}$$

for some error E_1 which is at most $O(\Delta x^2)$. Rearranging we have that

$$\frac{u(x + \Delta x) - u(x)}{\Delta} = \frac{du}{dx} + \frac{E_1}{\Delta x}. \tag{3.12}$$

We label $E_1/\Delta x$ as T_1 which is defined as *truncation error* (See subsection 3.3.1). It is clear from this that the left hand side is an approximation to $\frac{du}{dx}$. $\qquad\square$

3.3 Transforming Differential Equations to Difference Equations

Suppose now that we are given a partial differential equation of the form

$$L(u) = \frac{\partial u}{\partial t} - \mathcal{L}u \tag{3.13}$$

for some linear differential operator $\mathcal{L}$ which is a function $\mathcal{L}(x, u, x_x, ..., u_{x^n})$ for some $n \in \mathbb{N}$, that is that $L : \mathcal{C}^m \to \mathcal{C}^n$. We consider a grid as shown in Figure 3.1.

3.3.1 Truncation Error

Suppose that we have some difference equation $D : \mathcal{C}^m \to \mathcal{C}^n$ which is supposed to be an approximation to L. Denote ϕ be the exact solution to $D(u) = 0$, so $D(\phi) = 0$, and let Φ be the exact solution to $L(u) = 0$.
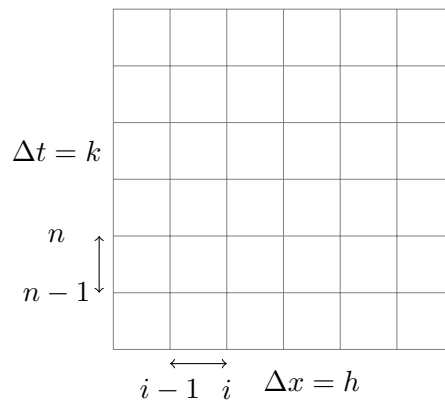

Figure 3.1: Mesh Grid example

Chapter 4

Method

This chapter outlines the method used to construct a finite difference scheme for the deterministic Jump Growth Equation, Equation 2.8. It begins with a discussion about the steady state of the McKendrick-von Foerster Equation and how this helps to solve the Jump Growth Equation. Following this we apply the mathematics in chapter 3 and Rosinger (2008) to construct a finite difference scheme that is stable and consistent, and thus convergent.

4.1 Steady State Solutions

In marine ecosystems it's been found that the abundance of organisms within weight classes is roughly constant (Sheldon et al. (1972)) if those weight classes are distributed logarithmically. Further, averaged over time, this abundance changes rather little (Datta et al. (2011)) suggesting that the system is near steady state. Benoît and Rochet (2004) found that the McKendrick-von Foerster Equation has a power law steady steady state of the form $\phi(w) \propto w^\gamma$. We combine this reasearch to now show that the the McKendrick-von Foerster Equation with diffusion (Equation 2.8) can be transformed using the logarithmic change of variables and appropriate change of function to have a constant solution if the work of Benoît and Rochet (2004) is correct.

4.1.1 Logarithmic Weight Index

It first helps to transform to a dimensionless variable $x = \log w$, with $\varphi(x)\mathrm{d}x = \phi(w)\mathrm{d}w$ which we will show makes our equations behave much more nicely under translation. First let us consider the feeding kernel function S (Equation 2.12), from which we can construct a new $\hat{S}(x) = S(\mathrm{e}^x)$ and substitute this in to the growth, death and diffusion functions (along with our change of variables and function) to get new functions $\hat{g}, \hat{\mu}, \hat{D}$ that satisfy

$$\varphi_t = -(\hat{g} \cdot \varphi)_x - \hat{\mu} \cdot \varphi + \frac{\mathrm{e}^{-x}}{2} \left((\hat{D} \cdot \varphi)_{xx} - (\hat{D} \cdot \varphi)_x \right). \tag{4.1}$$

These functions have the form

$$\hat{g}(x) \quad = \quad \int K\,e^{x' + (\alpha - 1)x}\,\hat{S}(x - x')\varphi(x')\,dx' \tag{4.2}$$

$$\hat{D}(x) \quad = \quad \int K^2\,e^{2x' + (\alpha - 1)x}\,\hat{S}(x - x')\varphi(x')\,dx' \tag{4.3}$$

$$\hat{\mu}(x) \quad = \quad \int K\,e^{\alpha x'}\,\hat{S}(x' - x)\varphi(x')\,dx' \tag{4.4}$$

and yield a steady state distribution that $\varphi(x) \propto e^{\gamma + 1}$. Finally by substituting in $\rho(x) = e^{\gamma}\,\varphi(x)$ we should yield a system which has a steady state $\rho(x) \propto 1$. This substitution gains the coefficients

$$\bar{g}(x) \quad = \quad \int K\,e^{(\alpha + 1)x'}\,\hat{S}(x - x')\rho(x')\,dx' \tag{4.5}$$

$$\bar{D}(x) \quad = \quad \int K\,e^{(\alpha + 1)x'}\,\hat{S}(x - x')\rho(x')\,dx' \tag{4.6}$$

$$\bar{\mu}(x) \quad = \quad e^{\gamma x}\int K\,e^{(\alpha + 1)x'}\,\hat{S}(x - x')\rho(x')\,dx' \tag{4.7}$$

Appendix A

Proof of Steady State

A.1 Change of Variables

Starting with the McKendrick-von Foerster Equation with diffusion (Equation 2.8) we first need to change to a dimensionless variable $x = \log w$, so that $\varphi(x)\partial x = u(w)\partial w$. In a first step this gives that

$$\mathrm{e}^{-x}\,\varphi_t = -(g(w)\,\mathrm{e}^{-x}\,\varphi)_w - \mathrm{e}^{-x}\,\mu(w)\varphi + \frac{1}{2}(D\,\mathrm{e}^{-x}\,\varphi)_{ww} \tag{A.1}$$

We then transform the derivatives from w to x using the chain rule

$$\frac{\partial}{\partial w} = \frac{\partial x}{\partial w}\frac{\partial}{\partial x} = \mathrm{e}^{-x}\,\frac{\partial}{\partial x}. \tag{A.2}$$

Which shows that

$$
\begin{aligned}
\mathrm{e}^{-x}\,\varphi &= -\mathrm{e}^{-x}\,\frac{\partial}{\partial x}\left(\hat{g}\varphi\right) - \mathrm{e}^{-x}\,\hat{\mu}(x)\varphi + \frac{\mathrm{e}^{-x}}{2}\frac{\partial}{\partial x}\left(\mathrm{e}^{-x}\,\frac{\partial}{\partial x}\left(\hat{D}\varphi\right)\right) \\
\varphi &= -\frac{\partial}{\partial x}\left(\hat{g}\varphi\right) - \hat{\mu}(x)\varphi + \frac{1}{2}\frac{\partial}{\partial x}\left(\mathrm{e}^{-x}\,\frac{\partial}{\partial x}\left(\hat{D}\varphi\right)\right) \\
&= -(\hat{g}\varphi)_x - \hat{\mu}(x)\varphi + \frac{\mathrm{e}^{-x}}{2}\left(\left(\hat{D}\varphi\right)_{xx} - \left(\hat{D}\varphi\right)_x\right).
\end{aligned}
\tag{A.3}
$$

Now we need to concentrate on the coefficient functions for growth, death and diffusion. First let us consider the growth function, $g(w)$ which from subsection 2.2.3 takes the form

$$g(w) = \int Kw'k(w,w')u(w')\,\mathrm{d}w' = \int Kw'w^\alpha S\left(\frac{w}{w'}\right)u(w')\,\mathrm{d}w' \tag{A.4}$$

then following the change of variables in Equation A.3 we take $\hat{g}(x) = \mathrm{e}^{-x}\,g(\mathrm{e}^x)$, and since $\varphi(x)\partial x = u(w)\partial w$ we can change from u to φ in the integral very simply and thus

$$\hat{g}(x) = \mathrm{e}^{-x}\,g(\mathrm{e}^x) = \int K\,\mathrm{e}^{x'}\,\mathrm{e}^{(\alpha-1)x}\,\bar{S}(x-x')\varphi(x')\,\mathrm{d}x', \tag{A.5}$$

where $\bar{S}(z) = S(\mathrm{e}^z)$. Similarly for the diffusion coefficient

$$D(w) = \int (Kw')^2 k(w,w')u(w')\,\mathrm{d}w' = \int (Kw')^2 w^\alpha S\left(\frac{w}{w'}\right)u(w')\,\mathrm{d}w' \tag{A.6}$$

we change variables so that

$$\hat{D}(x) = e^{-x} D(e^x) = \int K^2 \, e^{2x' + (\alpha - 1)x} \, \bar{S}(x - x')\varphi(x') \, \mathrm{d}x'. \tag{A.7}$$

The death term provides an easier change of variables with

$$\hat{\mu}(x) = \mu(e^x) = \int e^{\alpha x} \, \bar{S}(x' - x)\varphi(x') \, \mathrm{d}x' - \delta. \tag{A.8}$$

If we now assume that $e^{\gamma x} \rho(x) = \varphi(x)$, so that if the steady state of $\varphi(x) \propto e^{\gamma x}$ then the steady state of $\rho(x) \propto 1$, then we have that Equation A.3 implies

$$
\begin{aligned}
e^{\gamma x} \rho &= -(\hat{g} \, e^{\gamma x} \rho)_x - \hat{\mu} \, e^{\gamma x} \rho + \frac{e^{-x}}{2} \left((\hat{D} \, e^{\gamma x} \rho)_{xx} - (\hat{D} \, e^{\gamma x} \rho)_x \right) \\
&= -(\bar{g}\rho)_x - \bar{\mu}\rho + \frac{e^{-x}}{2} \left((\bar{D}\rho)_{xx} - (\bar{D}\rho)_x \right)
\end{aligned}
\tag{A.9}
$$

with the coefficient equations

$$\bar{g}(x) = \int K \, e^{x'} \, e^{(\alpha + \gamma - 1)x} \, \bar{S}(x - x')\varphi(x') \, \mathrm{d}x' \tag{A.10}$$

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