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# An Interactive Tool for the Computational Exploration of Integrodifference Population Models

Kennedy Agwamba  
*Harvey Mudd College*

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# An Interactive Tool for the Computational Exploration of Integrodifference Population Models

**Kennedy Agwamba**

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Jon Jacobsen, Advisor

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Rachel Levy, Reader



**Department of Mathematics**

May, 2016

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# Abstract

Mathematical modeling of population dynamics can provide novel insight to the growth and dispersal patterns for a variety of species populations, and has become vital to the preservation of biodiversity on a global-scale. These growth and dispersal stages can be modeled using integrodifference equations that are discrete in time and continuous in space. Previous studies have identified metrics that can determine whether a given species will persist or go extinct under certain model parameters. However, a need for computational tools to compute these metrics has limited the scope and analysis within many of these studies. We aim to create computational tools that facilitate numerical explorations for a number of associated integrodifference equations, allowing modelers to explore results using a selection of models under a robust parameter set.



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# Chapter 1

## Chapter 1: Introduction

### 1.1 Motivation & Background

The concept of population persistence is important with respect to the maintenance of biodiversity. Biodiversity is characterized by the variety of species and forms of life that inhabit a particular ecosystem. Preserving biodiversity is pertinent to humans for many reasons including the production of pharmaceuticals, sustenance, and aesthetics (Pearce 1991). Yet today, many would agree that environmental changes pose serious threats to biodiversity, manifested primarily in habitat loss and degradation (Dirzo and Raven 2003, Wilcove et al. 1998).

Mathematical models can predict the impact of such environmental change on the persistence of species population (Van Kirk and Lewis 1997, Jacobsen et al. 2014). Predictive measures of population dynamics are imperative in aiding conservation ecologists to take proper action to protect and preserve species vulnerable to extinction. Mathematical models often consider the species' means of growth and reproduction, given they seek to make quantitative assessments about a population's ability to persist under certain conditions. Yet, mathematical models differentiate themselves from one another based on the parameters and variables of interest, with the flexibility to numerically investigate both stochastic and deterministic processes.

Integrodifference models, in particular, have recently been used to analyze species which reproduce and spread in discrete time intervals across a finite domain (Van Kirk and Lewis 1997, Jacobsen et al. 2014). Integrodifference equations, a blend of difference and integral equations, allow

modelers to consider growth and dispersion in stages, dividing time into a period when growth is the population's primary function and a period when movement from one location to another becomes the population's primary function. This stage-based behavior is very realistic for several organisms, and integrodifference equations are highly versatile in their ability to exploit the recurrence relationship between the temporal and spatial properties of a population to predict the size and distributions of subsequent generations. Many mathematical and theoretical ecologists utilize this versatility to create integrodifference population equations which can model the growth and spread of a population affected by various changes to their habitat.

Organisms that are free-swimming in their juvenile/seed stages and sessile, or fixed in position, in their adult stages living in river ecosystems are an example of a community that can be modeled using integrodifference equations. Integrodifference models provide a better understanding of how factors, such as unidirectional stream flow, affect the physical environment and the population that inhabits it (Lutscher, Pachepsky, and Lewis 2010, Jacobsen and McAdams 2014). The southern bull-kelp of New Zealand is an example of a species that can be generalized as exhibiting separate growth and dispersal stages, which the model assumes to be continuous in space and occurring within fixed-time intervals. The unidirectional flow of the river both alters the physical environment and the dispersal patterns of the bull-kelp, limiting dispersion to one direction (Collins, Fraser, Ashcroft and Waters 2010).



**Figure 1.1** Southern Bull-Kelp of New Zealand

A given population's growth pattern can be modeled with knowledge of the initial population's density. In this case, growth can be treated as independent of space, depending only on the population density. The movement and activity associated with dispersion is modeled using a dispersal kernel. Dispersal kernels are used to patternize a dispersal event fixed within a bounded, habitable domain (Lutscher, Pachepsky, and Lewis 2010, Van Kirk and Lewis 1997, Jacobsen et al. 2014). A great degree of flexibility in integrodifference equations is derived from the dispersal kernel, which can be extended to consider either fixed, cyclic/periodic, or entirely random kernels. In the case of bull-kelp, using these discrete-time, continuous-space integrodifference equations, with dispersal kernels modeling the population's movement under the influence of unidirectional flow, has helped garner insight regarding the conditions in which the population will persist or desist (Collins, Fraser, Ashcroft and Waters 2010, Jacobsen et al. 2014).

The analysis of mathematical models for the quantitative assessment of population dynamics is important to ecologists and conservationists who would like to understand how factors such as disease, resource limitations, and climate change can impact populations over time (Jacobsen and McAdams 2014, Dirzo and Raven 2003, Wilcove et al. 1998). While numerous models have been constructed for the analysis of various ecological scenarios (Lutscher, Pachepsky, and Lewis 2010, Van Kirk and Lewis 1997, Jacobsen et al. 2014), many of these models are similar enough such that only single variables and/or parameters are created or modified to produce the variant model. Often, ecologists often use the same model to assess different scenarios. Yet, a comprehensive tool, which exploits these similarities by allowing modelers to define variables and parameters, does not exist. This project aims to create the computational tools necessary to conduct numerical exploration of integrodifference equations, allowing modelers to explore results using a selection of models under a robust parameter set. We hope mathematicians and ecologists alike will use this tool to produce and examine simulated predictions of associated integrodifference equations modeling relevant ecosystems.

## 1.2 Integrodifference Models and Dispersal Kernels

Integrodifference equations have been shown to accurately predict population dynamics for species with separate growth and dispersal stages (Kot and Schaffer, 1986; Van Kirk and Lewis, 1997). An integrodifference equation models the population as continuous in space (the habitat) and discrete in time (the dispersal event). If we consider a population  $n_t(x)$  distributed over a bounded domain  $\Omega$  at time  $t$ , we can model the successive population  $n_{t+1}(x)$  as

$$n_{t+1}(x) = \int_{\Omega} K(x, y) f(n_t(y)) dy \quad (1.1)$$

where  $f$  is a nonnegative, time-independent function which models the growth dynamics and  $K(x, y)$  is the dispersal kernel. The dispersal kernel models the probability density associated with a given organism starting at position  $y$  and settling at position  $x$  in a dispersal event. The computational tools we develop seek to explore integrodifference equations derived with similar motivations in modeling population dynamics, which take on this generic form.

Consider a population of aquatic insects in a stream where the larvae of these insects reside within the stream's benthos. These larvae periodically leap into the water column, where they fall subject to the flow of the stream. Lutscher, Pachepsky, and Lewis derived an expression for the dispersal kernel from a differential equation by considering individual movements through means of diffusion and advective flow, along with a constant settling rate for this biological system. The model assumes a given organism starts at an initial position, moves through a defined region by advective flow with Brownian motion, and resettles after being displaced. The modelers choose Brownian motion as a first approximation to variations in the flow of water. If we denote the density of these moving organisms with  $z(x, t)$ , then the change in density with respect to time is then given by

$$z_t = Dz_{xx} - vz_x - \alpha z, \quad (1.2)$$

where  $D$  is the diffusion coefficient,  $v$  is the advection velocity, and  $\alpha$  is the settling rate.

Given these parameters, Lutscher, Pachepsky, and Lewis conclude the dispersal kernel  $k(x)$  satisfies

$$k(x) = \int_0^{\infty} \alpha z(x, t) dt. \quad (1.3)$$

If we integrate Equation 1.2 over  $0 \leq t \leq \infty$ , we find that

$$\int_0^\infty z_t dt = z(x, \infty) - z(x, 0) = -z(x, 0).$$

Since  $\lim_{t \rightarrow \infty} z(x, t) = 0$ , we obtain

$$-z_t = D \int_0^\infty z_{xx} dt - v \int_0^\infty z_x dt - \alpha \int_0^\infty z dt. \quad (1.4)$$

We choose  $z(x, 0) = \delta_0(x - y)$  as the initial condition based on the assumption that a given organism starts at  $y$  at time  $t = 0$ . The expression for the dispersal kernel can now be plugged into Equation 1.4

$$-\delta_0 = \frac{D}{\alpha} \left( \int_0^\infty \alpha z(x, t) dt \right)_{xx} - \frac{v}{\alpha} \left( \int_0^\infty \alpha z(x, t) dt \right)_x - \int_0^\infty \alpha z(x, t) dt \quad (1.5)$$

which, recalling Equation 1.3, can be written as the ordinary differential equation

$$-\delta = \frac{D}{\alpha} k_{xx} - \frac{v}{\alpha} k_x - k. \quad (1.6)$$

Solving this ODE with asymptotic boundary conditions

$$\lim_{|x| \rightarrow \infty} z = 0 \quad \text{and} \quad \int_{-\infty}^\infty K(x) dx = 1 \quad (1.7)$$

yields the solution

$$k(x) = \begin{cases} A e^{a_1 |x-y|}, & x < 0 \\ A e^{a_2 |x-y|}, & x \geq 0 \end{cases} \quad (1.8)$$

where

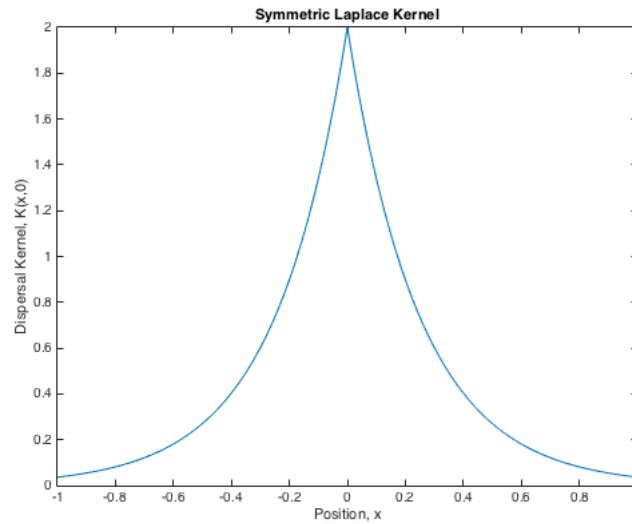
$$a_{1,2} = \frac{v}{2D} \pm \sqrt{\frac{v^2}{4D^2} + \frac{\alpha}{D}} \quad (1.9)$$

and

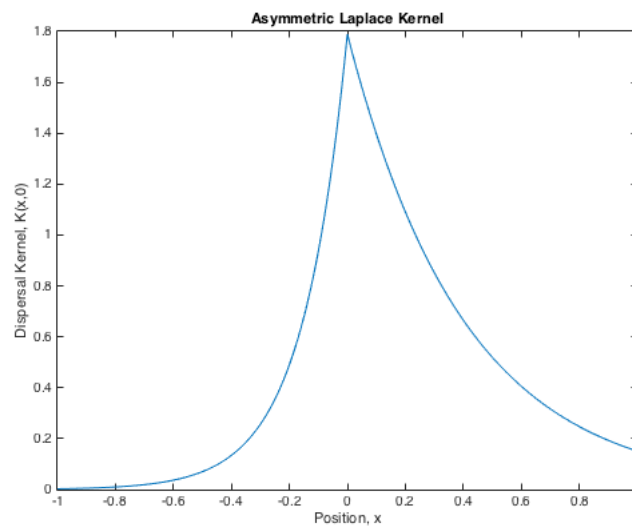
$$A = \frac{a_1 a_2}{a_2 - a_1} = \frac{\alpha}{\sqrt{v^2 + 4\alpha D}}. \quad (1.10)$$

Figures 1.2 and 1.3 show sample plots of the resulting dispersal kernels.





**Figure 1.2** An example of a symmetric Laplace kernel at  $y = 0$ . This represent the probability density for an organisms that starts at  $y = 0$  and settles at  $x$  following a dispersal event



**Figure 1.3** An example of an asymmetric Laplace kernel at  $y = 0$

Dispersal kernels model various forms of biological dispersal and therefore can be expressed in a multitude of ways. For the dispersal kernel  $K(x, y)$ , the kernel models the probability density of an individual, which starts at  $y$  settling at position  $x$  along a bounded domain  $\Omega$ . When we integrate the kernel over the span of the domain, this evaluates to the probability distribution for a population that was initially uniformly distributed over the domain. A dispersal kernel often has parameters that reflect factors associated with the environment contained in the domain.

For example, consider a habitat where the organisms contained within it experience unidirectional flow (e.g., wind, river flow) which skews the dispersion. With advective flow influencing the dispersal event, Equation 1.7 gives the asymmetric Laplace kernel for cases where  $v \neq 0$ , as seen in Figure 1.3. When  $v = 0$ , the dispersal kernel simplifies to the symmetric Laplace kernel, as seen in Figure 1.3. Figure 1.3 is asymmetrically distributed around the theoretical initial position with an apparent negative skew, where Figure 1.2, which assumes no unidirectional flow, is symmetrically distributed around the initial position  $y = 0$ .

### 1.3 Population Growth Models and The Asymptotic Growth Rate

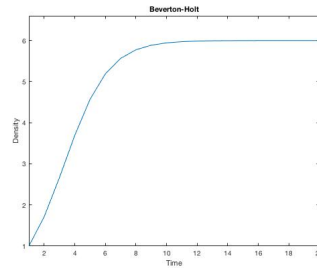
In Equation 1.1, we allow population growth dynamics to be modeled by a nonnegative, density-dependent growth function  $f(n_t)$ . These functions can be expressed with respect to the maximum per capita growth rate such that  $f(n_t) = g(n_t(x)) \cdot n_t(x)$ . Common growth functions of this variety include the Beverton-Holt (1957) model and the Ricker (1954) model. The Beverton-Holt model

$$f(n_t) = \frac{r n_t}{1 + (r - 1)n_t/K} \quad (1.11)$$

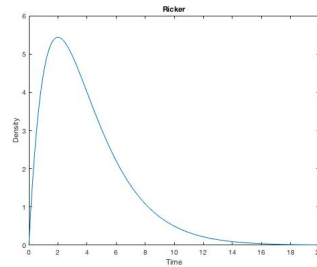
and the Ricker model

$$f(n_t) = n_t \cdot \exp \left[ r \left( 1 - \frac{n_t}{K} \right) \right] \quad (1.12)$$

both contain scalar parameters associated with the rate of proliferation in a given population,  $r$ , and the community's carrying capacity,  $K$ .



**Figure 1.4** Sample Beverton-Holt growth function for  $r = 2$  and  $K = 6$ .



**Figure 1.5** Sample Ricker growth function for  $r = 2$  and  $K = 4$ .

The Beverton-Holt and Ricker's model are known to achieve maximum per capita growth rate at arbitrarily low densities, increasing with decreasing population density (van Kirk and Lewis 1997). We can linearize expressions for  $f$  under the assumption that the maximum per capita growth rate is found locally as  $n \rightarrow 0$  for  $f'$ , analogous to capturing the first order term of the Taylor expansion for the nonlinear system as the variable of interest approaches 0. In particular, for the integrodifference model we will consider the linearization about  $n = 0$ , replacing  $f(n_t)$  with  $f'(0) \cdot n_t$  (note that we assume  $f(0) = 0$  for all our growth models).

Linearization is a key technique to understanding whether a given population will persist or go extinct, as modelers can then derive an asymptotic growth factor. This asymptotic growth factor often necessitates numerical simulations of the model to uncover for a given parameter set. The model in its nonlinear form is known to be difficult to numerically simulate. Similar to analyzing a nonlinear system of differential equations using the eigenvalues of the associated Jacobian, we can use linear stability analysis for the integrodifference model to gain a desired understanding of an infinite dimensional system for which the state of the system is given by a function rather than a vector.

We will invoke some key definitions necessary for the linear stability analysis of our system. First, let  $X$  be a normed vector space with norm  $\|\cdot\|$ . An operator  $T : X \rightarrow X$  is *completely continuous* if  $T$  is continuous and if  $B \subset X$  is bounded, then  $\overline{T(B)}$  is compact. An operator  $T$  is *Frechet differentiable at  $x$*  if there exist a linear operator  $L$  such that

$$\lim_{y \rightarrow 0} \frac{\|T(x+y) - T(x) - L(y)\|}{\|y\|} = 0.$$

Lastly, The *spectral radius* of  $T$  is defined as the supremum of the absolute values of the eigenvalues of  $T$ , or by Gelfand's formula,

$$\rho(A) = \lim_{k \rightarrow \infty} \|T^k\|^{1/k}.$$

With these definitions, we derive a constant associated with the long-term behavior of the system representing the population's response to growth and dispersal events for fixed and random kernels, which we will refer to as the asymptotic growth rate. The asymptotic growth rate is based on some critical assumptions made in the linear analysis of the equilibrium solution for Equation 1.1. When linearizing about the trivial solution  $n = 0$  for fixed kernels, Van Kirk and Lewis (1997) have shown there exists

a principal eigenvalue which serves as the asymptotic growth rate for the nonlinear model. While effective for assessing systems modeled using fixed kernels, we also hold interest in systems modeled using random kernel, for which no such eigenvalue exists. However, Jacobsen, Jin, and Lewis (2014) showed for models using random kernels there exists an analog to this principal eigenvalue that we denote using  $\Lambda$ .

If we let

$$\mathcal{T}(n_t) = \int_{\Omega} K(x, y) f(n_t(y)) dy, \quad (1.13)$$

then  $\mathcal{T}$  is a nonlinear operator that maps from  $L_2(\Omega)$  into  $L_2(\Omega)$  and is completely continuous. The equilibrium solution for the nonlinear model can be expressed as the fixed point equation

$$n_* = \mathcal{T} n_*. \quad (1.14)$$

Another property of  $\mathcal{T}$  is that it is Frechet differentiable, and its Frechet derivative  $\mathcal{L}$  is a completely continuous linear operator. The Frechet derivation, or linearization, of Equation 1.13 at the trivial state  $n_* = 0$  is defined by

$$\mathcal{L}(n_t) = \int_{\Omega} K(x, y) f'(0) n_t(y) dy. \quad (1.15)$$

To analyze the local stability of the fixed point of  $\mathcal{T}$ , we examine the spectral radius of the Frechet derivative  $\mathcal{L}$  at  $n_*$ . If the spectral radius of the Frechet derivative,  $\rho(\mathcal{T}'(n_*)) > 1$ , the equilibrium solution is unstable. Instability, in this case, is indicative of the action of a source, suggesting the given population will move away from the zero solution towards  $n_*$  and ultimately persist. If  $\rho(\mathcal{T}'(n_*)) < 1$ , the equilibrium solution is locally stable and moves towards the zero solution, implying the population will be unable to outgrow the diminishing effects of dispersal.

For fixed kernels,  $\rho(\mathcal{T}')$  is the principal eigenvalue of the operator  $\mathcal{L}$ . For time-dependent models, we show there exists a constant  $\Lambda$  that plays the same role as  $\rho(\mathcal{T}')$  in determining a threshold parameter. To make the growth rate and dispersal kernel time-dependent, we consider Equation 1.1 as

$$n_{t+1}(x) = F_t(n_t)(x) = \int_{\Omega} K_t(x, y) f_t(n_t(y)) dy, \quad (1.16)$$

where  $f_t$  and  $K_t$  are dependent on time step  $t$ , allowing integrodifference models to also explore the behavior of systems with cyclic or random growth

and dispersal patterns. If  $\{\alpha_t\}_{t \geq 0}$  is a set of independent identically distributed random variables from a set representing the range of various plausible environmental conditions, then we can rewrite Equation 1.16 as

$$n_{t+1}(x) = F_{\alpha_t}(n_t)(x) = \int_{\Omega} K_{\alpha_t}(x, y) f_{\alpha_t}(n_t(y)) dy. \quad (1.17)$$

In Jacobsen, Jin, and Lewis (2014), several assumptions are made about  $K_{\alpha_t}$  and  $f_{\alpha_t}$  to move towards the conclusion on the asymptotic growth rate being derived from the linearization of Equation 1.17. The average growth rate of the population over the first  $t$  time steps can be expressed as

$$\text{Avg. growth rate over first } t \text{ steps} = \left[ \frac{\int_{\Omega} n_t(x) dx}{\int_{\Omega} n_0(x) dx} \right]^{1/t}. \quad (1.18)$$

The parameter  $\Lambda$  is defined by taking the limit of this average as  $t \rightarrow \infty$

$$\Lambda := \lim_{t \rightarrow \infty} \left[ \frac{\int_{\Omega} n_t(x) dx}{\int_{\Omega} n_0(x) dx} \right]^{1/t}. \quad (1.19)$$

Equation 1.19 can be simplified to

$$\Lambda := \lim_{t \rightarrow \infty} \left[ \int_{\Omega} n_t(x) dx \right]^{1/t}, \quad (1.20)$$

as originally described in Jacobsen, Jin, Lewis (2014) with a proof of the limit's existence and independence from how the initial population distribution function is defined. This value  $\Lambda$  behaves similar to a principal eigenvalue as it is also associated with the long-term behavior of the system representing the population's response to growth and dispersion. Jacobsen, Jin, and Lewis demonstrated that if  $\Lambda > 1$ , the population will persist, but if  $\Lambda < 1$ , the population will go extinct. Consequently, the tool we've developed will allow modelers to numerically simulate integrodifference population models, and in particular, explore cases regarding population persistence involving random dispersal kernels that have yet to be examined in great detail.

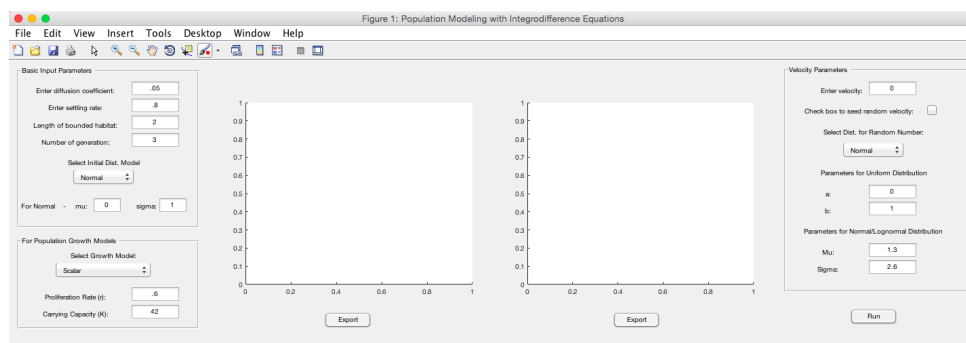


## Chapter 2

# Chapter 2: A MATLAB/Simulink Tool for Exploring Integrodifference Population Models

### 2.1 Design and Implementation

In this section, we offer a detailed look into the design, construction, and utility of the computational tools developed for the numerical exploration of integrodifference population model in MATLAB. Figure 2.1 provides a depiction of this tool to illustrate its appearance and various features.



**Figure 2.1** Complete GUI with embedded axes and parameter inputs for interactive simulations of population dynamics



We have developed a computational tool which explores the behavior of integrodifference equations as described in Chapter 1. The current version of the tool packages a set of MATLAB functions based on the models defined in Jacobsen et al., 2014 within an interactive, user-friendly GUI for the MATLAB/Simulink environment. The GUI divides inputs into three main subsections: "Basic Input Parameters", and "Population Growth Model", and "Velocity (Advection) Parameters". Basic input parameters includes the diffusion coefficient, the settling rate, the length of the bounded domain, the number of generations to simulate, and the shape of the initial population distribution. The diffusion coefficient  $D$  is a constant associated with the degree of randomness at which the organisms of interest diffuse through a medium. The settling rate  $\beta$  reflects the frequency at which an organism settles at a particular location. These terms shape the appearance of the dispersal kernel and thus its impact on the shape of the population distribution at the following time step. In the absence of advection, the average dispersal distance is given by

$$a = \sqrt{\frac{\beta}{D}}$$

in one-dimension. The length of this one-dimensional space in consideration is input as the parameter  $\Omega$ . The last two input parameters the user is responsible for deciding on are the number of generations/time steps they would like to simulate, and the distribution of the initial population. The simulation tool currently supports selecting either a normal or uniform distribution, supported by MATLAB's built-in continuous probability density functions.

The user is also able to select the growth model they would like to use from the "Population Growth Model" section. Currently supported growth models are the Beverton-Holt and Ricker's model, discussed in Chapter 1.3. The user can also choose to use a scalar value to influence growth dynamics. For example, if the user intends to analyze how various parameters contribute to the dispersal success function, as discussed by van Kirk and Lewis, the user would select the "Scalar" growth model, and set  $r = 1$ . Likewise, if the user was interested in a scenario where the resulting population doubled every generation, then the user would set  $r = 2$ .

The last set of parameters the user is responsible for are the advection-related parameters. The user is able to input a velocity value, simulating a

constant rate of unidirectional advection within the habitat. The user is also able to simulate randomness within a habitat by seeding random velocities based on a probability distribution. The shape of the dispersal kernel at each time step, as mentioned in Chapter 1.2 is given by

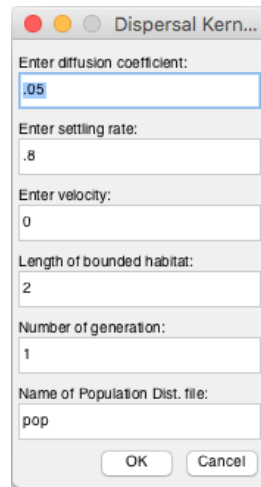
$$k(x) = \begin{cases} Ae^{a_1|x-y|}, & x < 0 \\ Ae^{a_2|x-y|}, & x \geq 0 \end{cases}$$

where

$$a_{1,2} = \frac{v}{2D} \pm \sqrt{\frac{v^2}{4D^2} + \frac{\alpha}{D}}.$$

By seeding random velocities, the dispersal kernel is redefined at each time step reflecting the magnitude that the randomly-seeded advection velocity has on the corresponding dispersal event. Note that when  $v = 0$ , the equation above simplifies to the mean dispersal distance  $a = \sqrt{\frac{\beta}{D}}$ . This feature is particularly interesting because integrodifference models considering random kernels are difficult to analytically solve. This tool gives modelers the capability to numerically explore integrodifference population models using random kernels.

Simulations of population dynamics with nonlinear growth models and random dispersal kernels are made possible by numerical integration and one-dimensional data interpolation in MATLAB. The dispersal kernel, the per capita growth function, and the population distribution are defined as function handles, and the product of those three function handles is numerically integrated using the built-in *integral* function. Following this integration, the result is an array of values. This array of values are treated as a set of query points to interpolate a function, which we use to define the population distribution following the simulated growth and dispersal event, in order to perform the calculations for subsequent time steps. These actions are contained within the main for-loop running for the number of generations as specified by the users and dominate the runtime performance of this tool. All prompted parameters are used to define these function handles, and therefore default values are put in as placeholders for which the user can change to explore unique growth and dispersal scenarios. All instantiated variables that can be defined prior to use are preallocated to prevent dynamic resizing of data structures in order to optimize runtime.



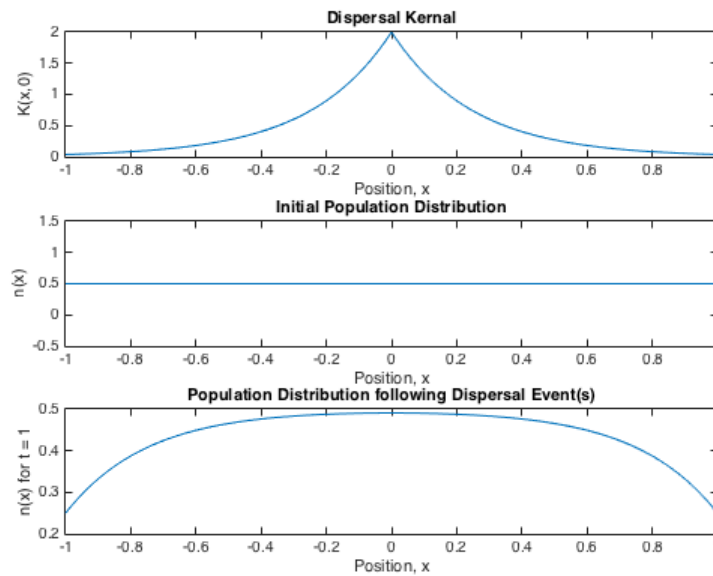
**Figure 2.2** Dialog box prompting users for parameter inputs resulting in the initial population distribution, the functioning dispersal kernel, and the population distribution at the final time step in one figure window

Another function contained within this tool utilizes a dialogue box to prompt the user to input values for key model parameters, including the diffusion coefficient, the settling rate, advection velocity, the length of the bounded domain, and the number of time steps/generations the user would like to simulate. Based on these inputs, the function produces a graph of the dispersal kernel. The dispersal kernel is currently defined as it is in Equation 1.8. The main function also prompts the user to provide the name (without the .m extension) of the function the user has created to define the initial population distribution. This function is plotted to provide a visual of  $n_t(x)$  at the 0th time step. The main function simulates one or more dispersal event using Equation 1.8, and the third plot produced is  $n_t(x)$ , at the time step  $t$ .

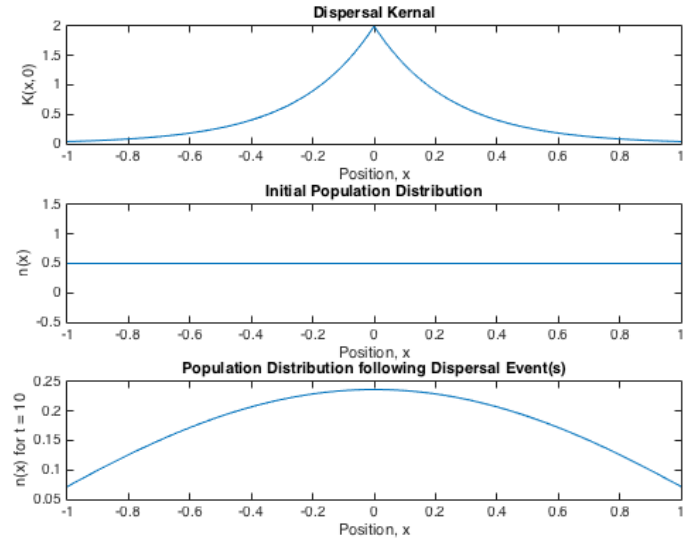
## 2.2 Key Insight and Discussion

This tool enables users to analyze the generational growth and dispersion dynamics of populations defined under a variety of distributions. For any predefined distribution, this tool is able to calculate the population distribution after a single time step or after several time steps.

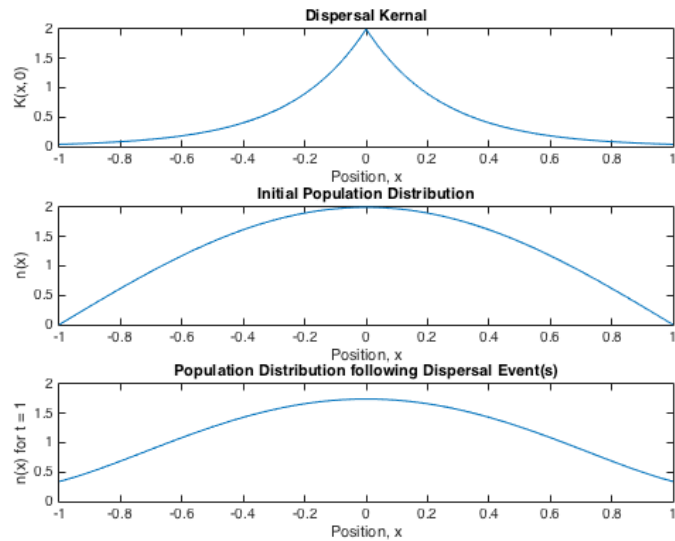
For example, in examining Figure 2.3 and 2.4, we can immediately distinguish the two plots by their difference in shape and scale along the vertical axis. Analyzing these figures and others created with various initial parameters offers the user an in-depth look at the dispersal success function defined by van Kirk and Lewis (1997). We can also examine different, user defined population distributions and analyze the resulting distribution after numerous dispersal events, as we show with Figures 2.5 - 2.11.



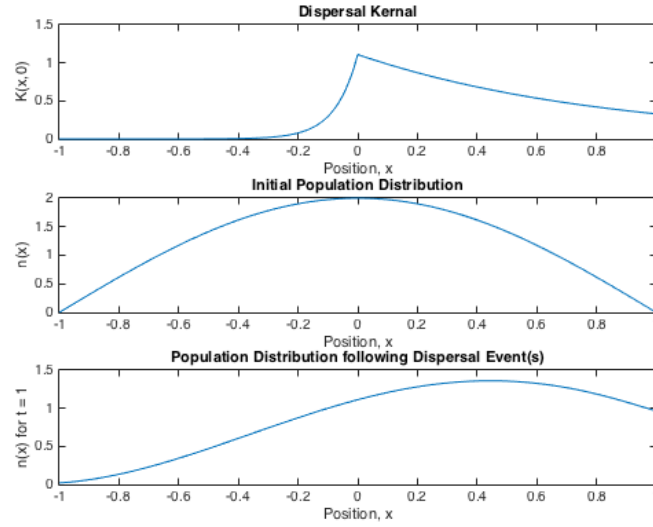
**Figure 2.3** Uniformly distributed population following a single dispersal event, exemplifying the dispersal success function as seen in van Kirk and Lewis (1997)



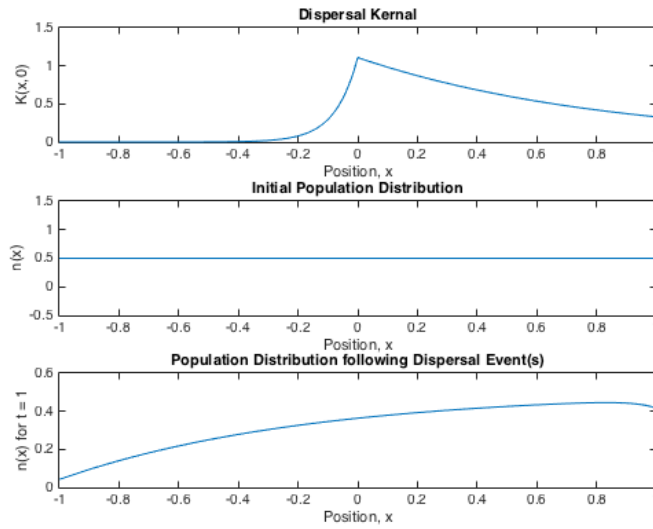
**Figure 2.4** Uniformly distributed population following 10 dispersal events



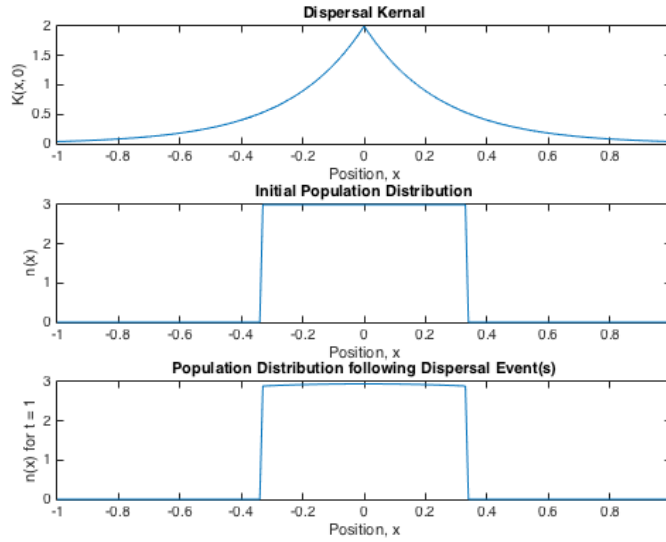
**Figure 2.5** Normally distributed population following a dispersal event with advection velocity set to 0



**Figure 2.6** Normally distributed population following a dispersal event with advection velocity set to 0.6

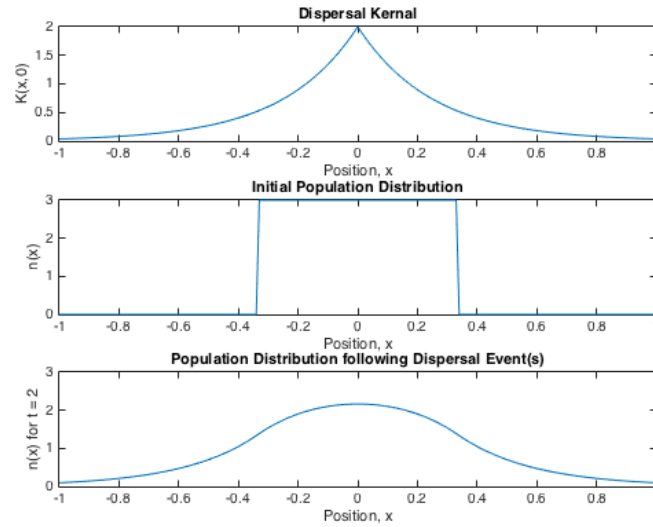


**Figure 2.7** Uniformly distributed population following a dispersal event with advection velocity set to 0.6

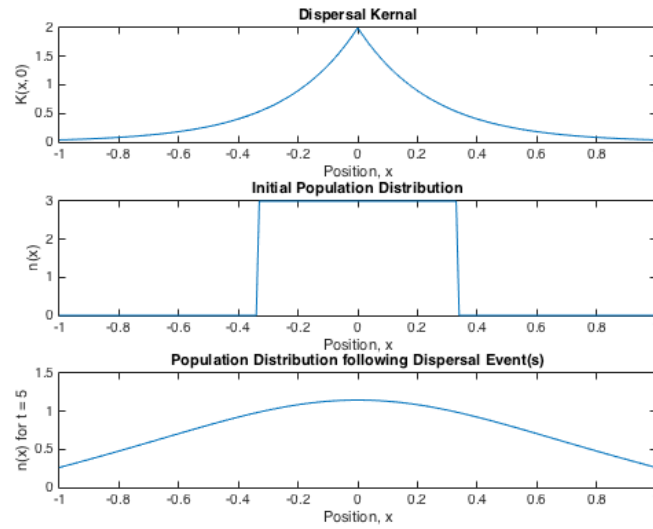


**Figure 2.8** Confined uniformly distributed population following a dispersal event

Figure 2.8 - 2.11 defines a uniform population distribution within a smaller confined region of the bounded domain. These figures could be seen as a simulation of the dispersion of organisms that were systematically introduced to a defined patch in the bounded habitat of interest. Going from  $n_t(x) = 1$  to  $n_t(x) = 2$ , and then to  $n_t(x) = 5$ , after the fifth dispersal event, it appears the population has become normally distributed, and therefore will assume the flattened distribution seen in Figure 2.4. In Figure 2.11, under the influence of asymmetric dispersion, we see the distribution begins to assume a negative skew similar to Figure 2.6.

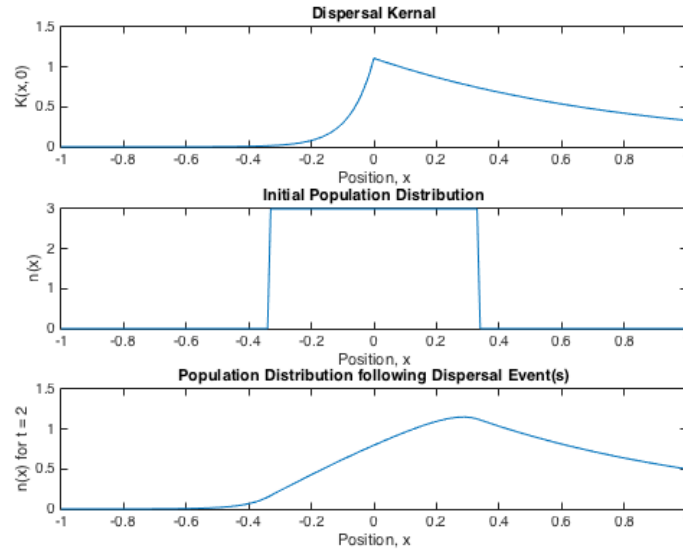


**Figure 2.9** Confined uniformly distributed population following two dispersal events



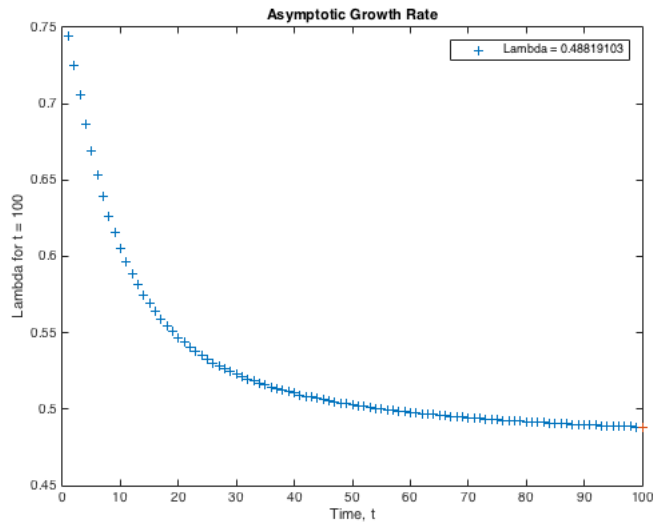
**Figure 2.10** Confined uniformly distributed population following five dispersal events



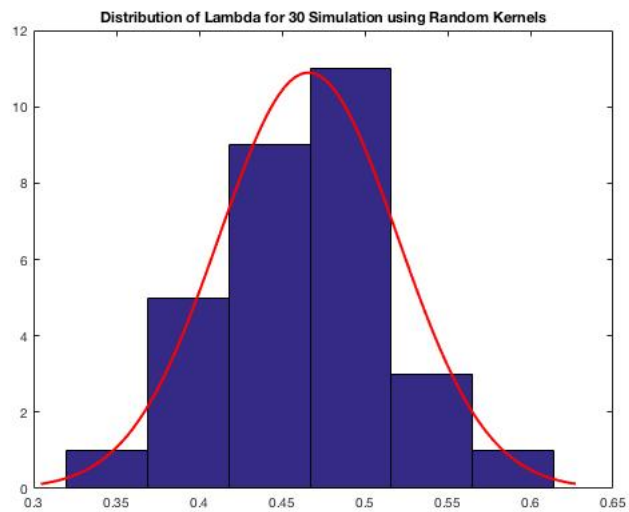


**Figure 2.11** Confined uniformly distributed population following two dispersal events with advection velocity set to 0.6

One of the primary purposes for developing this tool is to simulate population dynamics, which may suggest a particular population's tendency towards persistence or extinction. The population depicted in Figure 2.12 tends to extinction as the model lacks a function incorporating growth (i.e., per capita growth = 1). Populations that disperse without growth face extinctions within their bounded habitat as portions of the population flow out of the domain or die out. Previous studies which sought to examine population dynamics by integrodifference equations used analytical solutions which invoked the results of Equation 1.15 and these studies required fixed kernels. Under the same construction as Equation 1.15, we can simulate the long-term behavior of the system by simulating iterative calculations of  $\Lambda$ , as displayed in Figure 2.12.

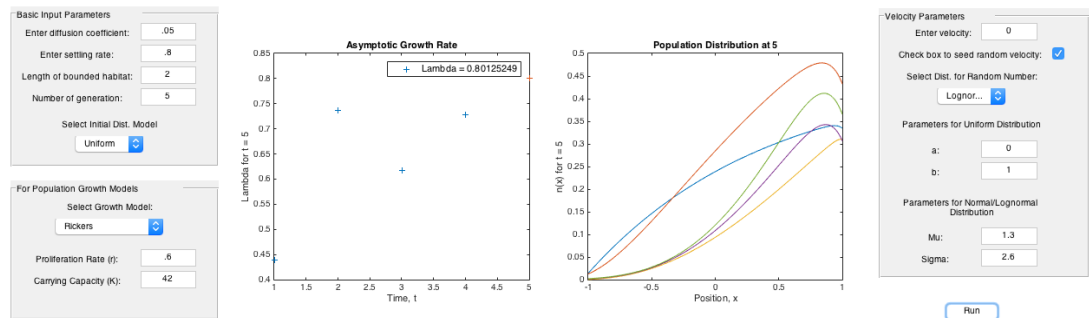


**Figure 2.12** Asymptotic growth rate of initially uniformly distributed population with no growth

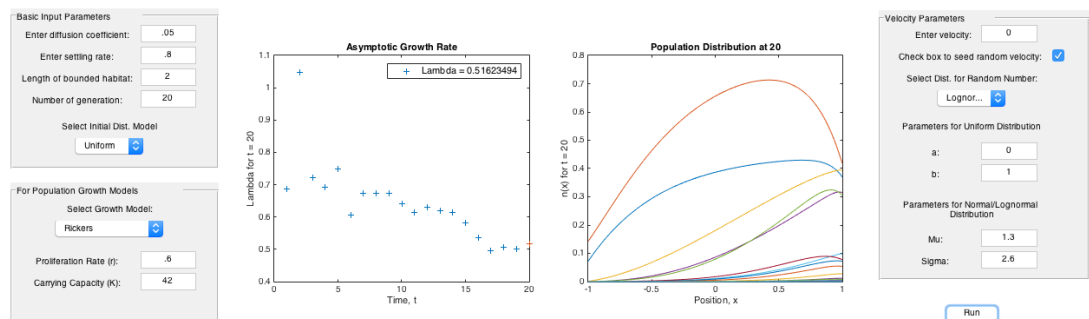


**Figure 2.13** Histogram and distribution fit of  $\Lambda$  values for 30 simulations of population dynamics for a uniformly distributed population using Ricker's growth model and random velocity based on a lognormal distribution

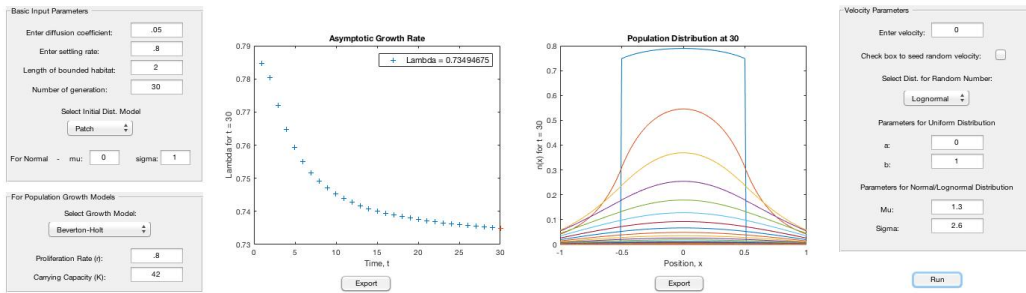
## 24 Chapter 2: A MATLAB/Simulink Tool for Exploring Integrodifference Population Models



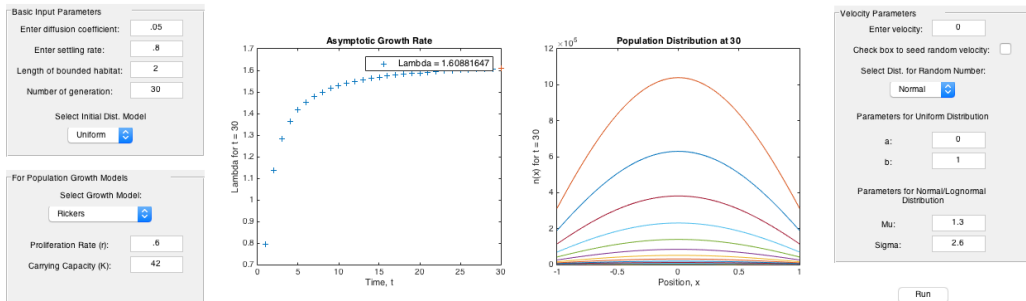
**Figure 2.14** Population dynamics after five time steps for uniformly distributed population using Ricker's growth model and random velocity based on a lognormal distribution



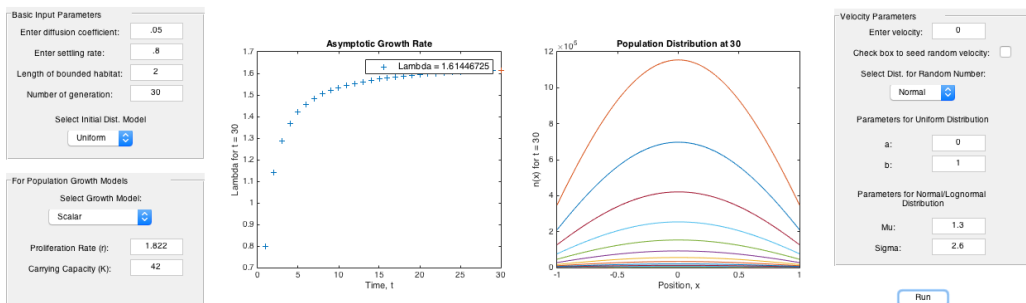
**Figure 2.15** Population dynamics after twenty time steps for uniformly distributed population using Ricker's growth model and random velocity based on a lognormal distribution



**Figure 2.16** Population dynamics after thirty time steps for uniformly distributed population contained within a larger bounded domain using Beverton-Holt's growth model under no advection



**Figure 2.17** Population dynamics after thirty time steps for uniformly distributed population using nonlinear Ricker's growth model under no advection



**Figure 2.18** Population dynamics after thirty time steps for uniformly distributed population using linearized form of Ricker's growth model based on  $f'(0)$  under no advection

Another purpose for developing this tool is to enable modelers to numerically uncover model solutions that were previously unexplored. We examine the numerically estimated values for  $\Lambda$  in 30 runs simulating population dynamics starting with a uniformly distributed population, with growth defined by Ricker's model and dispersion generationally defined by random advection based on a lognormal distribution. We allowed each simulation to reach 100 time steps. On average, these simulation converged to a lambda value of  $0.4660 \pm 0.0538$ , and appears to be convergence in accordance to a normal distribution centered around that mean with a slight right skew (Figure 2.13). In Figure 2.14 and 2.15, a population was also modeled using random dispersal kernels to provide a more realistic simulation of the stochastic nature of unidirectional advection in stream-like environments. In Figure 2.14 - 2.16, population dynamics were simulated using integrodifference equations containing nonlinear growth. Figure 2.18 allows the user to compare the population dynamics using the linearized growth model, but holding constant the initial distribution and all other parameter settings of Figure 2.17. All of these cases have yet to be well explored by mathematicians and ecologists alike.

## Chapter 3

# Chapter 3: Conclusion

In conclusion, we have developed a tool for the exploration of numerical solutions to complex integrodifference population dynamics. We have studied the tool's ability to assess various scenarios, ranging from the dispersal success function with no advection to population models with nonlinear growth and random kernels. We have illustrated the possibility of similar long-term behavior between linearized and nonlinear models. We also briefly examined the convergent behavior of  $\Lambda$  for population models using random kernels. All in all, integrodifference population models show tremendous ability and versatility in analyzing species population with discrete growth and dispersal stages. This tool allows users to explore a robust set of more realistic population models and maintains the capacity to be further developed for examining even more intriguing population models, with the ultimate goal of assisting ecologists in the preservation of biodiversity and the conservation of biological communities.

### 3.1 Future Work

The performance of the tool can be further optimized in a number of ways. Using the *tic - toc* stopwatch timer to measure performance based on internal time expenditure, 30 runs of 300 generation using the default parameters for a population that was initially uniformly distributed with growth and dispersion based on a linearized model and random dispersal kernels took an average of  $54.9777 \pm 9.0349$ . The fastest run lasted 43.6460 seconds and the slowest run lasted 72.0865 seconds.

When applying and analyzing the MATLAB performance profiler, the

highest performance cost was found in conducting the integration using MATLAB's built-in numerical integration function. It makes a call to MATLAB's codetools' *functionhintsfunc.m* that consumes 42.3 percent of the main callback function's performance time. Built-in functions can be more optimally used by considering good programming practices, such as preallocation, vectorization, and modular programming. Preallocation involves predefining the maximum amount of space to an array to circumvent dynamic resizing, which slows performance. Vectorization involves avoiding loops if a method or operation can be applied to a vector of objects or values. While preallocation and vectorization was considered and utilized in the process of coding this application, those means of optimization along with modular programming can be used to a greater extent to enhance performance. MATLAB also provides a parallel computing toolbox, which would enable optimal multi-core processing that has yet be explored.

The tool has yet to be used for significantly exploring questions regarding random kernels, nonlinear versus linear growth models, or domains outside of one-dimension space. Using this tool to explore such scenarios should offer new insight relating to integrodifference population models, and shifts the modeling paradigm closer and closer to modeling the reality observed in nature.

# Source Code

Available for download at:

[https://github.com/kendama/ipm\\_gui](https://github.com/kendama/ipm_gui)





# Bibliography

C. J. Collins, C. I. Fraser, A. Ashcroft and J. M. Waters, Asymmetric dispersal of southern bull-kelp (*Durvillaea antarctica*) adults in coastal New Zealand: Testing and oceanographic hypothesis, *Molecular Ecology*, 19 (2010), 4572-4580.

R. Dirzo and P. H. Raven, Global state of biodiversity and loss, *Annual Review of Environment and Resources*, 28 (2003), 137-167.

J. Jacobsen and T. McAdam, A Boundary Value Problem for Integrodifference Population Models with Cyclic Kernels, *Discrete and Continuous Dynamical System Series B*, 19 (2014), 3191-3207.

J. Jacobsen, Y. Jin, and M. A. Lewis, Integrodifference models for persistence in temporally varying river environments, *Journal of Mathematical Biology*, 70 (2014), 549-590.

F. Lutscher, E. Pachepsky and M. A. Lewis, The effect of dispersal patterns on stream populations, *SIAM Review*, 47 (2005), 749-772.

D. Pearce, An economic approach to saving the tropical forests, in *Economic Policy Towards the Environment*, (ed. D. Helm), Blackwell Publishers, (1991), 239-262.

D.C. Speirs, W.S.C. Gurney, Population persistence in rivers and estuaries. *Ecology*, 82 (2001), 1219-1237.

R. W. Van Kirk and M. A. Lewis, Integrodifference models for persistence in fragmented habitats, *Bulletin of Mathematical Biology*, 59 (1997), 107-137.

D. S. Wilcove, D. Rothstein, J. Dubow, A. Phillips, E. Losos, Quantifying Threats to Imperiled Species in the United States, *Bioscience*, 48 (1998), 607-615.