Deterministic and Stochastic Reaction-Diffusion Models in a Ring

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Abstract

It is known that Fisher's equation in one dimension supports traveling wave solutions in an unbounded domain. It is easily shown that solutions become stationary on a ring. In this study we divide a bounded domain into a large number of patches capable of supporting local populations. It is assumed that the local dynamics are governed by a logistic equation and that individuals disperse, but only to their nearest neighbors. Furthermore, it is assumed that local population growth and dispersal are stochastic events. Simulations are used to compute the rates of convergence to the stable states and our results are compared to those obtained analytically from Fisher's model on a ring.

1 Introduction

All organisms are discrete entities that normally interact with either neighboring species of their own or different species. This behavior is mostly seen in sessile organisms, such as terrestrial plants, marine macro organisms etc. Nevertheless, motile organisms also have their impact in the area in which they move. In our case, we do not deal with a day to day movement, but rather a global dispersal of individuals. Even though it seems interactions and dispersal between species and individuals in a space are a trivial solution, it has important consequences. In this project, we see that mathematical models can be used to include population dynamics to account for interaction and dispersal of individuals.

The concept of diffusion has been vastly studied in the past. Diffusion could broadly be described as the tendency for a group of particles initially concentrated near a point to spread out in time, gradually occupying an even larger space. A more general definition is exploring diffusion as a phenomenon by which the particle group as a whole spreads according to the irregular motion of each particle. The fundamental importance of the spatial distribution of organisms, emphasized by Skellam in his classic work, has recently been given high recognition in the literature of theoretical biology (see Okubo 1980).

The classic theory of diffusion was founded more than one hundred years ago by the physiologist A. Fick. The equation used by him is

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} \tag{1}$$

where D is the diffusion coefficient and N is the concentration of matter. Leading to a further step is the analysis of an interactive population diffusion system, also referred to as reaction diffusion. Such mechanism was proposed by Turing in one of the most important papers in theoretical biology and applied mathematics. These types of systems have been widely studied since 1970. The reaction diffusion equation is obtained when reaction kinetics (such as births and deaths) and diffusion are coupled. In a simple one-dimensional scalar case, this equation is,

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + f(N) \tag{2}$$

where N is the concentration, $f(N)$ is the demographic function and D is the diffusion coefficient.

One of the most popular cases of the nonlinear reaction diffusion equation was suggested by Fisher as a deterministic version of a stochastic model for the spatial spread of a favored gene in a population. Fisher's equation is an extension of the logistic growth population model. This is

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN\left(1 - \frac{N}{K}\right) \tag{3}$$

where K and D are positive. Note that, even though (3) is now referred to as Fisher's equation, it was first reported by Luther, (see Okubo,1980).

In an ecological context, "reaction" can be defined as the process of population change or species interactions in the absence of dispersal whilst diffusion describes the movement of individuals . Thus the reaction part of the reaction diffusion model could be the logistic equation, or any growth function. Looking at a given population divided into patches, we suppose that individuals have the probability of leaving the patches in any given interval of time. In section 2 of this paper, we define the deterministic model and the stochastic model is discussed in section 3. After discussing our models, we compare the results from the computer simulations to that of the deterministic results. Also the speed of propagation of the wave front is computed from both the stochastic simulations and the deterministic model. The results from each approach are recorded and then compared. The models are then used to see the importance of local fluctuations on the dynamics of a population.

2 Deterministic Model

The most common mathematical approach to spatial population models involves the analysis of the reaction diffusion equation. The reaction term is usually described by an exponential growth function or the logistic equation among others, while the diffusion term describes the movement of the individuals. Also the diffusion term corresponds to a simple passive spread. One of the most known equations and the one on which this paper will be focused is Fisher's equation. Fisher's equation is the combination of passive diffusive spread and the logistic growth of a population and it is given by

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN\left(1 - \frac{N}{K}\right) \tag{3}$$

where D is the diffusion coefficient, r is the intrinsic growth rate, K is the carrying capacity per unit of area, and N is the density of individuals at position x at time t.

Equation (1) for an unbounded domain gives traveling wave solutions (see Okubo, 1980). Let us now consider a population undergoing logistic growth with diffusion on a ring with a Gaussian normal distribution as the initial condition. We will first look for equilibrium points. Let

$$\frac{\partial N}{\partial t} = 0.$$

Since the equation does not depend on t anymore, then it can be written as

$$D\frac{d^2N}{dx^2} + \left(rN - \frac{r}{K}N^2\right) = 0.$$

Let

$$g = \frac{dN}{dx} \text{ and } g' = \frac{d^2N}{dx^2}$$

substituting it back into the previous equation yields

$$Dg' + rN - \frac{r}{K}N^2 = 0,$$

and writing the above equation in a matrix form we obtain

$$\begin{pmatrix} g' \\ \frac{dN}{dx} \end{pmatrix} = \begin{pmatrix} \frac{r}{kD}N^2 - \frac{r}{D}N \\ g \end{pmatrix}.$$

In order to find equilibria we let $g' = 0$ which leads to

$$\frac{r}{kD}N_\infty^2 - \frac{r}{D}N_\infty = 0,$$

and solving for N_∞ we obtain

$$\frac{r}{D}N_\infty\left(\frac{N_\infty}{K} - 1\right) = 0$$

Hence, the equilibrium points are $N_\infty = 0$ and $N_\infty = K$. Now we will analyze the stability of the nontrivial equilibrium of equation (3) by using the perturbation method around its equilibrium point $N_\infty = K$ (see Appendix). After the perturbation analysis the equation becomes

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} - rn. \tag{4}$$

In order to solve the equation above, we will transform it into a simpler equation. The important point is that, if there was no diffusion within the population ($D = 0$), then the population at each point x_0 would 'damp'exponentially to 0 according to

$$n(x,t) = n(x_0, 0)e^{-rt}.$$

Because of this observation, take

$$n(x,t) = e^{-rt}w(x,t),$$

where $w(x,t)$ would represent the population due to diffusion only. Substituting this expression into (4) we arrive at

$$\frac{\partial w}{\partial t} = D\frac{\partial^2 w}{\partial x^2}.$$

Solving this equation using the separation of variables method and applying the given boundary conditions we have:

$$w(x,t) = \sum_{m=1}^{\infty} B_m e^{-m^2 Dt}\cos(mx),$$

where

$$B_m = \frac{1}{\pi}\int_0^{2\pi} \phi(\xi)\cos(m\xi)d\xi,$$

where $\phi(x)$ is the initial distribution (which we assume to be close to K) and hence, the solution of problem (4) is

$$n(x,t) = e^{-rt}\sum_{m=0}^{\infty} B_m e^{-t(Dm^2)}\cos(mx).$$

However, it is easy to see that as $t \to \infty$, $n(x,t) \to 0$. Now

$$N(x,t) = n(x,t) + K,$$

which implies that the population perturbed about K will always converge to K, that is

$$\lim_{x\to 0} N(x,t) = K.$$

In addition to the perturbation method, a simple application of the maximum principle can be used to find that there are no non-constant periodic steady state solutions of equation (3) (see Appendix). Therefore, Fisher's equation supports constant solutions on a bounded domain in contrast to traveling wave solutions on an unbounded domain.

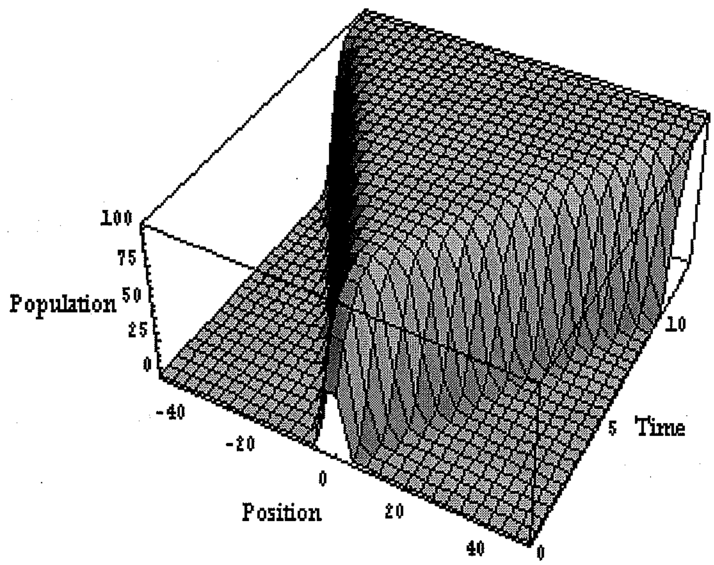

Figure 1: This figure shows how the population starts out as a Gaussian normal distribution, however, as time increases it converges to its carrying capacity which in this case is 100.

As we mentioned previously, with a large diffusion, our model would behave as though on an unbounded region where the solutions are traveling waves, and where the speed of propagation is given by the minimum velocity, that is $C_m = 2\sqrt{rD}$. It is important to see that the minimum velocity of propagation is equal to the ultimate speed of propagation.

3 Stochastic Model

In terms of randomness, diffusion can be defined as "a basically irreversible phenomenon by which matter, particle groups, population, etc., spread out within a given space according to individual random motion" (Okubo 1980). In our stochastic model, the dispersion process is based on a simple random walk in one dimension, and this random walk is performed by a group M of particles initially distributed in a certain pattern such as a normal distribution or equally concentrated in a certain number of patches. Each particle may either move to the left or to the right in fixed steps with the same probability of $\frac{1}{2}$. The space where the population is placed consists of a ring divided in a certain number of identical habitat patches equally connected to each other. The local dispersion, that is, movement within the same patch, is not relevant for this work: Rather we are interested in the global dispersion of individuals, which is the movement of an individual to the right or left patch. Only two events are involved in the dispersion process: these are the dispersion to the right, and the dispersion to the left.

The probability $P(m,n)$ that a particle will reach point m after n steps involves a birth-death process governed by a logistic growth, and it is given by (Murray 1989)

$$P(m,n) = \left(\frac{1}{2}\right)^n \frac{n!}{(\frac{(n+m)}{2})!(\frac{(n-m)}{2})!}.$$

The following are the parameters used in the stochastic model below:

$b =$ per-capita birth rate,

$\mu_0 =$ death rate at 0 density,

$\mu_1 =$ density-dependent death rate,

$K =$ carrying capacity,

$DR =$ dispersal rate to the right,

$DL =$ dispersal rate to the left,

$T =$ total number of patches,

$M =$ total number of individuals,

$N_i(t) =$ population at time t.

The logistic growth can be written as:

$$\frac{dN(t)}{dt} = bN(t) - (\mu_0 + \mu_1 N(t))N(t) = rN\left(1 - \frac{N}{K}\right)$$

where $r = b - \mu_0$, and the carrying capacity K is given by $\frac{b-\mu_0}{\mu_1}$.

In the stochastic model, one of four events takes place in each patch at time t. Therefore, the total number of events in a system of T patches is

$$T_E = 4T.$$

The total population M is initially distributed in each patch with a certain pattern, letting $N_i(t)$ be the population at time t in patch i.

EVENTS	**EFFECT**	**TRANS. PROB.**
Birth $P(i)$	$N(i) \rightarrow N(i) + 1$	$\frac{BN(i)}{\theta}$
Death $P(i)$	$N(i) \rightarrow N(i) - 1$	$\frac{(\mu_0+\mu_1 N(i))N(i)}{\theta}$
Disp. to the Right D_R	$N(i) \rightarrow N(i) - 1$ $N(i+1) \rightarrow N(i+1) + 1$	$\frac{D_R N(i)}{\theta}$
Disp. to the Left D_L	$N(i) \rightarrow N(i) - 1$ $N(i-1) \rightarrow N(i-1) + 1$	$\frac{D_L N(i)}{\theta}$

Figure 2: These are the probabilities at which the events occur, where $1 \leq i \leq T$ and θ is the sum 4of all the rates.

A) Normal distribution.

The total population M is distributed according to the normal distribution, given by

$$f(x) = \frac{M}{\sqrt{2\pi}\sigma} e^{-\frac{(x-\mu)^2}{2\sigma^2}},$$

where σ^2 is the variance, x is the patch number, μ is the mean position, and M is the total number of individuals.

B) Dirac Delta distribution.

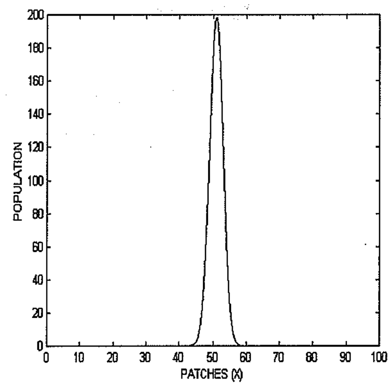

Figure 3: Population with a normal distribution over a linear space

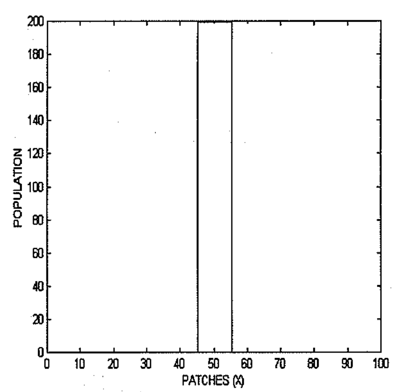

Figure 4: Population distributed uniformly over a number of patches

The total population is distributed in one patch.
The state space of our stochastic model is given by

$$N(t) = [N_1(t), N_2(t), N_3(t), ...N_T(t)]$$

where $N_1(t), N_2(t)$ and so forth specify the current population in each patch. The following are the events that may occur in each patch:

1. Birth of an individual
2. Death of an individual
3. Dispersion to the right
4. Dispersion to the left

As shown in the table in Figure 2, the probability that the event j takes place in the patch i is given by

$$\frac{R_{ij}}{\sum_{i=1}^{T}\sum_{j=1}^{4} R_{ij}},$$

where R_{ij} is the rate at which the event j will take place in the patch i. The time to the next event is an exponential random variable given by

$$\delta t = -\frac{\log(u)}{\theta},$$

where $\theta = \sum_{i=1}^{T}\sum_{j=1}^{4} R_{ij}$ is the sum of all the rates and u is a uniform random number (0,1).

4 Computer Simulations

Using the stochastic model we generated a series of simulations with the aid of a computer program written in Visual Basic (see Appendix). Different parameter values were used in our simulations. We fixed the values of the birth rate ($b = 4$), the carrying capacity ($K = 100$), the initial population ($M = 1000$), and the number of patches ($N = 100$), and only varied the values of the initial death rate and the dispersal rate between 0 and 4. The simulations were computed using two different initial conditions: one was a Gaussian normal distribution and the other was a Dirac delta function positioned in only one patch.

From the simulation results, we conclude that if we keep the dispersal rate constant and we increment the value of μ_0 the population tends to take longer to converge to the carrying capacity. In addition, the fluctuation decreases due to the fact that there are fewer people as μ_0 rises. However, when μ_0 is kept constant and dispersal rate is increased, dispersion increases throughout the ring. Therefore, the population reaches its steady state faster, though the population fluctuates about its equilibrium point due to local stochasticity. Graphical results and their analysis are found in Figures 5 through 12. The stochastic and deterministic graphs are plotted on the same set of axes, to facilitate the comparison. The plots reflect similarities between both results. In general, as time increases, the population approaches stability. The smooth graphs correspond to the deterministic solutions.

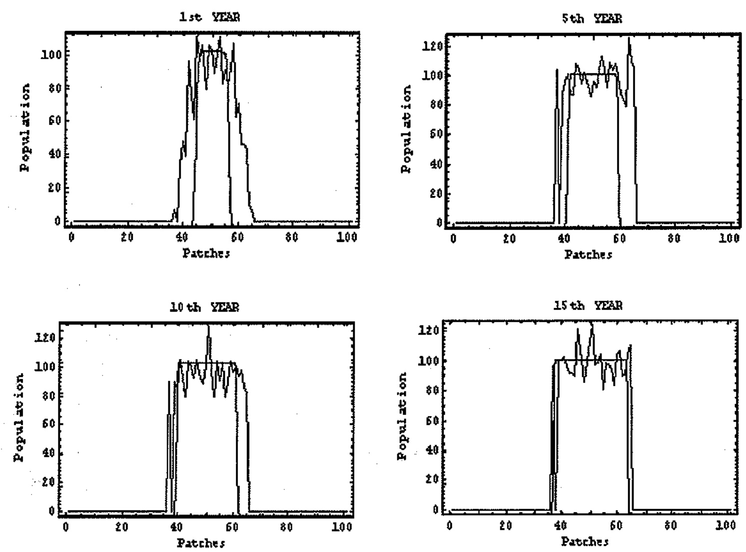

Figure 5: Population distribution at $\mu_0 = 1$ and $D = 0$.

It can be seen from the graphs that as time increases the population does not disperse and it only experiences logistic growth with an intrinsic growth rate equal to $b - \mu_0 = 3$, due to the fact that the dispersal rate is 0 (see Fig.5).

As time increases, the population grows logistically and also disperses.

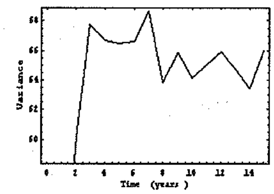

Figure 6: Since there is no dispersion the variance over time remains stable as the graph shows.

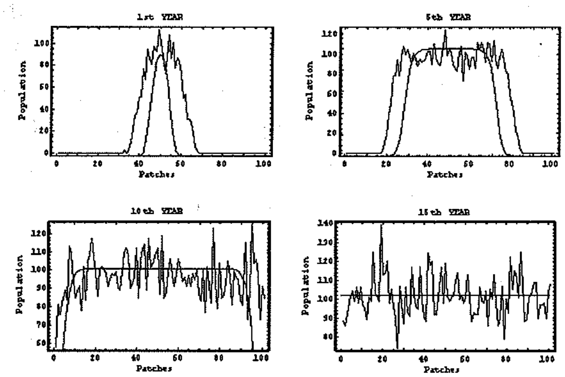

Figure 7: Population distributed at $\mu_0 = 1$ and $D = 2$.

At the 5th year we can see how the population has considerably dispersed and at the 10th year the population has almost dispersed throughout the whole ring and the carrying capacity has been reached. At the 15th year the population has already reached its equilibrium at the carrying capacity (Fig. 7). This conclusion is supported by looking at the plot of variance versus time (Fig. 8). The graph shows that the equilibrium is reached shortly after the 10th year.

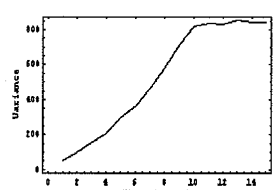

Figure 8: Variance versus time for a dispersed population

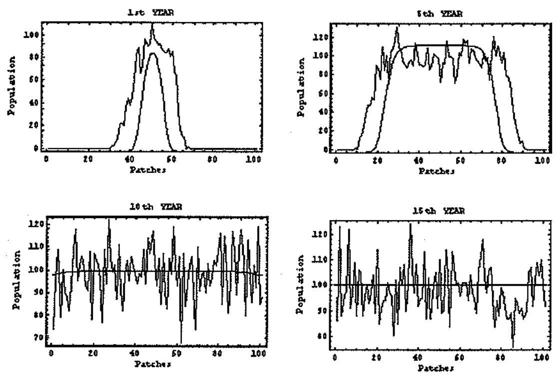

Figure 9: Population distributed at $\mu_0 = 1$ and $D = 3$.

As expected, the population in this case Figure 9 reaches its equilibrium in a shorter period of time than the one in Figure 7. The respective variance versus time graph Figure 10 shows that the equilibrium is reached at the 8th year, and after the 8th year the variance is stable.

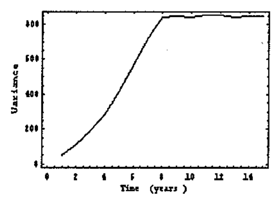

Figure 10: Variance versus time for a dispersed population

In the last example, the population grows logistically when the intrinsic growth rate is equal to 1 and disperses at a rate of 4 (Fig. 11). It can be observed how the variance stabilizes beyond the 15th year (Fig. 12). In fact, the stability all around the ring is reached at the 16th year and the population in each patch fluctuates around the carrying capacity ($K = 100$).

5 Speed of Propagation

As we have seen, a population that experiences logistic growth and dispersion in a ring eventually reaches its equilibrium at the carrying capacity (K). If we consider a ring composed of a large number of patches and

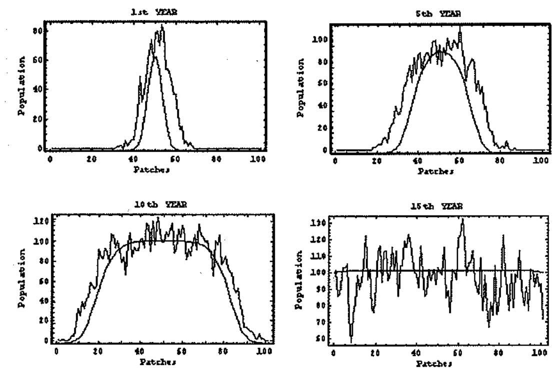

Figure 11: Population distributed at $\mu_0 = 3$ and $D = 4$.

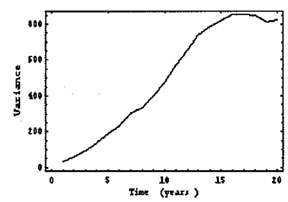

Figure 12: Plot of variance versus time for a dispersed population

a population is introduced to a localized region of the ring, the population follows a wavelike solution that expands in each direction until both wave fronts meet at a point of the ring and eventually the population reaches a steady state. In front of the wave is an uninvaded territory of the ring, and behind the wave the population is at the carrying capacity. In an unbounded domain, the rate at which the wave fronts propagate has been proved to be $2\sqrt{rD}$, where r is the intrinsic rate of increase of population growth (see Appendix). The same rate is applied to our bounded domain in order to know how fast the population goes to the steady equilibrium, considering a ring with a high number of patches and the fact that the wave front propagates in each direction without knowing that the domain is bounded. In order to compute the speed of propagation of the wave front for our stochastic model, the time at which the wave front reaches each of the patches is recorded and by using the least squares method we could find the slope - which is the speed of propagation of the wave front - of the line that best fits the points representing the patch number reached by the wave front at a certain time. Different thresholds were used to calculate the speed of propagation and were compared to the deterministic speed. However, the best approximation was obtained when the threshold was equal to 20% of the carrying capacity. The average of the results was calculated to get an accurate approximation of the solution.

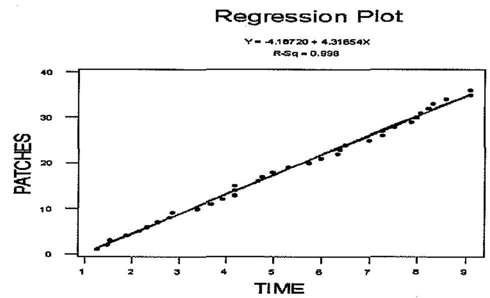

Figure 13: Parameters used: $r = 3$ and $D = 2$.

The speed of propagation of the wave fronts given by the stochastic simulations for this particular parameter set, is 4.32. However, using the same parameters to evaluate the rate using the deterministic model gives 4.89.

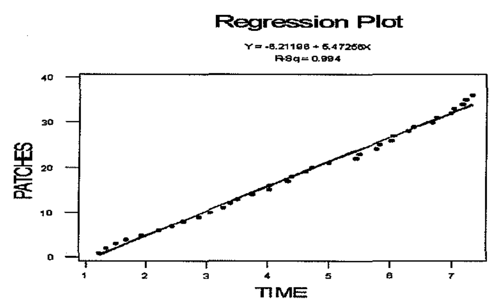

Figure 14: Parameters used: $r = 3$ and $D = 3$.

The speed of propagation of the wave fronts given by the stochastic model for this case is 5.46. Nevertheless, the value of the rate of convergence given by the deterministic model is 6.

After several trials of the stochastic simulations using different values for dispersal rates (D) and intrinsic growth rate (r), we obtained a slower speed of propagation from about 86% to 89% of the deterministic result.

6 Qualitative Explanation

In the stochastic model the dispersion occurs with discrete units of individuals, in contrast to the deterministic model, where dispersion occurs continuously and there is always movement of material. Therefore, a slower speed of propagation can be expected in the stochastic model due to the fact that you only have movement of a whole unit.

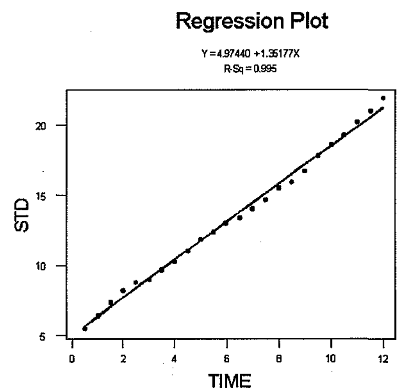

Figure 15: Parameters used: $r = 2$ and $D = 1$.

The above pictures show that the spatial variance and standard deviation in our stochastic model are quadratic and linear respectively over time.

7 Conclusions

The time that the population takes to reach the steady state depends on several factors, such as initial distribution, dispersal rate, intrinsic growth rate, carrying capacity and number of patches. When the total population is concentrated in one patch, it takes longer to converge to its stability than when the population is distributed normally along the ring. The intrinsic growth rate and the dispersal rate play a crucial role. The greater the values of r and d, the faster the constant state is reached. If the carrying capacity and the number of patches is enlarged then, more time will be needed to attain the steady state.

When the population is subjected to only diffusion, it spreads throughout the ring and the spatial variance increases linearly over time. On the other hand, when the population is subjected to both diffusion and reaction with a logistic growth, the spatial variance is quadratic over time and the standard deviation is linear while the wave fronts at each direction have not met each other. Once the population has spread all over the ring and is steady at the carrying capacity, the variance reaches a steady state and no longer increases.

The speed of propagation obtained from the stochastic model is slower than that computed from the deterministic model (from about 85% to 89% of the deterministic result).

8 Future Studies

Even though in our project we chose a constant dispersal rate for all the patches we could consider a dispersal rate that varies in each of the patches. For instance, the dispersal rate may be a linear function of local density or position, or any other function, along the patches.

Another option to explore could be varying the carrying capacity of the patches and considering individuals that disperse to the right or to the left with different probabilities, which depend on the number of individuals and on the carrying capacity of the patch.

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A Perturbation Analysis

We will solve Fisher's equation

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN(1 - \frac{N}{K}) \tag{3}$$

Using the perturbation method, we first let

$$N(x,t) = n(x,t) + N_\infty,$$

where we asssume $n(x,t)$ is small. Thus

$$\begin{aligned}
\frac{\partial n}{\partial t} &= D\frac{\partial^2 n}{\partial x^2} + r(n + N_\infty)(1 - \frac{n + N_\infty}{K}) & (5)\\
&= D\frac{\partial^2 n}{\partial x^2} + r(n + N_\infty) - \frac{r}{K}(n + N_\infty)^2 & (6)\\
&= D\frac{\partial^2 n}{\partial x^2} + r(n + N_\infty) - \frac{r}{K}(n^2 + 2nN_\infty + N_\infty^2). & (7)
\end{aligned}$$

Since n is small, we can neglect any nonlinear terms. Thus the previous equation can be written as

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} + r(n + N_\infty) - \frac{r}{K}(2nN_\infty + N_\infty^2).$$

Substituting the equilibrium point $N_\infty = K$ leads to the equation

$$\frac{\partial n}{\partial t} = D\frac{\partial^2 n}{\partial x^2} - rn.$$

A.1 Maximum Principle

Theorem A.1 *There are no positive non-constant periodic steady state solutions of*

$$\frac{\partial N}{\partial t} = \frac{\partial^2 N}{\partial x^2} + \alpha N - \beta N^2 \tag{8}$$

$$N(0,t) = N(2\pi, t) \tag{9}$$

Proof: Let $N(x) > 0$ and solve the steady state problem

$$\frac{\partial^2 N}{\partial x^2} + \alpha N - \beta N^2 = 0 \tag{10}$$
$$N(0) = N(2\pi) \tag{11}$$

This is a continuous function on the circle, but every continuous function on the circle achieves a maximum and a minimum. Let $N(x_0) = \max(N)$. Thus

$$\frac{\partial^2 N}{\partial x^2}|_{x_0} < 0, \tag{12}$$

so by (7) $\alpha N(x_0) - \beta(N(x_0))^2 > 0$, which implies $N(x_0) < \frac{\alpha}{\beta}$. Therefore, $\max(N) < \frac{\alpha}{\beta}$.

Similarly, let $N(x_1) = \min(N)$. Then

$$\frac{\partial^2 N}{\partial x^2}|_{x_1} > 0, \tag{13}$$

so by (7) $\alpha N(x_1) - \beta(N(x_1))^2 < 0$, which implies $N(x_1) > \frac{\alpha}{\beta}$.

Thus $\min(N) > \max(N)$, a contradiction, proves the theorem.

A.2 Speed of Propagation

We look for a solution of the reaction diffusion equation which represents a wave of stationary form propagating in the direction of positive x with velocity c. Thus we assume

$$N(x,t) = N(x - ct) = N(\xi) \tag{14}$$

where $\xi = x - ct (c > 0)$.

Substituting (10) into the logistic equation, and observing that

$$\frac{\partial}{\partial t} = -c\frac{d}{d\xi} \text{ and } \frac{\partial}{\partial x} = \frac{d}{d\xi},$$

we obtain the following ordinary differential equation for $N(\xi)$,

$$\frac{Dd^2N}{d\xi^2} + \frac{cdN}{d\xi} + \alpha N - \beta N^2 = 0. \tag{15}$$

By letting

$$g = -\frac{dN}{d\xi},$$

(12) can be cast in the form

$$Dg\frac{dg}{dN} - cg + \alpha N - \beta N^2 = 0.$$

At the point of inflection, $\frac{dg}{dN}$ is positive. If $\frac{g}{N}$ tends to a limit K as N tends to zero, i.e., at the very end of the advancing front, then K must satisfy the equation (Kendall,1948)

$$Dk^2 - ck + \alpha = 0.$$

Since K may tend to neither zero nor infinity, solutions exist only for

$$c^2 \geq 4\alpha D$$

or

$$c \geq 2\sqrt{\alpha D}$$

which guarantees that K has real roots. Fisher suggested that ultimately only the minimum velocity of advance $c_m = 2\sqrt{\alpha D}$, is possible. It is interesting to observe that this minimum velocity of propagation of a logistic population is equal to the ultimate speed of propagation of a Malthusian population; the carrying capacity of the resources, $\frac{\alpha}{\beta} = N_e$, for the logistic population has no contribution to the wave speed. (see Okubo, 1980).

A.3 Stochastic Simulator

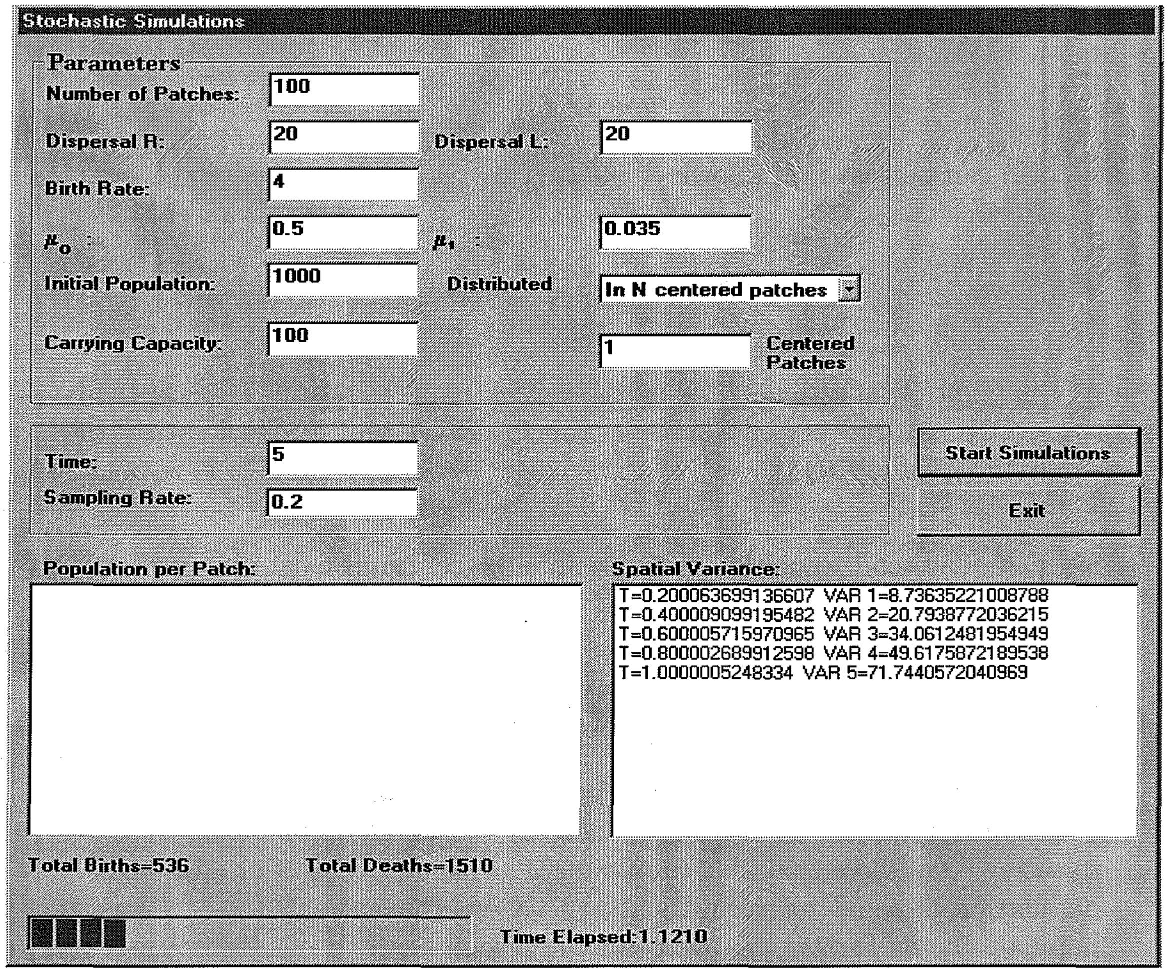

Figure 16: Stochastic Simulator Interface. The program receives from the user a series of parameters. It allows the initial population to be initially distributed as a delta function or as a gaussian distribution. Also, the user can set the time during which the simulation will be running and the output files are stored according to the sampling rate.