Anomalous Biennial Oscillations in a Fisher Equation with a Discretized Verhulst Term

C. Walsh,[1] T. S. Ray,[1, 2] and Naeem Jan[1]

The dynamics of a biological population governed by a modified Fisher equation is studied by means of Monte Carlo simulations. Reproduction of the population occurs at discrete times, while transport caused by diffusion and conduction takes place on shorter time scales. The discrete reproduction, modeled with a set of coupled logistic maps, exhibits phenomena which are not evident in the usual continuum version of the Fisher equation. Several mechanisms for biennial oscillations of the total population are investigated. One of these shows an ordered coupling between random diffusive motion and the chaotic attractor of the logistic map.

1. INTRODUCTION

The dynamics of a population of biological species subject to environmental constraints is an important and challenging problem. The overwhelming number of variables influencing the dynamics makes it difficult to achieve an appreciation of general features. However, in many instances, complex interactions between a species and its environment combine simply to yield a distinct pattern. It has often been found that these patterns may be captured in highly simplified mathematical models of population dynamics. Because the models are quite general, one expects the results to apply to many different species in a variety of ecosystems.

[1] Department of Physics, St. Francis Xavier University, Antigonish, Nova Scotia B2G 1C0, Canada.
[2] Division of Science, Northeast Missouri State University, Kirksville, Missouri 63501.

One such mathematical model which has been applied to population dynamics is the Fisher equation[1, 2]

$$\frac{\partial u(\mathbf{r}, t)}{\partial t} = D\nabla^2 u(\mathbf{r}, t) + u(\mathbf{r}, t)[1 - u(\mathbf{r}, t)] \tag{1}$$

This equation models the spatial movement of the species $u(\mathbf{r}, t)$ as a diffusive process. The second term on the right-hand side of Eq. (1) models the reproduction of the species at position $\mathbf{r}$ as a standard Verhulst process. This term can be broken down further into two terms. The first is linear in $u(\mathbf{r}, t)$, representing the growth of the population in proportion to its present size. The second term is quadratic in $u(\mathbf{r}, t)$, and it has the effect of curtailing population growth. It is meant to model environmental factors which inhibit growth, such as a limited food supply, an increase in the number of predators, and the increased likelihood of epidemics in large populations.

The behaviour of Eq. (1) has been investigated both through analytic techniques and by Monte Carlo simulation.[1−5] Furthermore, extra terms have been added in some studies to model advection of the population (e.g., a school of fish being carried by ocean currents), as well as convection, where the size of the population is proportional to its rate of movement.[4, 5] The results predict that a population initially localized in space expands outward at a constant rate. The presence of a convective term causes an asymmetry in the expansion.

It is important to realize, however, that Eq. (1) is a continuum approximation to population dynamics. This is not necessarily appropriate as a model for many species, especially those which reproduce at specific times during the year. In this case a better model would allow for reproduction to occur at discrete time intervals, with overall movement of the population taking place on much shorter time scales. This leads to important differences in the dynamics, stemming from the fact that the discrete version of the Verhulst term in Eq. (1) is markedly different in its behaviour from the the continuum version.

The discrete Verhulst process, with an additional factor r, is commonly known as the logistic map:

$$u_{t+1} = ru_t(1 - u_t) \tag{2}$$

The logistic map has figured prominently in studies of chaos for systems with few degrees of freedom (see, e.g., ref. 6). Different values of r produce a variety of steady-state properties. When $0 < r < 1$, the logistic map has a fixed point at zero. For $1 < r < 3$, the logistic map has a nonzero fixed

point, which monotonically increases starting from zero over the interval. For $r > 3$, the steady-state attractor is a limit cycle, which first oscillates between two values and, for higher r, becomes quadruply valued. The period doubling in the limit cycle keeps occurring until a critical value of r is reached at which point the attractor becomes chaotic.

This paper studies the effect of a discrete reproductive process in a modified Fisher equation through Monte Carlo simulations. This involves placing logistic maps on a two-dimensional grid and coupling them with diffusive and conductive processes to simulate various terms in the Fisher equation. Coupled maps have been studied in previous work, in the context of turbulence.[7, 8] The present model has some results which are similar, but the biological approach reveals a host of phenomena which do not arise in these other works. These results also do not appear in studies of the continuous Fisher equation. Many, but not all, of the new results are traceable to properties of a single logistic map. They account for steady states where, for example, the population approaches a limit cycle, and also where the system exhibits cooperative effects so that all subpopulations reproduce in tandem. On the other hand, there are some surprising effects that arise from the effect of having many maps, as a result of subtle couplings between diffusive and reproductive processes.

The work presented here applies to many types of species. However, the particular species in the minds of the authors was selected to be the Atlantic cod. Their ocean home was simulated as a two-dimensional lattice. The variable $u(\mathbf{r}, t)$, representing a general biological population, will be referred to as a cod population for the remainder of the paper.

2. THE MODEL AND SIMULATION DETAILS

The modified Fisher equation used in the simulations is given by

$$\frac{\partial u(\mathbf{r}, t)}{\partial t} = D\nabla^2 u(\mathbf{r}, t) + \mathbf{g}(u(\mathbf{r}, t), \mathbf{r}) \cdot \nabla u(\mathbf{r}, t)$$

$$+ \sum_{k=1}^{\infty} ru(\mathbf{r}, t)[1 - u(\mathbf{r}, t)] \delta(t - k\Delta t) \tag{3}$$

The δ-functions in the last term on the right-hand side ensure that reproduction only occurs once every time interval Δt. This is called a "year" throughout the rest of the paper, although it is more general.

The effect of the second term is to cause the local population to move according its value and to the properties of the particular region of space. It is meant to model the conduction of the cod according to spatial gradients

in the food supply per number of cod. The function $g(u(\mathbf{r}, t), \mathbf{r}) \cdot \nabla u(\mathbf{r}, t)$ introduces a nonlinearity into the problem, similar to that of the convection term in other work[4, 5] in addition to that in the logistic terms. It is dependent on both the local population and the spatial coordinates. The form chosen appears overly complicated, but is easy to implement in the simulations:

$$g(u(\mathbf{r}, t), \mathbf{r}) = [1/(1 + \exp\{-|\nabla[f(\mathbf{r})/u(\mathbf{r}, t)]|\}) - 1/2] \nabla[f(\mathbf{r})/u(\mathbf{r}, t)] \quad (4)$$

The Monte Carlo simulations were run on a square lattice of size 20×20, representing a region of ocean. A few of the simulations involved a larger lattice of size 80×80. These larger simulations were run mainly to check for finite size effects in the smaller ones.

The simulations are defined as follows. On each lattice site, called a "cell," a population of cod u_i resides, where $0 < u_i < 1$. Here, the subscript i labels the particular cell. The values of u_i are allowed to change through diffusive, conductive, and reproductive processes. Reflective boundary conditions are maintained, so that movement of cod never results in cod entering or exiting the system. These boundary conditions introduce inhomogeneities into the system and fluctuations that occur near the edge may decay more slowly because of the reflective walls than fluctuations that occur near the center of the system. The results presented below are expected to be insensitive to these boundary conditions.

Another variable defined at every cell represents the local food supply, and is denoted by f_i. An additional array is set up identical in size to the first, which stores the distribution of food. The mean value of the food f_m is chosen to be a number on the unit interval. The distribution is uniform about the mean with extreme values $f_m \pm \varepsilon$. The quantity ε is a parameter which can be set externally, and it is called the "food noise". The food distribution once set is fixed for the duration of the simulation. There is no suggestion that the demise of the cod population is related to an inadequate food supply. We have assumed that the food density and its regional variation are controlled by factors other than the cod population, which has a rather limited impact. We are not simulating a prey/predator situation.

The diffusion term in Eq. (3) is implemented in the simulations by means of a random walk. A fraction of the population in a given cell is moved with probability 4/5 to one of its four nearest neighboring cells. No motion may also occur with probability 1/5. The fraction of the population which is moved in a single diffusion step is always αu, where $0 < \alpha < 1$ is an adjustable parameter. This procedure is applied to each cell in the system,

52 times per yearly reproductive cycle (representing a time scale of 1 week between diffusive moves).

The conduction step, representing the second term in Eq. (3), occurs biweekly, or once every two diffusion steps. For each cell, one of the four nearest neighbours is chosen for consideration. The "food density," or food per cod, is computed for both the cell and its selected neighbour. If the food density is lower in the neighbour, no cod moves, and the process stops. If the food density is higher in the neighbour, an amount of cod in the cell is moved to the neighbour. If $y = f_n/u_n - f_i/u_i$ equals the difference in food densities between the cell labelled by i and its neighbour, labelled by n, then the amount of cod depleted in cell i, Δu_i, is found from the following formula for y greater than 0:

$$\Delta u_i = u_i \frac{(1 - e^{-y})}{2(1 + e^{-y})} \tag{5}$$

The cod that is removed from cell i is added to the cod in cell n. This functional form for determining the magnitude of the flow of cod from a lower food density to a cell with a higher food density is somewhat arbitrary, although there are several desirable features. A more appropriate function will be species dependent and should also reflect properties such as local currents, migratory paths, etc. The amount of cod which moves increases monotonically with food density gradient, but Eq. (5) ensures than no more than half of the cod population will migrate from any cell to its neighbour.

Every year, after 52 diffusion steps with 26 intervening conduction steps, the logistic map was applied to each cell to determine the new population of cod. The logistic map parameter r was held constant for some of the simulations. In others, r was set according to the amount of cod and food in each cell. The exact implementation is described in the next section. Unless otherwise stated, all maps are initialized at the onset of the simulation with values between 0 and 1 drawn from a uniform distribution.

3. RESULTS

In the first set of results, the behaviour of the total cod population has been investigated for fixed values of the logistic map parameter r. This implies that the dependence of the reproduction rate of cod on the local food supply is neglected. The understanding gleaned from these studies helps to clarify the more complicated simulations, where r is set for each cell according to the values of f_i and u_i.

Three distinct regimes of the logistic map were selected for the simulation studies with constant r. The first of these is where the logistic map moves toward a nonzero fixedpoint attractor. The logistic map parameter was chosen to be $r = 3/2$, giving a fixed point-solution for the cod population of $1/3$. The other two values of r chosen for study were $r = 3.25$, corresponding to the double limit cycle attractor, and $r = 4.00$, giving a chaotic attractor.

Of primary concern for the simulations with constant r is the effect that diffusion and conduction along the food gradients has on the total population. Without any diffusion or conduction, each cod subpopulation residing in its own cell independently approaches the logistic map attractor. If the attractor is a fixed point, with a value u^*, the total population approaches a value Nu^*, where N is the total number of cells in the system.

3.1. Fixed-Point Regime

In the fixed-point regime, with $r = 3/2$, both diffusion and conduction were observed to depress the mean total cod population. When only diffusive movement is simulated, the total population fluctuates about a fixed mean value which is measurably less than that of a system without diffusion.

The depression of the mean value is a nonlinear effect, which is caused by the stochastic noise associated with the diffusive process. It is commonly observed in many simple systems.[6] In fact, if one adds white noise independently to N uncoupled logistic maps, it can be shown that, for small noise amplitude η with $r = 3/2$,

$$\langle u \rangle = \frac{r-1}{2r} + \frac{r-1}{2r} \left[1 - \frac{2r^2}{(r-1)^2} \eta^2 \right]^{1/2} \tag{6}$$

However, the cod simulations do not obey this equation, because the conservation of cod couples the noise between different maps. Every diffusive move takes a certain amount of cod from one cell and places that same amount in an adjacent cell. Applying the logistic map to each cell causes the maps to approach the fixed-point value $u^* = 1/3$ monotonically from either below or above, depending upon the initial value. Summing all of the maps together to get the total cod population leads to an overall canceling of noise values about the mean. Naively, one may assume that the variance σ in the total population is a measure of the noise η appropriate for a single cell as described by Eq. (6). This is found not to be the case and the use of σ in Eq. (6) leads to a value of $\langle u \rangle$ which is too large compared to that observed for the coupled system.
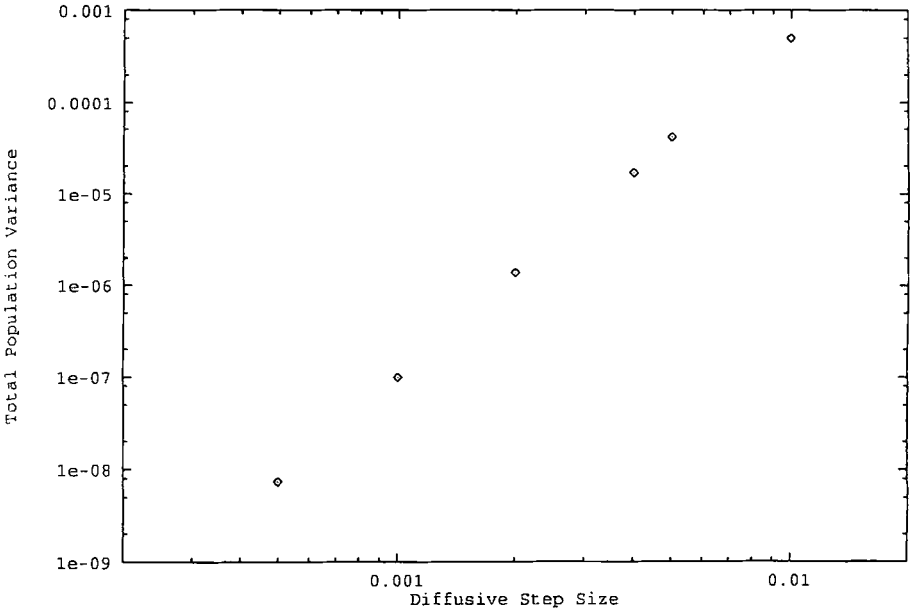
Fig. 1. Variance of the total cod population about the mean versus diffusive step size for fixed $r = 3/2$.

The scaling properties of the variance with the noise amplitude may be determined by imagining a simpler problem in which two logistic maps coevolve. Stochastic noise with a given amplitude is added to each map between time steps. The maps are independent, except that if a given amount of noise is added to one map, the same amount of noise is subtracted from the second map. According to the logistic equation (2), the sum of the two maps in the next time step will differ from twice that of a single map by a term proportional to D^2. This term scales as the standard deviation of the maps from the mean value. The variance should therefore scale as D^4. Figure 1 shows the variance of the total cod population as a function of the diffusive step size. To a high degree of accuracy, the relation $\sigma^2 \sim D^4$ is obeyed, in accordance with the scaling argument for two maps.

Now the effect of the conduction will be considered without diffusion. An amount of food taken from a random sample of a distribution is placed in each cell. The distribution was chosen to be uniform about a mean value equal to 0.8. The allowed values fell between $0.8 \pm \varepsilon$, where ε (called the "food noise") is a variable parameter.

The conduction of cod attempts to make the food density (food/cod) equal in all cells. Even if this is only partially accomplished, the deviation
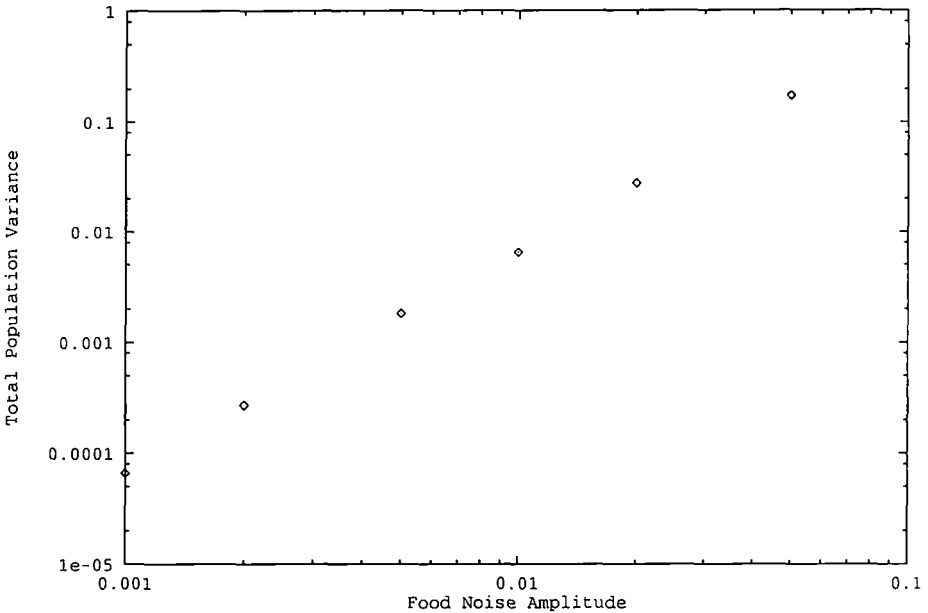
Fig. 2.   Variance of the total cod population about the mean versus food noise for fixed
$r = 3/2$.

of cod in each cell from the mean should scale as the food noise ε. The total population will have a standard deviation which also scales as ε, so that the variance will scale as ε^2. Figure 2 shows the simulation data for conduction without diffusion where $r = 3/2$. The variance is observed to scale as ε^2, as expected.

It is interesting to compare the scatter of points about the mean for the diffusive and conductive simulations. The conservation of cod in the diffusive process reduces the noise to somewhat below the white noise value. However, the observed noise in the total population for the purely conductive process is much smaller (for $\varepsilon \sim D$). This implies that the conductive process is strong enough to drive the system each year to approximately the same state before reproduction. Figure 3 illustrates these observations. The maps $u(\mathbf{r}, t)$ are initialized randomly with values between 0 and 1 drawn from a uniform distribution at the start, $t = 0$. In the case of no diffusion and no conduction, $u(\mathbf{r}, t)$ approaches u^* from below. Maps with values near to 1 flow to near 0 at the next iterate, while those near 0 slowly approach 1/3 from below. Contrast this behaviour with the case of no diffusion but conduction with small "food noise." Conduction under
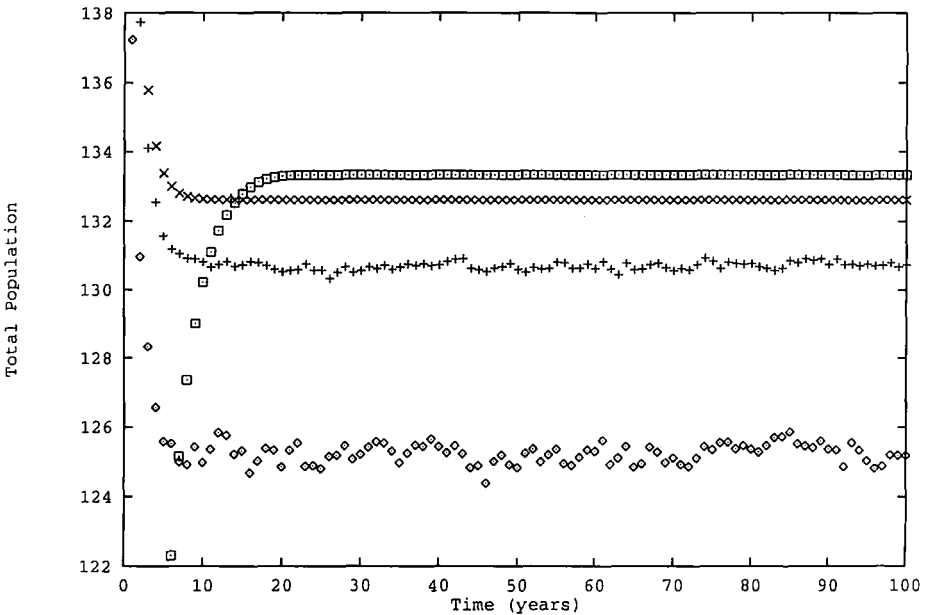
Fig. 3. Total population versus time for fixed $r = 3/2$. Squares: no diffusion or conduction. Crosses: no diffusion, conduction with food noise $\varepsilon = 0.01$. Diamonds: diffusion with diffusive step size $D = 0.1$, no conduction. Plusses: diffusion with $D = 0.1$, conduction with food noise $\varepsilon = 0.01$.

these conditions leads to a cod density u_i in each cell of approximately $1/2$ and hence the coupled system approaches its asymptotic limit from above.

When both conduction and diffusion are turned on with $r = 3/2$, a competition takes place between the two processes. Conduction attempts to drive the system to a state predetermined by the food distribution, where the food per cod is equal in every cell. The diffusive motion tries to randomly move the cod, and thus competes with the quenched disorder of the food distribution. The end result is that the noise in the total cod population is greater than that of a purely conductive process, but less than a purely diffusive one. The effect is exhibited in Fig. 3.

3.2. Double Limit Cycle Regime

When the parameter r is chosen so that the attractor is a double-valued limit cycle, without diffusion or conduction of cod, the total population oscillates between two numbers. The actual values of these numbers
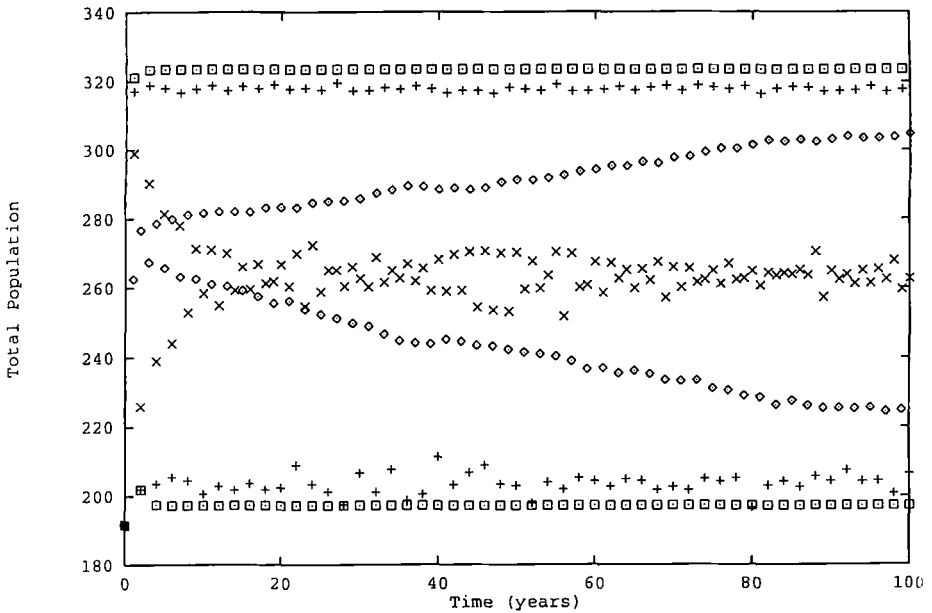
Fig. 4.   Total population versus time for fixed $r = 3.25$. Diamonds: no conduction, diffusion with diffusive step size $D = 0.01$. Crosses: no conduction, diffusive step size $D = 0.1$. Squares: conduction with food noise $\varepsilon = 0.1$, no diffusion. Plusses: both conduction and diffusion with $D = 0.1$, $\varepsilon = 0.1$.

depend upon how many cells are on one particular leg of the limit cycle at a given time, which in turn is a function of the initial conditions. For random initial cell values, the total population will typically oscillate within $N \pm \sqrt{N}$ times the mean of the two limit cycle values.

With a small amount of diffusive motion, the total population behaves in a manner similar to that of a system without noise. There is a small amount of noise detectable, but no other appreciable difference. As the diffusive step size is increased, there is an increasing probability for a map on one leg of the limit cycle to cross over to the other leg. This causes disruptions of the initial pattern so that the system exhibits "bursts" of activity where more maps are consistently on one half of the limit cycle for several cycles. In principle, the average number of years for these bursts to cycle should be determined by the diffusive step size.

The effect of conduction without diffusion is strikingly different. When the noise in the food supply is set to zero, the system "locks" into a state where every map is on the same leg of the limit cycle. The conduction tends to drive the system to a state where the food density is the same in every

cell. If the food noise is small, this will cause the cod in all maps to equalize. As the food noise is increased, the system still exhibits the limit cycle pattern, although there is some noise which is qualitatively similar to case where only diffusive motion is allowed. The mode-locking behavior is similar to that of the coupled circle maps in the work of Stassinopoulis et al.[8]

When both conduction and diffusion of cod are allowed to occur, there is competition between the two processes, as was observed for the case where the attractor is a fixed point. For most values of the diffusive step and the food noise, the system locks up so that all maps are on the same leg of the double limit cycle. There is a certain amount of noise observed, as when the food noise is high for the purely conductive case. Figure 4 shows all three of the above cases.

3.3. Chaotic Regime

When the logistic parameter is fixed at $r = 4.00$, the system is in the chaotic regime, where successive values of the logistic map are statistically uncorrelated. For $r = 4.00$, all values of the logistic map between zero and one are allowed, and they are sampled from a distribution which is approximately uniform (near the endpoints of the unit interval, the distribution is higher than toward the middle). Without any diffusion or conduction, the total population has a mean value of $N/2$. The standard deviation of the total population from the mean depends on N in the usual manner according to the central limit theorem: $\sigma \sim N^{1/2}$.

If diffusion of the cod is introduced without conduction, a remarkable effect occurs in the chaotic regime. Figure 5 shows that the system immediately goes into a state where the total cod population oscillates between two values. Although the behavior is similar in appearance to the double limit cycle, the mechanism is very different. It is caused by a biennial oscillation of the system distribution. Initially, the distribution of maps is uniform between zero and one. When diffusion acts, the cod populations spread out, so that most cells have a population near $1/2$. This results in a distribution for the cod population which resembles a normal distribution, peaked at a value of $1/2$. Next, the logistic map acts and moves the cell populations to higher values near one. This effect occurs because of the way the maps are folded and mixed by the chaotic attractor. Values near $1/2$ are always mapped near the high end of the unit interval when $r = 4.00$.

The next set of diffusive steps have subtle effects. Cell populations are predominantly high, so that random motion of the cod will still give a distribution for the system with a high mean. The shape of this distribution, however, is highly asymmetrical, tapering down toward $1/2$ while
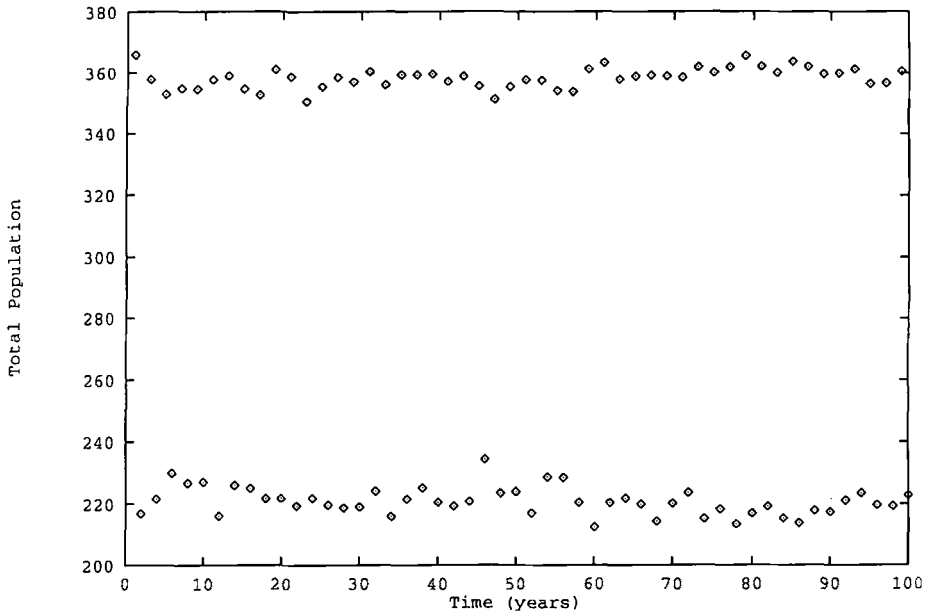
Fig. 5. Total population versus time for fixed $r = 4.00$, diffusion having diffusive step size $D = 0.01$.

remaining large at one. Finally, when the logistic map acts for the second time, the end result resembles a uniform distribution (again caused by the properties of the chaotic attractor), and the biennial cycle can begin anew. This subtle interplay among the logistic map in the chaotic regime, diffusion, the size of the diffusion step, and the constraint that the population is limited to a maximum of 1 is responsible for the stability of the biennial oscillations.

The interplay between the chaotic attractor and the diffusive motion seems to be fairly stable. Larger systems (80×80) show the same behaviour, and are stable for longer times than the smaller systems. This would indicate that instability arises as a finite-size phenomenon. The conductive process also produces a similar effect, as does both conduction and diffusion together.

3.4. Simulation With *r* Dependent Upon the Food Density

In an effort to make a more realistic simulation of cod population dynamics the logistic map parameter *r* was set for each cell as a function

of the food density for the particular cell. This means that r depends generally on the cell coordinates as well as time. The scheme chosen has a certain amount of arbitrariness, but it is designed to model the dependence of reproduction on the food source in a simple manner so that general features of the behaviour will be easy to understand and nontrivial at the same time.

The value of r for each cell was reset every reproductive cycle according to the following procedure:

1. food − cod < 0, $0 < r < 1$ (fixed point equal to zero)

2. $0 <$ food − cod < 0.25, $1 < r < 2.25$ (fixed point greater than zero)

3. $0.25 <$ food − cod < 0.5, $2.25 < r < 3.50$ (limit cycle regime)

4. $0.5 <$ food − cod, $r = 4.00$ (chaotic regime)

For each range, r is selected from a uniform distribution. The first condition models an inadequate food supply to support the cod. The logistic parameter is selected so that the population will rapidly decrease. Condition 2 allows the cell population to approach a nonzero fixed point when there is an adequate food supply. Condition 3 models an abundant food supply, so that the population can grow significantly in short intervals of time. The allowed values of r are within the double and quadruple limit cycle regime. Finally, when the food supply is so large as to not appreciably constrain the population growth, r is set so that the population can change to any value on the unit interval.

In the simulations, the mean value of the food was set to 0.8. Without any food noise or diffusion, the system exhibits an apparently double-valued limit cycle, with a small amount of noise (see Fig. (6). This behaviour is a result of oscillations of the system between the above cases 2 and 3. The biennial mechanism is of a third type, which differs from both the double limit cycle with fixed $r = 3.25$ and the chaos–diffusion interplay. Instead, the maps are reaching a steady state where, at some time step, all of them have values such that $0 <$ food − cod < 0.25. Condition 2 is realized, and all maps are given some $1 < r < 2.25$. Application of the logistic map equation brings all of the cell populations down significantly from their previous values. They now reach a level where $0.25 <$ food − cod < 0.50. This makes all of the maps satisfy condition 3, so that they are subjected to an r value in the double and quadruple limit cycle range. Because they have a low value, they are close to one of the lower branches of the cycles. When the logistic equation is applied once again, the populations will jump to values close to an upper branch of one of the limit cycles. Now, all maps satisfy condition 2, and the process repeats.
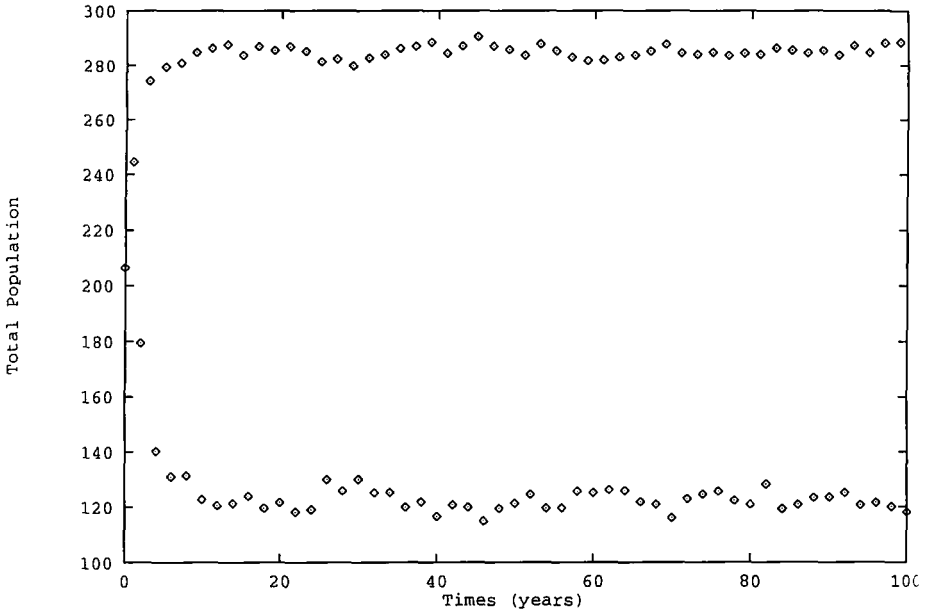
Fig. 6. Total population versus time for r dependent on food per cod in each cell.

The fact that the total system follows the cycle in tandem, rather than a certain percentage existing on each leg, is caused by the same mode-locking phenomenon observed for constant $r = 3.25$. When conduction is allowed to move the cod, they tend to become equal in all cells. One can easily check this by turning the conduction off and noting that the maps become unsynchronized.

4. CONCLUSION

The simulation results presented here for a modified Fisher equation with reproduction occurring after discrete time intervals yield an interesting variety of effects. The results are clearly different and much richer than those of the continuous Fisher equation. In many instances, a biennial oscillation in the total population is observed. Of the three possible mechanisms found here, the one for fixed r in the chaotic regime is perhaps the most surprising. The interplay between random diffusion and the chaotic attractor leads to an ordering of the population which can only be seen in a statistical manner from the behaviour of the population distribution of the cells.

The cycles that appear on a short time scale may also be changed in the long term by transport of the cod. For example, diffusion of cod can eventually interrupt the biennial oscillations in the cases where r is fixed independent of the food supply. This is a possible mechanism for long-time cycles in cod population.

A good area for future work is the effect that harvesting a portion of the population has for discrete reproduction. Preliminary studies indicate that the total population will fall precipitously to zero after several years if a fixed quota above a certain threshold is removed annually, although for quotas below this threshold the total population is relatively high and stable. This could be relevant to the drop in population of many species, including the Atlantic cod as a result of overharvesting.

ACKNOWLEDGMENTS

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