Predator-Prey Models with Diffusion and Time Delay

IRINA KOZLOVA $^1$, MANMOHAN SINGH $^1$ AND ALAN EASTON $^{1,2}$

$^1$ School of Mathematical Sciences, Swinburne University of Technology, Hawthorn, Victoria, AUSTRALIA.
$^2$ Present address:
School of Natural and Physical Sciences, University of PNG, National Capital District, PAPUA NEW GUINEA.

Abstract: Luckinbill [1] demonstrated in a laboratory that populations of Paramecium aurelia as a prey and Didinium nasutum as a predator could exhibit sustained oscillatory behaviour. Harrison [2] modelled this data for testing predator-prey models and successfully demonstrated the general features of the experiment including the sustained oscillations. We have studied the above models in order to determine the effect of diffusion and time delay. It has been shown that the inclusion of these terms gives rise to different growth patterns. It has been observed that while diffusion accelerates the process of growth or extinction of a population, the time delay modifies the process of growth or extinction of the population and the properties of the cyclic steady state. These results can be used to obtain a better fit to field data and improve predictions in the behaviour of predator-prey systems.

Key-Words: Paramecium, Didinium, diffusion, Lotka-Volterra, response functions and time delay.

1 Introduction

This paper is devoted to predator-prey models based on Luckinbill’s [1] experiment with Paramecium aurelia as a prey together with Didinium nasutum as a predator.

Paramecium aurelia is a small unicellular organism of the ciliate genus. It is elongated, ranges in size from 120 to 300 $\mu$m and lives mostly in freshwater ponds, where it feeds on various bacteria, small protozoans, algae and yeasts. Didinium nasutum is also a well-known protozoan ciliate, which lives in freshwater habitats and feeds on other ciliates, especially Paramecium, which is several times larger.

It is actually different in shape from Paramecium, thicker and less oblong, egg-shaped with size 80–170 $\mu$m in length and 60–80 $\mu$m in diameter.

Luckinbill’s [1] experiment with Paramecium aurelia and Didinium nasutum was successful in maintaining oscillatory behaviour because it was conducted in 6 ml of cerophyl medium thickened with methyl cellulose to stabilise the system. This experiment was modelled by Harrison [2] by fitting the parameters in Lotka-Volterra models in order to find the best fit between the selected model and the observed population densities. He used different kinds of functional responses, including re-
sponses with the predator mutual interference, ratio-dependency, Leslie and sigmoid types. He also used a delay component in the predator numerical response. However, he was not completely satisfied with accuracy of the results because the solutions were very dependent on the initial conditions and the population densities fell too low between the cycles. Jost and Arditi [3] noted that different parameters were found for the basic growth and carrying capacity parameters and caution that the approach may not identify the appropriate features of the model. Haefner [4] explains in some detail the reasons for success of the Luckinbill’s experiment. He also underlines the importance of understanding the features of the models selected before the validation process is attempted.

This paper investigates the models used by Harrison with extensions to include spatial dependence. The main point of this paper is to examine the role of the time delay in the numerical response of the predator.

2 Equations

Let \( u(x, t) \) be the prey population density and \( v(x, t) \) be the predator population density. The logistic predator-prey model with inclusion of a predator time delay effect and diffusion consists of the equations

\[
\frac{\partial u}{\partial t} = \rho \left( 1 - \frac{u}{K} \right) u - \omega v f_1(u, v) + d_1 \frac{\partial^2 u}{\partial x^2} \tag{1}
\]

\[
\frac{\partial v}{\partial t} = -\gamma v + \sigma v f_2(u, v) + d_2 \frac{\partial^2 v}{\partial x^2}, \tag{2}
\]

where

\[
f_1(u, v) = f(u(x, t), v(x, t)),
\]

\[
f_2(u, v) = f(u(x, t - \tau), v(x, t)),
\]

\( \rho \) is the specific growth rate of prey in the absence of predator, \( K \) is the carrying capacity of the prey, \( \omega \) is the maximum number of prey that can be eaten by a predator per unit time, \( \gamma \) is the mortality rate of predator in the absence of prey, \( \sigma \) is a conversion efficiency to predator biomass, \( \tau \) is the time delay constant and \( d_1 \) and \( d_2 \) are diffusivity constants. The delay is introduced in the numerical response term in the equation (2) to consider the effect of a time delay on the population densities of the prey and predator. As seen, the population density \( u(x, t) \) is replaced by \( u(x, t - \tau) \), where \( \tau \) is delay term.

All of the computations are carried out over the domain \([-2, 2]\) so that the effect of diffusion can be observed. The boundary conditions applied for this domain are

\[
\frac{\partial u(-2, t)}{\partial x} = \frac{\partial v(-2, t)}{\partial x} = 0,
\]

\[
\frac{\partial u(2, t)}{\partial x} = \frac{\partial v(2, t)}{\partial x} = 0.
\]

In each numerical experiment, we use the initial condition

\[
u_0 = 15 \text{sech}^2(10x), \quad -2 \leq x \leq 2,
\]

\[
v_0 = \begin{cases} 
0, & -2 \leq x < -0.5, \\
6, & -0.5 \leq x \leq 0.5, \\
0, & 0.5 < x \leq 2,
\end{cases}
\]

![Figure 1: Initial conditions for the prey and predator.](image)

This is chosen with \( u \) initially concentrated at the origin in the centre of the domain uniformly occupied by \( v \). It is graphed at intervals \( \Delta x = 0.1 \) in Figure 1.
3 Response Functions and Data Values

In this paper, we use the response functions and associated data values used by [2]. The responses are

1. \( f(u, v) = \frac{u}{\phi + u} \),
2. \( f(u, v) = \frac{u}{(\phi + u)(1 + \beta v)} \),
3. \( f(u, v) = \frac{u}{\phi + u}(1 - (1 + \mu u) e^{-\mu u}) \).

In these equations, \( \phi \) is a saturation constant, \( \beta \) is the predator interference constant and \( \mu \) is a constant. Response function 1 is the standard Holling type 2 response for which \( \phi \) is the half saturation constant, the level of prey at which half of the maximum consumption rate occurs.

There are ten parameters \( (\rho, K, \omega, d_1, \gamma, \sigma, d_2, \phi, \beta \text{ and } \mu) \) to be chosen in the model equations including the response functions. In the calculations below the response parameters \( \mu = 0.107 \) and \( \beta = 0.00728 \) and the carrying capacity parameter \( K = 898 \) are not changed. Diffusion parameters are taken in two sets, \( d_1 = d_2 = 0 \) and \( d_1 = 0.2, d_2 = 0.1 \), to present cases without and with diffusion accordingly. The other five parameters are considered in groups called Data 1, Data 2 and Data 3.

<table>
<thead>
<tr>
<th></th>
<th>( \rho )</th>
<th>( \omega )</th>
<th>( \phi )</th>
<th>( \sigma )</th>
<th>( \gamma )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Data 1</td>
<td>1.85</td>
<td>25.5</td>
<td>284.1</td>
<td>12.4</td>
<td>2.07</td>
</tr>
<tr>
<td>Data 2</td>
<td>1.93</td>
<td>10.76</td>
<td>60.6</td>
<td>8.80</td>
<td>2.90</td>
</tr>
<tr>
<td>Data 3</td>
<td>1.90</td>
<td>5.74</td>
<td>3.44</td>
<td>3.72</td>
<td>2.27</td>
</tr>
</tbody>
</table>

All of the response functions have the general features of having value zero when \( u = 0 \) and increasing toward 1 as the population density of the prey \( u \) increases. Response functions 1 and 2 behave in a similar manner even though the population density in 2 depends on the predator \( v \) as well as the prey. However, for 2 the response is significantly reduced for large values of the predator density.

4 Numerical Calculations

The model equations (1) and (2) are solved numerically using the operator splitting method [5] which has been successfully applied previously by the authors. The differential equation system is split into a pair of non linear reaction equations

\[
\frac{1}{2} \frac{\partial u}{\partial t} = \rho \left(1 - \frac{u}{K}\right) u - \omega v f_1(u, v), \quad (3)
\]

\[
\frac{1}{2} \frac{\partial v}{\partial t} = -\gamma v + \sigma v f_2(u, v), \quad (4)
\]

which are used for the first half of the time step, and a pair of linear diffusion equations

\[
\frac{1}{2} \frac{\partial u}{\partial t} = d_1 \frac{\partial^2 u}{\partial x^2}, \quad (5)
\]

\[
\frac{1}{2} \frac{\partial v}{\partial t} = d_2 \frac{\partial^2 v}{\partial x^2}, \quad (6)
\]

which are used for the second half of the time step.

The numerical method used for the reaction equations and the diffusion equations is the forward Euler scheme. Then equations (3) and (4) become

\[
\bar{u}_{j}^{n+1/2} = u_{j}^{n} + \Delta t \times \left( \rho \left(1 - \frac{u_{j}^{n}}{K}\right) u_{j}^{n} - \omega v_{j}^{n} f_{1}(u_{j}^{n}, v_{j}^{n}) \right), \quad (7)
\]

\[
\bar{v}_{j}^{n+1/2} = v_{j}^{n} + \Delta t \times \left( -\gamma v_{j}^{n} + \sigma v_{j}^{n} f_{2}(u_{j}^{n}, v_{j}^{n}) \right), \quad (8)
\]

where \( u_{j}^{n} \) and \( v_{j}^{n} \) indicate the approximate values of \( u \) and \( v \) at the positions \( x_{j} = -2 + j \Delta x, \ j = 0, 1, \ldots \) and time \( t_{n} = n \Delta t, \ n = 0, 1, \ldots \), and \( \bar{u}_{j}^{n+1/2} \) and \( \bar{v}_{j}^{n+1/2} \) indicate the representative values at the half time step.

Similarly, equations (5) and (6) become

\[
u_{j}^{n+1} = \bar{u}_{j}^{n+1/2} + \frac{d_{1} \Delta t}{\Delta x^2} \times \left( \bar{u}_{j-1}^{n+1/2} - 2 \bar{u}_{j}^{n+1/2} + \bar{u}_{j+1}^{n+1/2} \right), \quad (9)
\]

\[
u_{j}^{n+1} = \bar{v}_{j}^{n+1/2} + \frac{d_{2} \Delta t}{\Delta x^2} \times \left( \bar{v}_{j-1}^{n+1/2} - 2 \bar{v}_{j}^{n+1/2} + \bar{v}_{j+1}^{n+1/2} \right). \quad (10)
\]
The numerical schemes (9) and (10) for the diffusion equations give stable solutions provided 
\[ \frac{d_i \Delta t}{(\Delta x)^2} \leq 0.5, \ i = 1, 2. \]
These conditions are satisfied for the calculations of all cases of this paper using the increment value \( \Delta x = 0.1 \) and the time step \( \Delta t = 0.00005 \) days. The value of \( \Delta t \) has been chosen after examining the convergence of calculated values of \( u \) and \( v \) we have solved equations (1) and (2) with response function 1, Data 1 for various values of \( \Delta t \) from 0.01 to 0.00000005. The solution consists of a sequence of the prey and predator pulses with increasing amplitude toward the steady state limit cycle. As the time step is decreased, the peak values become smaller approaching the converged solution until the time step \( \Delta t = 0.0005 \). We choose a time step \( \Delta t = 0.00005 \) to ensure that the solution has converged.

5 Results and Discussion

![Figure 2](image1.png)

Figure 2: Predator-prey solutions for response function 1 and Data 1. (a) Transient output of \( u \) and \( v \), (b) output without and with diffusion with no delay, (c) output without and with diffusion with time delay.

![Figure 3](image2.png)

Figure 3: Predator-prey solutions for response function 2 and Data 2. (a) Transient output of \( u \) and \( v \), (b) output without and with diffusion with no delay, (c) output without and with diffusion with time delay.

In all the graphs in Figures 2-4 we have given the transient outputs and the time sequences of the solution for the population densities \( u \) and \( v \) for each of the three sets of response functions and data sets for no diffusion and with diffusion, no delay and with delay \( \tau = 2 \) hours. Each figure presents pictures in 3 rows and 2 columns. Row order for each case includes the transient outputs, time sequences without delay and time sequences with delay \( \tau = 2 \). The order of the columns is without diffusion and with diffusion. The transient outputs are shown as spatial curves for \( u \) and \( v \) at times \( t = 0.5, 1.0, 1.5, \ldots, 10 \) days through the domain \([-2, 2]\). Time sequences for the prey and predator are shown as density distributions in time at the position \( x = 0 \), i.e. at the middle point of the space interval \([-2, 2]\). In each of the Figures 2-4 the case with no diffusion in row (b) is the result from Harrison’s model [2]. To illustrate delay effect from a wider point of view, we conclude with a series computations with delays of 0, 1, 3 and 5 hours presented as phase planes in Figure 5. In all of the cases illustrated, the time sequences continue up to 60 days.
function 1 and Data 1. Solutions exhibit the oscillations with some growing and some decaying. With no delay, the cases with and without diffusion show the initial growth of the prey is limited by the growth of the predator until the predator population density decreases due to the small population density of the prey. While the prey is at a subsistence level the predator population density continues to reduce until it reaches such a small level that an outbreak of the prey can occur. This growth is finally limited by the predator and the procedure is repeated. The population densities of \( u \) and \( v \) grow to a steady pattern of steady cycles of periods of almost zero population density followed by pulses with amplitudes close to 760 and 300 for the prey and predator respectively. The distances between the successive pulses also increase close to a period of 10-days and the maximum amplitudes of the pulses increase toward their steady state values. For the no diffusion cases first pulses reach smaller values than with diffusion, and it also takes a longer time to reach the steady cyclic state. It is clear that diffusion accelerates the process.

With time delay, the steady state prey and predator peak values close to 890 and 520 are approached more quickly, and the time interval between successive cycles is increased to approximately 20 days. Diffusion again accelerates the process of reaching steady state values.

Figure 3 presents the outputs using the response function 2 and Data 2. With no delay, the steady state solutions consist of regular oscillations of prey and predator pulses with magnitudes approximately 520 and 180 accordingly. The first prey and predator peak pulse values are much smaller than without diffusion, and very close in values to others for diffusion one. Time periods between peaks are also greater. The final pattern is reached more quickly with diffusion and in fewer oscillations. With time delay, the cyclic steady state is achieved sooner and is reached after only three pulses.

Figure 4 presents the outputs using the response function 3 and Data 3. Here the steady state solutions consist of regular oscillations of prey and predator pulses with magnitudes approximately 520 and 180 accordingly. The first prey and predator peak pulse values are much smaller than without diffusion, and very close in values to others for diffusion one. Time periods between peaks are also greater. The final pattern is reached more quickly with diffusion and in fewer oscillations. With time delay, the cyclic steady state is achieved sooner and is reached after only three pulses.
pattern is achieved very quickly in three or four of the cycles. With diffusion the first peaks are much higher than without it. With time delay the maximum values are larger and the time between peaks is greater. There are more pulses for the time period here compared with Figures 2 and 3. This is a result of the response function which is much smaller than the other responses for small prey values. Hence the growth of the predator reduces more quickly and the prey values increase more quickly.

In order to examine more closely the influence of delay on the population growth process, the results for response function 2 and Data 2 have been calculated with delay coefficients $\tau = 0, 1, 3$ and 5 for comparison with the solution for point of view, we include $\tau = 2$ shown in Figure 3. The results are presented in Figure 5 as phase-plane plots. The trajectories are traversed anticlockwise with increasing values toward the limit cycles. The graphs show that increasing the delay coefficient $\tau$ significantly increases the peak values of the pulses and increases the time interval between the pulses. With the inclusion of diffusion the trajectories grow to their steady cyclic pattern more quickly.

6 Conclusion

Each the graphs from Figures 2 - 4 show that there is a cyclic steady state. It is interesting to note that this is not necessarily the case if the response functions are used with the other data sets. Then steady states may be constant values. The inclusion of diffusion accelerates the process of reaching the final growth pattern. Increasing the time delay leads to increased values of local extrema for both the prey and predator and an increased time between their occurrence. This was best seen in the phase-plane plots.

These results underline the importance of the choice of appropriate features of predator-prey interactions in mathematical biology. Time delay in the numerical response has the physiological meaning that the conversion of prey biomass to predator biomass is delayed. It could occur in natural situations. Including delay when modelling biological processes could significantly improve the realism of the model as well as the accuracy of the predictions for the chosen data.

References


