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Non-Linear Bifurcation Analysis of Reaction-Diffusion Activator-Inhibator System

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Abstract. The paper first deals with the linear stability analysis of an activator-inhibitor reaction diffusion system to determine the nature of the bifurcation point of the system. The non-linear bifurcation analysis determining the steady state solution beyond the critical point enables us to determine characteristic features of the spatial inhomogeneous pattern formation arising out of the bifurcation of the state of the system.

Key words: Bifurcation Analysis, Critical point, Dissipative structure, Reaction-diffusion, Activator-inhibitor.

1. Introduction

Recently, reaction-diffusion systems have been playing a significant role in different fields of science such as chemical reactions, electronic devices, combustion processes neuron structures, population of organisms etc. [1]. Turing was the first to present stability analysis which shows that the reaction and diffusion of chemicals can give rise to spatial structure and to suggest that this in turn could be a key event in the formation of biological pattern [2]. The works of Prigogine, Nicolis [3] and others [4] have advanced the theory to a great extent after which it culminated in the foundation of the theory of dissipative structure. The study of dissipative structures, a term originally introduced by them in the context of biochemical reactions has now turned into an interdisciplinary subject covering wide range of fields offering challenging problems to modern scientists [5]. Segal and Jackson [6], who were first to stress the role of dissipative structure in the context of ecology, have pointed out that the couplings between the diffusion of species and non-linear population dynamics could give rise to instabilities of the inhomogeneous steady state and hence transition to a new space dependent regime. This type of mechanism is playing a dominant role in explaining the cause of a great number of patchy distribution in population dynamics. Most of the works are based on Lotka-Volterra type of systems. An exception is the important work of Laplante [7], who investigated a non Lotka-Volterra type of diffusion predator-prey model and analytically studied the instabilities giving rise to inhomogeneous steady-state solution.

In the present paper, we have considered a non-linear activator-inhibitor reaction diffusion system which is of the non Lotka-Volterra system type [1]. It is hardly necessary to point out that the non-linearity of the model equation plays a vital role in the phenomena of dissipative structure and pattern formation. The purpose of the present paper is to analyze the general mechanics and principles underlying the pattern formation in the non-linear activator-inhibitor reaction diffusion system. In Section 2, we have first briefly described the model equation pointing out its biological (or chemical) significance and at least justifying the presence of the non-linear term in the model equation from its heuristic origin. Then a linear stability analysis of the system has been carried out and instability leading to inhomogeneous steady state solution has been investigated. In Section 3, we have presented a full non-linear bifurcation analysis which enabled us to determine the explicit form of the steady state solution, bifurcating beyond the critical point. The numerical solution has been represented graphically to show its agreement with the analytical solution. Section 4 (conclusion) deals with a careful discussion of the results so obtained in biological perspective.

2. Model Equation: Biological Significance and Linear Stability Analysis

We consider an Activator-Inhibitor reaction diffusion system governed by the system of equations [1]:

$$\begin{aligned} \frac{\partial X}{\partial t} &= \frac{X^2}{Y} - bX + D_X \frac{\partial^2 X}{\partial r^2} \\ \frac{\partial Y}{\partial t} &= X^2 - Y + D_Y \frac{\partial^2 Y}{\partial r^2} \end{aligned} \tag{2.1}$$

where X and Y are concentrations of two reactants of species, b (> 0) is a parameter, D_X and D_Y are the diffusion coefficients. The physical interpretation of the model is that X activates Y, through the term X^2 and both X and Y are degraded linearly proportional to their concentrations, given by the terms $-bX$ and $-Y$. This linear degradation is referred to as first order kinetics reversed. The term $\frac{X^2}{Y}$ shows a negative feedback by Y in the production of X, since an increase in Y decreases the production of X and hence indirectly a reduction in itself. The term X^2 depicts the enhanced reaction rate when two molecules of X are present. The larger is Y, the smaller is the production of X. This is an example of feedback inhibition [1, 8]. The effect of the non-linear term $\frac{X^2}{Y}$ in the first model equation is to limit the maximal activator production rate so that an activator peak will not grow indefinitely. The above model equation (2.1) is heuristically a simplified form of the original reaction kinetic model equation due to Gierar and Meinhardt [9]. The interest of biologists in the development of pattern formation in biological systems was largely aroused due to the contributions by Meinhardt and Gierar [9–11]. Their work predominantly consists of numerical simulation of reaction diffusion system in various geometry. The results often bear a realisitic likeness to patterns commonly found in nature such as in phyllotaxis, bristle-like pattern, irregularly spaced structures such as stomata, ontogenic development of higher organism etc. [12].

We now want to analyze the behavior of the system predicted by the model equation (2.1). The complexity of the non-linear partial differential equation (2.1) first leads to the following stability analysis presented below and later to the non-linear bifurcation analysis to be presented in the next section. As a first step to the solution of the system of Equation (2.1) along with the investigation of characteristic behavior, let us consider the homogeneous (with diffusion absent) steady state given by

$$X^* = \frac{1}{b}, \quad Y^* = \frac{1}{b^2} \tag{2.2}$$

which are space and time independent. For physical acceptability, we must have X^* and $Y^* > 0$, implying $b > 0$, which represent uniform steady state solution of the (truncated) Equation (2.1). If diffusion is added now, (2.2) will no longer be solutions of the enlarged system. To avoid this, we should assume either the Dirichlet's or Neumann's boundary conditions. Here, we choose Neumann's boundary condition or zero fluxes on boundaries:

$$\frac{\partial X(0,t)}{\partial t} = \frac{\partial X(k,t)}{\partial t} = \frac{\partial Y(0,t)}{\partial t} = \frac{\partial Y(k,t)}{\partial t} = 0 \quad (0 \le r \le k). \tag{2.3}$$

The main reason for choosing zero flux boundary conditions is that we are interested in self-organization of pattern; zero flux conditions imply no external input [1].

The stability of the homogeneous steady state (X^*, Y^*) is not guaranteed for all values of the parameter b. If the linear stability analysis of the reaction diffusion system with Neumann boundary condition confirms that the uniform (homogeneous) steady state is unstable, the path of the system will then bifurcate after the value of the parameter crosses a critical value (critical value or bifurcation point). Both the stability and bifurcation of the system path depend essentially on the values of the parameter. The linear stability analysis presented below will predict the existence of such a bifurcation point, if any.

We now give small perturbation to our steady state (2.2) such that

$$x(r,t) = X(r,t) - X^*, \; y(r,t) = Y(r,t) - Y^* \text{ and } \frac{x}{X^*} \ll 1; \quad \frac{y}{Y^*} \ll 1. \tag{2.4}$$

Around the steady state (2.2), the time evolution of these perturbations will then simply be described by the linear system:

$$\frac{\partial}{\partial t}\begin{pmatrix} x(r,t) \\ y(r,t) \end{pmatrix} \equiv L \begin{pmatrix} x(r,t) \\ y(r,t) \end{pmatrix} \tag{2.5}$$

where the linear parabolic operator is defined by

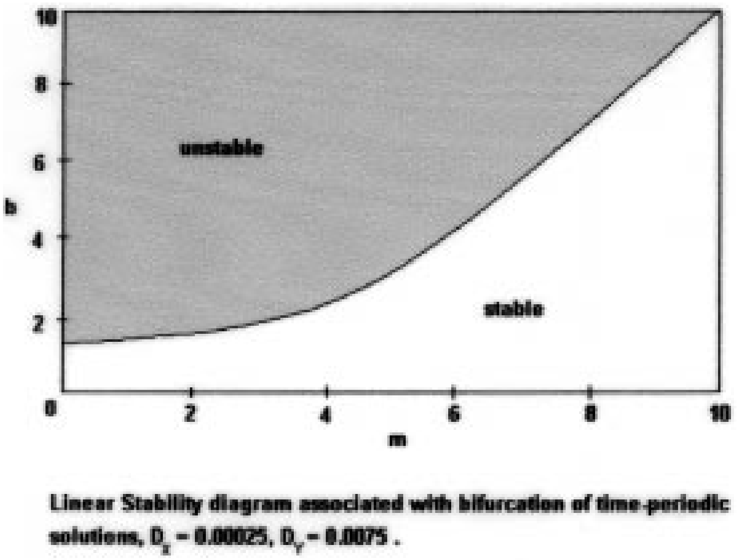

Figure 1. Linear stability diagram associated with bifurcation of time-periodic solutions, $D_X = 0.00025$, $D_Y = 0.0075$.

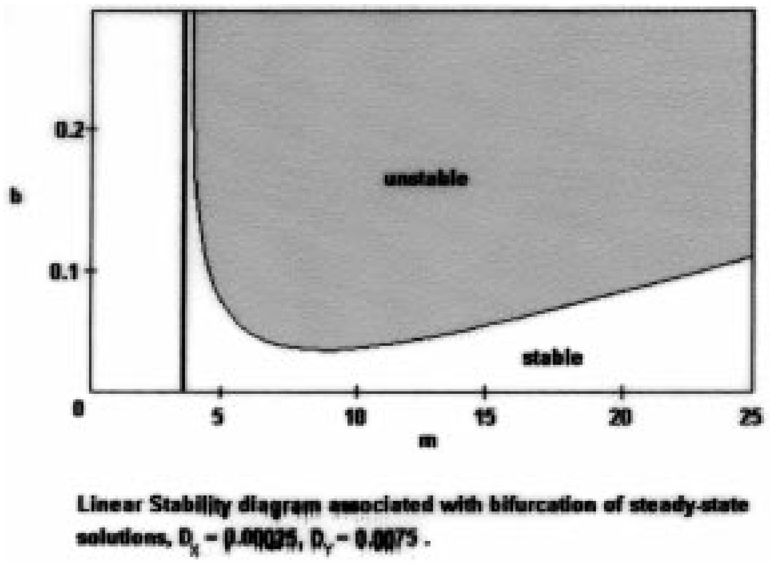

Figure 2. Linear stability diagram associated with bifurcation of steady-state solutions, $D_X = 0.00025$, $D_Y = 0.0075$.

$$L \equiv \begin{pmatrix} b + D_X \frac{\partial^2}{\partial r^2} & -b^2 \\ \frac{2}{b} & -1 + D_Y \frac{\partial^2}{\partial r^2} \end{pmatrix}. \tag{2.6}$$

The solution to (2.5) satisfying the boundary conditions (2.3) will be of the form

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} e^{\lambda_m t} \cos\left(\frac{m\pi r}{k}\right), \quad m = 0, 1, 2, \ldots \tag{2.7}$$

the λ_m's being the real or complex eigenvalues of our operator L. The characteristic equation is

$$\lambda_m^2 + \left(D_X \frac{m^2\pi^2}{k^2} - b + 1 + D_Y \frac{m^2\pi^2}{k^2}\right)\lambda_m + \left(1 + D_Y \frac{m^2\pi^2}{k^2}\right)\left(D_X \frac{m^2\pi^2}{k^2} - b\right) + 2b = 0. \tag{2.8}$$

The solution of the equation yields:

$$\lambda_m = \frac{-\left(D_X \frac{m^2\pi^2}{k^2} - b + 1 + D_Y \frac{m^2\pi^2}{k^2}\right) \pm \sqrt{\left(1 + D_Y \frac{m^2\pi^2}{k^2} + b - D_X \frac{m^2\pi^2}{k^2}\right)^2 - 8b}}{2}. \tag{2.9}$$

From this expression we get the following results:

(i) λ_m is complex if $\left(1 + D_Y \frac{m^2\pi^2}{k^2} + b - D_X \frac{m^2\pi^2}{k^2}\right)^2 - 8b < 0.$ (2.10)

(ii) A complex eigenvalue has a positive real part if the coefficient of λ_m in (2.8) is negative, or if

$$b > 1 + \frac{m^2\pi^2}{k^2}(D_X + D_Y). \tag{2.11}$$

Figure 1 represents b as a function of m along the critical curve

$$\tilde{b}_m = 1 + \frac{m^2\pi^2}{k^2}(D_X + D_Y). \tag{2.12}$$

The points on the curve $\tilde{b}_m$ corresponding to integer values of m are necessarily bifurcation points of time-periodic solutions.

(iii) If λ_m is real, one may have one positive root provided

$$\left(1 + D_Y \frac{m^2\pi^2}{k^2}\right)\left(D_X \frac{m^2\pi^2}{k^2} - b\right) + 2b < 0$$

$$\text{or, } b > \frac{D_X \frac{m^2\pi^2}{k^2}\left(1 + D_Y \frac{m^2\pi^2}{k^2}\right)}{-1 + D_Y \frac{m^2\pi^2}{k^2}}. \tag{2.13}$$

Figure 2 represents b as a function of m along the critical curve

$$b_m = \frac{D_X \frac{m^2\pi^2}{k^2}\left(1 + D_Y \frac{m^2\pi^2}{k^2}\right)}{-1 + D_Y \frac{m^2\pi^2}{k^2}}. \tag{2.14}$$

Thus, the points on the curve b_m corresponding to integer values of m are necessarily bifurcation points of steady-state solutions.

The steady state (2.2) first becomes unstable through real eigenvalues, thus leading to the emergence of a new time-independent steady-state solution. The critical wave number m_c corresponding to the onset of instability will then be given by the integer for which the expression b_m takes its minimum, namely,

$$m_c \equiv \text{nearest integer to } \left\{ \frac{(1+\sqrt{2})k^2}{\pi^2 D_Y} \right\}^{\frac{1}{2}}. \tag{2.15}$$

The value of b corresponding to this critical mode is then given by (2.13)–(2.15) as

$$b_{m_c} \equiv b_c \approx \frac{D_Y}{D_X}(1+\sqrt{2}). \tag{2.16}$$

From the above relation, we see that the critical mode and hence the stability or instability of the system is determined by the mobility ratio $\frac{D_Y}{D_X}$.

In the neighborhood of b_c $(b > b_c)$, one thus has $\lambda_{m_c} \approx 0$ (from 2.9), and the evolution of perturbation is now described by:

$$\begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} x_0 \\ y_0 \end{pmatrix} \cos\left(\frac{m_c \pi r}{k}\right) \tag{2.17}$$

which is obviously the characteristic of the emergence of a new inhomogeneous steady state solution to which (2.17) is a first approximation.

3. Non-Linear Bifurcation Analysis

In this section, our aim is to produce explicit form of the steady state solutions bifurcating beyond the critical value b_c (first bifurcation point). The first step is to insert decomposition

$$\begin{aligned} x &= X - X^* \\ y &= Y - Y^* \end{aligned} \tag{3.1}$$

into the initial population dynamics (2.1) and keeping the non-linear contributions in x and y, we obtain for the steady state $\frac{\partial X}{\partial t} = 0 = \frac{\partial Y}{\partial t}$:

$$L_C \begin{pmatrix} x \\ y \end{pmatrix} = \begin{pmatrix} p(x,y) \\ q(x,y) \end{pmatrix} \tag{3.2}$$

where $L_C \equiv \begin{pmatrix} b_c + D_X \frac{\partial^2}{\partial r^2} & -b_c^2 \\ \frac{2}{b_c} & -1 + D_Y \frac{\partial^2}{\partial r^2} \end{pmatrix}$ is the operator L evaluated at the critical point of the first bifurcation point,

$$\begin{aligned} p(x,y) &= -(b-b_c)x + (b^2 - b_c^2)y + b^2(b^2y-1)(x-by)^2 \\ q(x,y) &= -2\left(\frac{1}{b} - \frac{1}{b_c}\right)x - x^2. \end{aligned} \tag{3.3}$$

We now assume, in the neighborhood of the critical point b_c an expansion of b, x and y in terms of a small parameter ϵ whose exact form will be determined later:

$$\mu = b - b_c = \epsilon\mu_1 + \epsilon^2\mu_2 + \dots \tag{3.4}$$

$$\begin{pmatrix} x \\ y \end{pmatrix} = \epsilon \begin{pmatrix} x_0 \\ y_0 \end{pmatrix} + \epsilon^2 \begin{pmatrix} x_1 \\ y_1 \end{pmatrix} + \epsilon^3 \begin{pmatrix} x_2 \\ y_2 \end{pmatrix} + \dots . \tag{3.5}$$

We now introduce the expansion into (3.2) and identify equal powers of ϵ. We then obtain a set of relations of the form:

$$L_C \begin{pmatrix} x_i \\ y_i \end{pmatrix} = \begin{pmatrix} p_i \\ q_i \end{pmatrix} \quad \text{where} \quad i = 0, 1, 2, 3, \dots \tag{3.6}$$

together with the boundary conditions

$$\frac{\partial x_i(0,t)}{\partial t} = \frac{\partial x_i(k,t)}{\partial t} = \frac{\partial y_i(0,t)}{\partial t} = \frac{\partial y_i(k,t)}{\partial t} = 0. \tag{3.7}$$

Here, p_i and q_i are expressions involving the unknown parameters μ_i and solutions (x_i, y_i). The first few expressions are

$$\begin{aligned} p_0 &= q_0 = 0 \\ p_1 &= -\mu_1 x_0 + 2b_c\mu_1 y_0 - b_c^2(x_0 - b_c y_0)^2 \\ q_1 &= \frac{2\mu_1}{b_c} x_0 \\ p_2 &= -\mu_1 x_1 - x_0\mu_2 + (2b_c\mu_2 + \mu_1^2)y_0 - 2b_c\mu_1(x_0 - b_c y_0)^2 + b_c^4(x_0 - b_c y_0)^2 \\ q_2 &= \left(\frac{2}{b_c}\mu_2 + \mu_1^2\right) x_0. \end{aligned} \tag{3.8}$$

Since L_c has zero as a simple eigenvalue, (3.6) has a solution if and only if the functions p_i, q_i given by (3.8) obey a solvability condition. This condition determines the coefficients μ_i and is given by the Fredholm alternative whose form is here:

$$\int_0^k dr \begin{pmatrix} p_i \\ q_i \end{pmatrix} (x^T, y^T) \equiv 0 \tag{3.9}$$

where (x^T, y^T) is the eigenvalue corresponding to a null eigenvalue of the adjoint of L_c and obeying the boundary condition (2.3), namely

$$\begin{pmatrix} x^T \\ y^T \end{pmatrix} = \begin{pmatrix} d_1 \\ d_2 \end{pmatrix} \cos\left(\frac{m_c \pi r}{k}\right) \tag{3.10}$$

with

$$\frac{d_1}{d_2} = \frac{b_c^2}{b_c - D_X \frac{m_c^2 \pi^2}{k^2}}. \tag{3.11}$$

Using the expression (3.8) for p_1 in the solvability condition (3.9), together with (3.10) one finds:

$$\mu_1 \int_0^k dr \cos^2\left(\frac{m_c \pi r}{k}\right) = \frac{b_c^2 (d_1 - b_c d_2)^2}{2 b_c d_2 - d_1} \int_0^k dr \cos^3\left(\frac{m_c \pi r}{k}\right). \tag{3.12}$$

The coefficients of μ_1 on the l.h.s is always positive. On the other hand, the r.h.s vanishes (whether m_c is even or odd) owing to the presence of cosine terms in the solvability condition and we conclude that $\boldsymbol{\mu_1 = 0}$. The coefficient μ_2 is computed by first determining $\begin{pmatrix} x_1 \\ y_1 \end{pmatrix}$. We solve the equation

$$L_C \begin{pmatrix} x_1 \\ y_1 \end{pmatrix} = \begin{pmatrix} p_1 \\ q_1 \end{pmatrix} \tag{3.13}$$

by introducing the Fourier Series expansion

$$\begin{pmatrix} x_1 \\ y_1 \end{pmatrix} = \sum_{m=1}^{\infty} \begin{pmatrix} h_m \\ j_m \end{pmatrix} \cos\left(\frac{m \pi r}{k}\right). \tag{3.14}$$

It appears that $h_m = j_m = 0$ for $m \neq 2m_c$. Therefore, we only consider the case when $m = 2m_c$. Substituting (3.14) in (3.13) for $m = 2m_c$ we get,

$$\begin{pmatrix} b_c - D_X \frac{4m_c^2\pi^2}{k^2} & -b_c^2 \\ \frac{2}{b_c} & -1 - D_Y \frac{4m_c^2\pi^2}{k^2} \end{pmatrix} \begin{pmatrix} h_{2m_c} \\ j_{2m_c} \end{pmatrix} = \begin{pmatrix} t_{2m_c} \\ z_{2m_c} \end{pmatrix} \tag{3.15}$$

where

$$t_{2m_c} = \frac{2}{k} \int_0^k p_1 \cos\left(\frac{2m_c \pi r}{k}\right) dr = -b_c^2 (d_1 - b_c d_2)^2 \tag{3.16}$$

$$z_{2m_c} = \frac{2}{k} \int_0^k q_1 \cos\left(\frac{2m_c \pi r}{k}\right) dr = 0. \tag{3.17}$$

Solving (3.15) we get,

$$h_{2m_c} = \frac{\left(D_X \frac{4m_c^2\pi^2}{k^2} - b_c\right) b_c^2 (d_1 - b_c d_2)^2}{\left(1 + D_Y \frac{4m_c^2\pi^2}{k^2}\right)\left(D_X \frac{4m_c^2\pi^2}{k^2} - b_c\right) + 2b_c} \tag{3.18}$$

$$j_{2m_c} = \frac{-2b_c (d_1 - b_c d_2)^2}{\left(1 + D_Y \frac{4m_c^2\pi^2}{k^2}\right)\left(D_X \frac{4m_c^2\pi^2}{k^2} - b_c\right) + 2b_c}. \tag{3.19}$$

Thus we can determine (x_1, y_1). To obtain an explicit value of the coefficient μ_2, we once again use the solvability condition – this time for p_2 and we get the expression for μ_2 as

$$\frac{\mu_2}{d_1^2} = \frac{3}{8} b_c^2 \left(D_X \frac{m_c^2\pi^2}{k^2}\right)^2 \left(b_c - D_X \frac{m_c^2\pi^2}{k^2}\right) = \psi\left(m_c, b_c, \frac{D_X}{k^2}\right). \tag{3.20}$$

The explicit expression in this case is of no importance. The point is to realize that the sign of ψ determines the nature of the bifurcating solution. Here ψ is positive if

$$b_c > D_X \frac{m_c^2\pi^2}{k^2} \tag{3.21}$$

and from (3.4)

$$\varepsilon \approx \pm \left(\frac{b - b_c}{\mu_2}\right)^{1/2}. \tag{3.22}$$

Thus the bifurcating branches are supercritical $(b > b_c)$. This means that the steady state pattern which is generated by the system is stable.

The bifurcating solutions near $b = b_c$ can be calculated to a first approximation by inserting this value of ε in the expression (3.5) and by retaining the first two terms one gets:

$$x(r) = \pm \left(\frac{b - b_c}{\psi}\right)^{\frac{1}{2}} \cos\left(\frac{m_c \pi r}{k}\right)$$

$$+ \left(\frac{b - b_c}{\psi}\right) \frac{\left(D_X \frac{4m_c^2\pi^2}{k^2} - b_c\right)\left(\frac{D_X m_c^2\pi^2}{k^2}\right)^2}{\left(1 + D_Y \frac{4m_c^2\pi^2}{k^2}\right)\left(D_X \frac{4m_c^2\pi^2}{k^2} - b_c\right) + 2b_c} \cos\left(\frac{2m_c \pi r}{k}\right) \tag{3.23}$$

$$y(r) = \pm \left(\frac{b - b_c}{\psi}\right)^{\frac{1}{2}} \cos\left(\frac{m_c \pi r}{k}\right)$$

$$- \left(\frac{b - b_c}{\psi}\right) \frac{\frac{2}{b_c}\left(\frac{D_X m_c^2\pi^2}{k^2}\right)^2}{\left(1 + D_Y \frac{4m_c^2\pi^2}{k^2}\right)\left(D_X \frac{4m_c^2\pi^2}{k^2} - b_c\right) + 2b_c} \cos\left(\frac{2m_c \pi r}{k}\right) \tag{3.24}$$

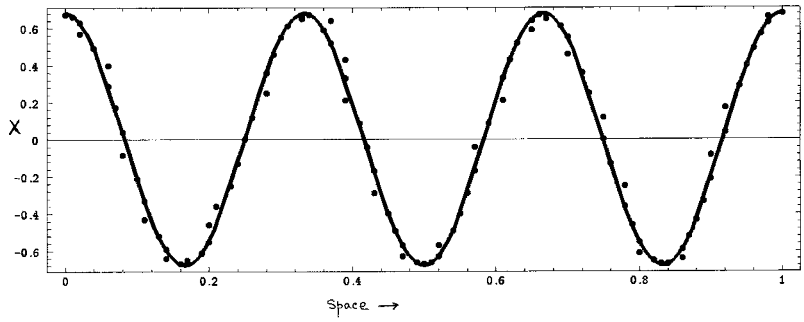

Figure 3. Non-uniform steady solution for $b = 2.5$, $b_c = 2.48$, $m_c = 6$, $k = 1$, $D_X = 2.5 \times 10^{-4}$, $D_Y = 7.5 \times 10^{-3}$. Heavy line: Analytical curve given by 3.23. Dots: Computer solution by direct integration of 2.1.

The above two expressions (3.23) and (3.24) give the explicit form of the steady state solution, bifurcating beyond the critical point.

For illustration we consider $D_X = 2.5 \times 10^{-4}$, $D_Y = 7.5 \times 10^{-3}$, $m_c = 6$, $k = 1$, $b = 2.5$, $b_c = 2.48$. This branch is drawn in Figure 3 where we also plotted the result obtained from the direct computer integration of (2.1). Fairly nice agreement is obtained with the analytical curves given by (3.23) and (3.24).

4. Conclusion

In this paper we have tried to shed some light on the stability and bifurcation behavior of a model reaction-diffusion system in which a variety of reaction kinetic behaviors such as autocatalysis, activation and inhibition etc is incorporated. Let us now look into the biological or chemical significance of the results obtained. We first consider the linear stability analysis. The evolution equation (2.12) of perturbation (x, y) predicts the formation of chemical pattern or formation of colonies in predator prey system. We consider model equation (2.1) to represent a prey-predator system, the homogeneous state (2.2) becoming unstable for $b < b_c$, any fluctuation in concentration population density will be amplified and the system will reversibly evolve to a new regionalized distribution of reactants or species. From (2.17), we also see that the degree of regionalism is to a good approximation, given by m_c, which is inversely proportional to D_Y, the mobility of the reactant (or predator Y). This shows that the patchy distribution of reaction depends on the mobility of the inhibitor Y. The expression (2.16) shows the dependence of the parameter b corresponding to the critical mode on the mobility ratio $\frac{D_Y}{D_X}$, the greater is the value of $\frac{D_Y}{D_X}$, the larger is the domain of instability.

The non-linear bifurcation analysis leads to the expression (3.23) and (3.24) for steady state solution bifurcating beyond the critical point. They correspond to second order correction to harmonics of the critical mode. These corrections, as expected, are relatively small and do not differ significantly from the first order mode (2.17). The overall shape of the spatial wave is determined by the critical mode m_c. The agreement between the analytical results (3.23) and (3.24) and numerical integration of (2.1) is very good near the first bifurcation point, which we have focused on in our study. And finally the paper, in the spirit of studying a dynamical problem of feedback mechanism, may play a significant role both in Chemical Kinetics and Ecology, in various forms and in different contexts [13–15].

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