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Bifurcation Analysis of Two Biological Systems: A Tritrophic Food Chain Model and An Oscillating Networks Model

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Applied Mathematics

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Abstract

In this thesis, we apply bifurcation theory to study two biological systems. Main attention is focused on complex dynamical behaviors such as stability and bifurcation of limit cycles. Hopf bifurcation is particularly considered to show bistable or even tristable phenomenon which may occur in biological systems. Recurrence is also investigated to show that such complex behavior is common in biological systems.

First we consider a tritrophic food chain model with Holling functional response types III and IV for the predator and superpredator, respectively. Main attention is focused on the stability and bifurcation of equilibria when the prey has a linear growth. Coexistence of different species is shown in the food chain, showing bistable or even tristable phenomenon. Hopf bifurcation is studied to show complex dynamics due to the existence of multiple limit cycles. In particular, normal form theory is applied to prove that three limit cycles can bifurcate from an equilibrium in the vicinity of a Hopf critical point.

Further investigation is focused on the recurrence behavior in oscillating networks of biologically relevant organic reactions. This model has one unique equilibrium solution. Analysis is first given to the stability and bifurcation of the equilibrium. Then, particular attention is focused on recurrence behavior of the system when the equilibrium become unstable. Numerical simulations are compared with the analytical predictions to show a very good agreement.

Keywords: Food chain model, oscillating network, organic reaction, stability, saddle-node bifurcation, Hopf bifurcation, limit cycle, bistable, tristable, recurrence

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Chapter 1

Introduction

1.1 Overview

Bifurcation analysis has always played an important role in the study of practical dynamical systems, such as biological models, physical models, and chemical models. For example, as it has been shown, a railway vehicle has stable motion in low speeds, but when it reaches a high speed, the motion becomes unstable. The main purpose of nonlinear analysis on the dynamics of railway vehicles is to study bifurcation, nonlinear lateral stability and hunting behavior of vehicles in tangent track. As an indispensable part of bifurcation theory, Hopf bifurcation is a very important type of bifurcation and often occurs in almost all physical systems, yielding periodic oscillations. In particular, Hopf bifurcation can occur in many biological systems such as the Lotka-Volterra model of predator-prey interaction (known as paradox of enrichment), the Hodgkin-Huxley model for nerve membranes [1], the Selkov model of glycolysis, the Belousov-Zhabotinsky reaction and the Lorenz attractor. Thus, considering Hopf bifurcation is of great importance in studying biological and physical systems.

Hopf bifurcation is also known as Poincaré-Andronov-Hopf bifurcation, named after Henri Poincaré, Eberhard Hopf, and Aleksandr Andronov [2]. In the mathematical theory of bifurcations, Hopf bifurcation appears from a critical point at which the system's stability changes and a periodic motion arises. More precisely, Hopf bifurcation occurs in a dynamical system from an equilibrium solution when the linearized system contains a pair of purely imaginary eigenvalues at the equilibrium solution. With a general assumption for a dynamical system, the equilibrium solution loses its stability at a critical point and a family of small-amplitude limit cycle bifurcates from the equilibrium. Further, for post-critical behaviors, Hopf bifurcation can be classified as two types: supercritical and subcritical. Assume that a dynamical system undergoes a Hopf bifurcation from an equilibrium of the system, the normal form associated with the Hopf bifurcation can be written as

$$\frac{dz}{dt} = z[(\lambda + i) + c|z|^2], \quad (1.1)$$

where z , c are both complex and λ is a parameter. If we write $c = \alpha + i\beta$, α is called the first Lyapunov constant. There exists a unique limit cycle bifurcating from the equilibrium $z = 0$

for $\lambda > 0$, with the solution given by

$$z(t) = \sqrt{-\frac{\lambda}{\alpha}} e^{(1+\beta r^2)it}. \quad (1.2)$$

If $\alpha < 0$ (or $\alpha > 0$), then the bifurcation is called supercritical (or subcritical). Therefore, if the first Lyapunov constant (focus value) is negative, then the limit cycle is orbitally stable and the bifurcation is supercritical. Otherwise the limit cycle is unstable and the bifurcation is subcritical.

Recently, there have been many studies on the subject of Hopf bifurcation. Among them, the main research is focused on the analysis of limit cycles and stability. Yu *et al.* [34] studied a bacteriophage model that includes prophage, focusing on asymptotic behavior of the solutions, and proved the existence of a supercritical Hopf bifurcation and stable limit cycles. Zhang *et al.* [35] studied a newly autoimmune four-dimensional disease model, and proved the existence of a supercritical Hopf bifurcation, leading to a family of stable limit cycles. The study of Hopf bifurcation has also been used to investigate the behaviors in simple disease models arising in epidemiology, in-host disease and autoimmunity (e.g., see [36]). Recently, there are also some studies on the tritrophic food chain models, in which the coexistence of multiple species is shown by proving the existence of a stable limit cycle. For example, Francois and Llibre [11] used averaging theory to prove the existence of a stable periodic orbit contained in the region where all variables are positive. Castellanos *et al.* [8] studied linear growth of the prey and functional response of Holling type III [62] for the middle and top species, and showed a double zero-Hopf bifurcation in the positive octant of \mathbb{R}^3 using the averaging theory. In [4], the authors studied the case when the prey has linear growth, while the middle and top species have functional responses Holling types II and III [62], respectively, and proved the existence of a stable limit cycle in the region of interest. In [6], the authors considered the case when the prey has logistic growth, while the predator and superpredator have the functional responses Lotka-Volterra type and Holling type II [62], respectively, forming a differential system based on the Leslie-scheme. In the paper, the authors also computed the first Lyapunov coefficient explicitly and showed the existence of a stable limit cycle. Moreover, they demonstrated by simulation a strange attractor which provides evidence that the model exhibits chaotic dynamics.

In this thesis, our study focuses on the stability and bifurcation of limit cycles due to Hopf bifurcation. In particular, we consider two models: a tritrophic food chain model and an oscillating networks model. For the food chain model, we mainly investigate the case when the model is characterized by that the prey growth rate is linear in the absence of the predators, while the functional responses for the middle and top species in the chain are Holling type III and Holling type IV, respectively. For the oscillating network model, our main attention is focused on Hopf bifurcation and the recurrence phenomenon induced by Hopf bifurcation.

To study our two models, we need the basis of stability and bifurcation theory for nonlinear dynamical systems. In the following, we briefly introduce some of the fundamental theory and methodology.

1.1.1 Linear theory

Firstly, we present some results and formulas for general dynamical systems to study the stability of equilibrium solutions. Consider the general nonlinear differential system:

$$\dot{x} = f(x, \mu), \quad x \in \mathbb{R}^n, \quad \mu \in \mathbb{R}^m, \quad f : \mathbb{R}^{n+m} \mapsto \mathbb{R}^n, \quad (1.3)$$

where the dot denotes differentiation with respect to time t , x and μ are the n -dimensional state variable and m -dimensional parameter variable, respectively. Assume that the nonlinear function $f(x, \mu)$ is analytic with respect to x and μ . Suppose that an equilibrium solution of Eq.(1.3) is given in the form of $x_e = x_e(\mu)$, which is determined from $f(x, \mu) = 0$. In order to analyze the stability of x_e , evaluating the Jacobian of system (1.3) at $x = x_e(\mu)$ yields $J(\mu) = D_x f|_{x=x_e(\mu)}$. If all eigenvalues of $J(\mu)$ have nonzero real parts, then the system is said to be hyperbolic, that means no complex dynamics exists in the vicinity of the equilibrium. Otherwise, at least one of the eigenvalues of $J(\mu)$ has zero real part at a critical point, defined by $\mu = \mu_c$, and bifurcations may occur from $x_e(\mu)$. To determine the stability of the equilibrium, we firstly find the eigenvalues of the Jacobian $J(\mu)$, which are the roots of the characteristic polynomial equation:

$$\begin{aligned} P_n(\lambda) &= \det[\lambda I - J(\mu)] \\ &= \lambda^n + a_1(\mu)\lambda^{n-1} + a_2(\mu)\lambda^{n-2} + \cdots + a_{n-1}(\mu)\lambda + a_n(\mu) = 0. \end{aligned} \quad (1.4)$$

For a fixed value of μ , if all the roots of the polynomial $P_n(\lambda)$ have negative real part, then the equilibrium is asymptotically stable for this value of μ . If at least one of the eigenvalues has zero real part as μ is varied to cross a critical point μ_c , then the equilibrium becomes unstable at μ_c and bifurcation occurs from this critical point. When all the roots of $P_n(\lambda)$ have negative real part, we call $P_n(\lambda)$ a stable polynomial, otherwise an unstable polynomial.

In general, for $n \geq 3$, it is hard to find the roots of $P_n(\lambda)$. Thus we use the Routh-Hurwitz Criterion [46] to analyze the local stability of the equilibrium solution $x = x_e(\mu)$. The criterion gives necessary and sufficient conditions under which the equilibrium is locally asymptotically stable, i.e. all the roots of the the characteristic polynomial $P_n(\lambda)$ have negative real part. These conditions are given by

$$\Delta_i(\mu) > 0, \quad i = 1, 2, \dots, n, \quad (1.5)$$

where $\Delta_i(\mu)$ is called the i th-principal minor of the Hurwitz arrangements of order n , defined as follows (here, order n means that there are n coefficients a_i ($i = 1, 2, \dots, n$) in Eq. (1.4), which construct the Hurwitz principal minors):

$$\begin{aligned} \Delta_1 &= a_1, \\ \Delta_2 &= \det \begin{bmatrix} a_1 & 1 \\ a_3 & a_2 \end{bmatrix}, \\ \Delta_3 &= \det \begin{bmatrix} a_1 & 1 & 0 \\ a_3 & a_2 & a_1 \\ a_5 & a_4 & a_3 \end{bmatrix}, \\ &\dots, \\ \Delta_n &= a_n \Delta_{n-1}. \end{aligned} \quad (1.6)$$

Assume that as μ is varied to reach a critical point $\mu = \mu_c$, at least one of Δ_i 's becomes zero. Then the fixed point $x_e(\mu_c)$ becomes unstable, and μ_c is called critical point. It can be seen from Eq. (1.5) that if $a_n(\mu) = 0$, but other Hurwitz arrangements are still positive (i.e. $\Delta_n = 0$, $\Delta_i(\mu) > 0$, $i = 1, 2, \dots, (n-1)$), then $P_n(\lambda) = 0$ has one zero root. In this case, system (1.3) has a simple zero singularity and a static bifurcation occurs from x_e . In other cases, for example, Hopf bifurcation occurs at a critical point when $P_n(\lambda) = 0$ has a pair of purely imaginary eigenvalues $\pm i\omega$ ($\omega > 0$) at this point. However, the pair of purely imaginary eigenvalues are often difficult to be determined explicitly for high dimensional systems. Here, we present the following theorem without computing the eigenvalues of the Jacobian of a general system. The theorem gives the necessary and sufficient conditions for determining a Hopf critical point based on the Hurwitz criterion. Its proof can be found in [57].

Theorem 1.1.1 [57] The necessary and sufficient conditions for system (1.3) to have a Hopf bifurcation at an equilibrium solution $x = x_e$ is $\Delta_{n-1} = 0$, with other Hurwitz conditions being still held, i.e. $a_n > 0$ and $\Delta_i > 0$, for $i = 1, \dots, n-2$.

Next, we present a method for computing focus values. There are many methods developed for computing the focus values of planar vector fields, such as Poincaré Takens method [16], the perturbation method [58], the singular point value method [23], etc. But, for higher dimensional dynamical systems, the computation is much involved. In the next two subsections, we briefly introduce the method of normal forms for computing the focus values of general n -dimension dynamical systems. The general normal form theory can be found in [16, 10] and computations using computer algebra systems can be found in [17, 29].

1.1.2 Normal form theory

Consider the following general n -dimensional differential system:

$$\dot{z} = Az + f(z), z \in R^n, f : R^n \rightarrow R^n, \quad (1.7)$$

where Az and $f(z)$ represent the linear and nonlinear parts of the system, respectively. We assume that $z = 0$ is a fixed point of the system, which implies that $f(0) = Df(0) = 0$. It is also assumed that $f(z)$ is analytic and can be expanded in Taylor series about z , and system (1.7) only contains stable center manifolds. In the computation of normal forms, the first step is usually to introduce a linear transformation into (1.7) such that the linear part of (1.7) can be changed into the Jordan canonical form. Without loss of generality, suppose that under the linear transformation $z = T(x, y)$, system (1.7) becomes

$$\begin{aligned} \dot{x} &= J_1 x + f_1(x, y), \quad x \in R^k, \quad f_1 : R^n \rightarrow R^k, \\ \dot{y} &= J_2 y + f_2(x, y), \quad y \in R^{n-k}, \quad f_2 : R^n \rightarrow R^{n-k}, \end{aligned} \quad (1.8)$$

where $J_1 = \text{diag}(\lambda_1, \lambda_2, \dots, \lambda_k)$, and $J_2 = \text{diag}(\lambda_{k+1}, \lambda_{k+2}, \dots, \lambda_n)$, with $\text{Re}(\lambda_j) = 0$, $j = 1, 2, \dots, k$ and $\text{Re}(\lambda_j) < 0$, $j = k+1, \dots, n$.

Next, we apply center manifold theory [5] to system (1.8), yielding to that y can be expressed as $y = H(x)$, satisfying $H(0) = DH(0) = 0$. Therefore, the first equation of (1.8) can be rewritten as

$$\dot{x} = J_1 x + f_1(x, H(x)) = J_1 x + f_1^2(x) + f_1^3(x) + \dots + f_1^s(x) + \dots, \quad (1.9)$$

where $f_1^j \in M_j, j = 2, 3, \dots, M_j$ defining a linear space of vector fields whose elements are homogeneous polynomials of degree j . Equation (1.9) describes the dynamics on the center manifold of system (1.8), and $H(x)$ can be determined from the following equation:

$$DH(x)[J_1x + f_1(x, H(x))] - J_2(H(x)) - f_2(x, H(x)) = 0. \quad (1.10)$$

Next, by using normal form theory, we introduce the near-identity transformation:

$$x = u + Q(u) = u + q^2(u) + q^3(u) + \dots + q^s(u) + \dots, \quad (1.11)$$

where $q^j \in M_j, j = 2, 3, \dots$ into (1.9) to obtain the normal form,

$$\dot{u} = J_1u + C(u) = J_1u + c^2(u) + c^3(u) + \dots + c^s(u) + \dots, \quad (1.12)$$

where $c^j \in M_j, j = 2, 3, \dots$

In the view point of computation, computing center manifold and normal form seems to be straightforward. However, to design an efficient algorithm is not an easy task. Recently, an explicit recursive formula has been developed for computing the normal form together with center manifold for general n -dimensional differential systems associated with semisimple singularities. We omit the detailed formulas and algorithms, as well as the Maple program here, which can be found in [29].

1.1.3 Bifurcation of multiple limit cycles

Now we turn to discuss how to determine the maximal number of limit cycles which may bifurcate from a Hopf critical point. Suppose that we have obtained the normal form of system (1.7), given in the polar coordinates up to the $(2k + 1)$ th order term:

$$\begin{aligned} \dot{r} &= r(v_0 + v_1r^2 + v_2r^4 + \dots + v_kr^{2k}), \\ \dot{\theta} &= \omega_c + t_1r^2 + t_2r^4 + \dots + t_kr^{2k}, \end{aligned} \quad (1.13)$$

where r and θ denote the amplitude and phase of motion, respectively. v_k and t_k are expressed in terms of the original system's coefficients. v_k is called the k th-order focus value of the origin. The zero-order focus value v_0 is obtained from linear analysis.

To find k small-amplitude limit cycles of system (1.7) around the origin, we first find the conditions based on the original system's coefficients such that $v_0 = v_1 = v_2 = \dots = v_{k-1} = 0$ (note that $v_0 = 0$ is automatically satisfied at the critical point), but $v_k \neq 0$. Then appropriate small perturbations are performed to prove the existence of k limit cycles. In the following theorem, we give sufficient conditions for the existence of small-amplitude limit cycles. (The proof can be found in [17].)

Theorem 1.1.2 [17] Suppose that the focus values depend on k parameters, expressed as

$$v_j = v_j(\epsilon_1, \epsilon_2, \dots, \epsilon_k), \quad j = 0, 1, \dots, k, \quad (1.14)$$

satisfying

$$\begin{aligned} v_j(0, \dots, 0) &= 0, \quad j = 0, 1, \dots, k-1, \quad v_k(0, \dots, 0) \neq 0, \\ \text{and } \det \left[\frac{\partial(v_0, v_1, \dots, v_{k-1})}{\partial(\epsilon_1, \epsilon_2, \dots, \epsilon_k)}(0, \dots, 0) \right] &\neq 0. \end{aligned} \quad (1.15)$$

Then, for any given $\epsilon_0 > 0$, there exist $\epsilon_1, \epsilon_2, \dots, \epsilon_k$ and $\delta > 0$ with $|\epsilon_j| < \epsilon_0, j = 1, 2, \dots, k$ such that the equation $\dot{r} = 0$ has exactly k real positive roots (i.e. system (2.1) has exactly k limit cycles) in a δ -ball with its center at the origin.

1.2 Two biological models studied in the thesis

This thesis is focused on the study of a tritrophic food chain model and an oscillating networks model of biologically relevant organic reactions. Particular attention is given to stability of equilibrium solutions and bifurcations.

1.2.1 A tritrophic food chain model

The general tritrophic food chain model with three species is described by the following three ordinary differential equations [7]:

$$\begin{aligned}\frac{dx}{dt} &= h(x) - f(x)y, \\ \frac{dy}{dt} &= c_1 y f(x) - g(y)z - \mu y, \\ \frac{dz}{dt} &= c_3 g(y)z - d_2 z,\end{aligned}\tag{1.16}$$

where x , y and z represent respectively the densities of the bottom, the middle and the top species in the chain. The function $h(x)$ represents the growth rate of prey in the absence of the other species, and $h(x)$ is assumed linear in this study. The functions $f(x)$ and $g(y)$ are the functional responses of the predator y and superpredator z , respectively. All the parameters are positive. The parameters c_1 and c_3 represent the benefits from the consumption of food, and the parameters μ and d_2 represent the mortality rate of the corresponding predators. For ecological study, the region of interest in \mathbb{R}^3 is the positive octant $\Omega = \{(x, y, z) \in \mathbb{R}^3 | x > 0, y > 0, z > 0\}$.

We consider the case when f is Holling type III and g is Holling type IV, which are given explicitly in the form of

$$f(x) = \frac{a_1 x^2}{x^2 + b_1}, \quad g(y) = \frac{a_2 y}{y^2 + b_2},\tag{1.17}$$

where a_1, b_1, a_2, b_2 are positive parameters.

1.2.2 An oscillating networks model of biologically relevant organic reactions

To study oscillations in oscillating networks, a simple kinetic model is constructed in [54], described by the following three ordinary differential equations:

$$\begin{aligned}\frac{dA}{dt} &= k_1 S A - k_2 I A - k_3 A - k_0 A + k_4 S, \\ \frac{dI}{dt} &= k_0 I_0 - k_0 I - k_2 I A, \\ \frac{dS}{dt} &= k_0 S_0 - k_0 S - k_4 S - k_1 S A,\end{aligned}\tag{1.18}$$

where $A = [\text{RSH}]$, $I = [\text{maleimide}]$, $S = [\text{AlaSEt}]$, I_0 and S_0 are the concentrations of maleimide and AlaSEt fed into the reactor, respectively, k_i , $i = 1, 2, 3, 4$, are rate constants and k_0 is the space velocity. From the linear stability analysis of this model [39], we find that increasing k_0 from lower to higher values causes two transitions. The first one is from a stable focus to a stable orbit via an Andronov-Hopf bifurcation [48], and the second one is from a stable orbit to a single stable equilibrium via a saddle-node or fold bifurcation [48].

1.2.3 Outline of the thesis

In Chapter 2, we focus on Hopf bifurcation in a tritrophic food chain model (1.16) with Holling functional response types III and IV. We provide a summary on the linear analysis of system (1.16). And we find three limit cycles around the Hopf singular point in system (1.16) by using normal form theory. Conclusion and discussions are presented at the end of this chapter.

In Chapter 3, we are devoted to the stability analysis of the equilibria in an oscillating networks model of biologically relevant organic reactions (1.18). We first present a summary on the stability of equilibria of the model by the Routh-Hurwitz Criterion, and then identify saddle-node and Hopf bifurcations arising from the equilibrium. Numerical simulations are given to show the good agreement between simulations and analytical predictions. Conclusion and discussions are drawn at the end of this chapter.

Finally, we conclude the thesis in Chapter 4 and also discuss some potential future research.

Chapter 2

Multiple Limit Cycles in a Food Chain Model

2.1 Introduction

After the pioneering work of Lotka and Volterra [24, 30], the study of ditrophic food chains has received and been continuously receiving much attention in mathematical ecology. The classical ecological models of interacting populations often have focused on two species. Continuous time models of two interacting species, usually called prey-predator models, have been analyzed extensively, and some notable achievements have been made, for example, see [3, 21]. Mathematically, these models can exhibit only two basic patterns: Trajectories approach a steady state or a limit cycle. However, the ecological communities in nature have been observed to exhibit much more complex dynamics. Price *et al.* [28] argued that community behavior must be based on three or more trophic levels. Continuous time models with three species have been reported to have more complicated patterns. Existence of limit cycles, multiplicity of attractors, and catastrophic bifurcations are the characteristics of the models which have been used to explain complex behaviors observed in the field. The research in the past two decades has demonstrated that the complex dynamical behavior, including quasi-periodic motion or even chaos, can arise in continuous time ecological models with three or more species. Much attention has been paid to the study of the transition from periodic oscillation to chaotic motion. Understanding the mechanism of generating such behaviors constitutes an exercise of paramount importance. In the late 1970s, some interest in the mathematics of tritrophic food chain models emerged. One important model is called tritrophic food chain because each population except the lowest eats only the one on the immediate lower trophic level [12]. Our attention in this article is to investigate whether or not three species can exist simultaneously. The typical ecological interaction has been studied from a mathematical point of view through a differential equation system, showing the coexistence of species translating to the existence of a stable limit cycle. Some authors dealt with the problem of persistence [12, 13], but did not provide information on the number and the geometry of the attractors. Hogeweg and Hesper [20] showed through simulation that a particular food chain model can behave chaotically, however, this paper did not receive much attention. Later, Hastings and Powell showed in [18] that food chains behave chaotically on a “tea-cup” strange attractor, and the three populations

have diversified time responses increasing from bottom to top. Around the same time, Muratori and Rinaldi [26] performed a singular perturbation analysis to confirm that the tea-cup geometry is the result of the interaction between high frequency (prey-predator) oscillation and low frequency (predator-top-predator) oscillation. Since then, particular effort has been devoted to the study of the complex dynamics of food chain systems, and bifurcation analysis has been the major tool of investigation.

The general tritrophic food chain model with three species is described by the following three ordinary differential equations [7]:

$$\begin{aligned}\frac{dx}{dt} &= h(x) - f(x)y, \\ \frac{dy}{dt} &= c_1 y f(x) - g(y)z - \mu y, \\ \frac{dz}{dt} &= c_3 g(y)z - d_2 z,\end{aligned}\tag{2.1}$$

where x , y and z represent respectively the densities of the bottom, the middle and the top species in the chain. The function $h(x)$ represents the growth rate of prey in the absence of the other species, and $h(x)$ is assumed linear in this study. The functions $f(x)$ and $g(y)$ are the functional responses of the predator y and superpredator z , respectively. All the parameters are positive. The parameters c_1 and c_3 represent the benefits from the consumption of food, and the parameters μ and d_2 represent the mortality rate of the corresponding predators. For ecological study, the region of interest in \mathbb{R}^3 is the positive octant $\Omega = \{(x, y, z) \in \mathbb{R}^3 | x > 0, y > 0, z > 0\}$.

In this chapter, we consider the case when f is Holling type III and g is Holling type IV, which are given explicitly in the form of

$$f(x) = \frac{a_1 x^2}{x^2 + b_1}, \quad g(y) = \frac{a_2 y}{y^2 + b_2},\tag{2.2}$$

where a_1, b_1, a_2, b_2 are positive parameters.

The rest of the chapter is organized as follows. In section 2.2, we provide a linear analysis of system (2.1), in particular on the stability and bifurcation of the positive equilibrium. In section 2.3, we prove the existence of three limit cycles around the positive equilibrium, arising from Hopf bifurcation. In section 2.4, numerical simulation is presented in good agreement with our analytical theory. Finally, the conclusion and discussion is drawn in section 2.5.

2.2 Bifurcation analysis of system (2.1)

In this section, we consider the differential system (2.1) where the functional responses are given in (2.2) and the growth rate of prey is linear. So, the function h is written as $h(x) = \rho x$

and the differential system that we will analyze has the form,

$$\begin{aligned}\dot{x} &= \left(\rho - \frac{a_1 xy}{b_1 + x^2} \right) x, \\ \dot{y} &= \left(-\mu + \frac{a_1 c_1 x^2}{b_1 + x^2} - \frac{a_2 z}{b_2 + y^2} \right) y, \\ \dot{z} &= \left(-d_2 + \frac{a_2 c_3 y}{b_2 + y^2} \right) z.\end{aligned}\tag{2.3}$$

It is obvious that $p_b = (0, 0, 0)$ is a boundary equilibrium solution of system (2.3). The Jacobian matrix of system (2.3) evaluated at the equilibrium p_b is given by

$$\begin{bmatrix} \rho & 0 & 0 \\ 0 & -\mu & 0 \\ 0 & 0 & -d_2 \end{bmatrix},$$

which clearly shows that p_b is a saddle point.

Because it is hard to obtain the explicit expression of the positive equilibrium solution of system (2.3), we derive the conditions based on the system parameters for the existence of the positive equilibrium in the region of interest. Moreover, we study the stability and find the conditions under which Hopf bifurcation occurs from the positive equilibrium. In [7], the authors have given the conditions for the existence of the positive equilibrium, and a single limit cycle bifurcating from this positive equilibrium. Here, our main result is to prove the existence of three limit cycles. First, we cite some results from [7].

It should be noted that for practical systems proving the existence of a single limit cycle is usually not difficult, but proving the existence of two limit cycles is quite challenge. It is extremely difficult to prove the existence of three limit cycles. Very few articles have been published to discuss the existence of three limit cycles, for example, see [33, 14].

Lemma 2.2.1 [7] For system (2.6) with positive parameters, the point $p_0 = (x_0, y_0, z_0) \in \Omega$ is an equilibrium if and only if the parameters a_1 , b_2 and the third coordinate of p_0 satisfy

$$\begin{aligned}a_1 &= \frac{\rho(b_1 + x_0^2)}{x_0 y_0}, \quad b_2 = \frac{y_0}{d_2}(a_2 c_3 - d_2 y_0), \quad z_0 = \frac{c_3}{d_2}(-\mu y_0 + c_1 x_0 \rho), \\ y_0 &< \frac{a_2 c_3}{d_2}, \quad -\mu y_0 + c_1 x_0 \rho > 0.\end{aligned}\tag{2.4}$$

Corollary 2.2.2 [7] *With the conditions given as in Lemma 2.2.1, if*

$$c_1 = \frac{k_1 + \mu c_3 y_0}{c_3 x_0 \rho}, \quad y_0 < \frac{a_2 c_3}{d_2}\tag{2.5}$$

with $k_1 > 0$, then $z_0 > 0$ and the equilibrium is inside Ω , given in the form of $p_0 = (x_0, y_0, \frac{k_1}{d_2})$.

With the parameter values given in Lemma 2.2.1 and Corollary 2.2.2, system (2.3) becomes

$$\begin{aligned} \dot{x} &= \rho x - \frac{\rho x^2 y (b_1 + x_0^2)}{x_0 y_0 (b_1 + x^2)}, \\ \dot{y} &= -\frac{a_2 d_2 y z}{y_0 (a_2 c_3 - d_2 y_0) + d_2 y^2} + \frac{x^2 y (b_1 + x_0^2) (k_1 + \mu c_3 y_0)}{c_3 x_0^2 y_0 (b_1 + x^2)} - \mu y, \\ \dot{z} &= d_2 z \left(\frac{a_2 d_2 c_3 y}{y_0 (a_2 c_3 - d_2 y_0) + d_2 y^2} - 1 \right). \end{aligned} \quad (2.6)$$

The Jacobian matrix of system (2.6) evaluated at $p_0 = (x_0, y_0, \frac{k_1}{d_2})$ is given as follows:

$$J_{p_0} = \begin{bmatrix} \frac{(x_0^2 - b_1)\rho}{x_0^2 + b_1} & -\frac{x_0\rho}{y_0} & 0 \\ \frac{2b_1(k_1 + \mu c_3 y_0)}{c_3 x_0^2 (b_1 + x_0^2)} & \frac{2d_2 k_1}{a_2 c_3^2} & -\frac{d_2}{c_3} \\ 0 & \frac{k_1(a_2 c_3 - 2d_2 y_0)}{a_2 c_3 y_0} & 0 \end{bmatrix}.$$

Which, in turn, yields a cubic characteristic polynomial, given by

$$P_1(\lambda) = \lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0, \quad (2.7)$$

where the coefficients A_1, A_2, A_3 are expressed in terms of the parameters in system (2.6) as

$$\begin{aligned} A_1 &= \frac{c_3^2 \rho (b_1 - x_0^2) a_2 - 2d_2 k_1 (b_1 + x_0^2)}{(b_1 + x_0^2) c_3^2 a_2}, \\ A_2 &= \frac{1}{(b_1 + x_0^2) c_3^2 a_2 y_0} \{ [(-2y_0 d_2^2 + (a_2 c_3 - 2\rho y_0) d_2 \\ &\quad + 2a_2 c_3 \rho) b_1 + d_2 x_0^2 (a_2 c_3 - 2d_2 y_0 + 2\rho y_0)] k_1 + 2a_2 b_1 c_3^2 \mu \rho y_0 \}, \\ A_3 &= \frac{d_2 k_1 \rho (b_1 - x_0^2) (a_2 c_3 - 2d_2 y_0)}{(b_1 + x_0^2) c_3^2 a_2 y_0}. \end{aligned} \quad (2.8)$$

Based on the characteristic polynomial (2.7), we consider possible bifurcation from the equilibrium p_0 , including both static and dynamic (Hopf) bifurcations. The static bifurcation occurs when $P_1(\lambda) = 0$ has zero roots (zero eigenvalues). Thus we let $A_3 = 0$ to get $b_1 = x_0^2$, which yields $A_1 < 0$. Thus, the static bifurcation occurs in the unstable region, which is not interesting physically.

Theorem 2.2.3 *In system (2.6), if one of the following conditions is satisfied,*

$$\begin{aligned} \text{I) } & 0 < x_0 < \sqrt{b_1}, \quad 0 < y_0 < \frac{a_2 c_3}{2d_2}, \quad k_1 \leq k_L, \quad \mu > 0; \\ \text{II) } & 0 < x_0 < \sqrt{b_1}, \quad 0 < y_0 < \frac{a_2 c_3}{2d_2}, \quad k_L < k_1 < k_U, \quad \mu > \mu_0; \end{aligned} \quad (2.9)$$

then the equilibrium $p_0 = (x_0, y_0, \frac{k_1}{d_2})$ is local asymptotically stable. Here,

$$k_L = \frac{a_2 c_3^2 \rho^2 (b_1 - x_0^2) [b_1 (a_2 c_3 - d_2 y_0) + d_2 y_0 x_0^2]}{d_2 (b_1 + x_0^2) [d_2 (b_1 + x_0^2) (a_2 c_3 - 2d_2 y_0) + 2d_2 \rho y_0 x_0^2 + 2b_1 \rho (a_2 c_3 - d_2 y_0)]},$$

$$k_U = \frac{c_3^2 \rho (b_1 - x_0^2) a_2}{2d_2 (b_1 + x_0^2)}.$$

Proof According to the Hurwitz criterion, first we have

$$\begin{aligned} A_1 > 0 &\implies c_3^2 \rho (b_1 - x_0^2) a_2 > 0 \iff b_1 - x_0^2 > 0 \implies 0 < x_0 < \sqrt{b_1}; \\ A_1 > 0 &\implies c_3^2 \rho (b_1 - x_0^2) a_2 - 2d_2 k_1 (b_1 + x_0^2) > 0 \implies k_1 < \frac{c_3^2 \rho (b_1 - x_0^2) a_2}{2d_2 (b_1 + x_0^2)} \iff k_1 < k_U; \\ A_3 > 0 &\implies (b_1 - x_0^2) (a_2 c_3 - 2y_0 d_2) > 0 \implies 0 < y_0 < \frac{a_2 c_3}{2d_2}. \end{aligned} \tag{2.10}$$

Then, we compute $\Delta_2 = A_1 A_2 - A_3$ to obtain

$$\begin{aligned} \Delta_2 &= \frac{2}{(b_1 + x_0^2)^2 c_3^4 a_2^2 y_0} \Delta_{2a}, \\ \Delta_{2a} &= (b_1 + x_0^2) y_0 \rho c_3^4 b_1 a_2^2 A_1 \mu - k_1 \{-2y_0 (x_0^2 + b_1) d_2^2 + [(a_2 c_3 - 2\rho y_0) b_1 \\ &\quad + x_0^2 (a_2 c_3 + 2\rho y_0)] d_2 + 2a_2 b_1 c_3 \rho\} d_2 (x_0^2 + b_1) (k_1 - k_L). \end{aligned} \tag{2.11}$$

Now, solving Δ_{2a} for μ , we obtain the critical value,

$$\mu_H = \frac{k_1 [d_2 (b_1 + x_0^2) (a_2 c_3 - 2y_0 d_2 + 2\rho y_0) + 2b_1 \rho (a_2 c_3 - 2d_2 y_0)] (k_1 - k_L)}{2b_1 a_2 c_3^2 \rho y_0 (k_U - k_1)}. \tag{2.12}$$

Further, it can be verified that $k_L < k_U$:

$$\begin{aligned} k_L < k_U &\iff \frac{a_2 c_3^2 \rho^2 (b_1 - x_0^2) [b_1 (a_2 c_3 - d_2 y_0) + d_2 y_0 x_0^2]}{d_2 (b_1 + x_0^2) [d_2 (b_1 + x_0^2) (a_2 c_3 - 2y_0 d_2) + 2d_2 \rho y_0 x_0^2 + 2b_1 \rho (a_2 c_3 - d_2 y_0)]} < \frac{c_3^2 \rho (b_1 - x_0^2) a_2}{2d_2 (b_1 + x_0^2)}, \\ &\iff \frac{\rho [b_1 (a_2 c_3 - d_2 y_0) + d_2 y_0 x_0^2]}{[d_2 (b_1 + x_0^2) (a_2 c_3 - 2y_0 d_2) + 2d_2 \rho y_0 x_0^2 + 2b_1 \rho (a_2 c_3 - d_2 y_0)]} < \frac{1}{2}, \\ &\iff 2\rho [b_1 (a_2 c_3 - d_2 y_0) + d_2 y_0 x_0^2] < [d_2 (b_1 + x_0^2) (a_2 c_3 - 2y_0 d_2) + 2d_2 \rho y_0 x_0^2 + 2b_1 \rho (a_2 c_3 - d_2 y_0)], \\ &\iff d_2 (b_1 + x_0^2) (a_2 c_3 - 2y_0 d_2) > 0. \end{aligned} \tag{2.13}$$

Thus, besides $A_1 > 0$, $A_2 > 0$, $A_3 > 0$ under the conditions given in (2.10), the above discussion shows that $\Delta_2 > 0$ for $k_1 \leq k_L$ ($\mu > 0$) or $k_L < k_1 < k_U$ ($\mu > \mu_H$). Hence,

$$\begin{aligned} \text{if } k_1 \leq k_L &\implies \Delta_2 > 0 \text{ for } \mu > 0 \implies \text{equilibrium point is stable, or} \\ \text{if } k_L < k_1 < k_U &\implies \Delta_2 > 0 \text{ for } \mu > \mu_0 \implies \text{equilibrium point is stable.} \end{aligned} \tag{2.14}$$

Next, we derive the conditions for Hopf bifurcation. According to Theorem 1.1.1, Hopf bifurcation occurs from the equilibrium p_0 at $\mu = \mu_H > 0$ when the following conditions hold,

$$0 < x_0 < \sqrt{b_1}, \quad k_L < k_1 < k_U, \quad 0 < y_0 < \frac{a_2 c_3}{2d_2}. \quad (2.15)$$

Under the conditions in (2.15), we rewrite $P_1(\lambda)$ as

$$P_1(\lambda) = \frac{F_1 F_2}{y_0 a_2 c_3^2 [a_2 c_3^2 \rho (b_1 - x_0^2) - 2k_1 d_2 (b_1 + x_0^2)] (b_1 + x_0^2)}, \quad (2.16)$$

where

$$\begin{aligned} F_1 &= a_2 c_3^2 (b_1 + x_0^2) \left[\lambda + \frac{2d_2 (k_U - k_1)}{a_2 c_3^2} \right], \\ F_2 &= 2y_0 d_2 (b_1 + x_0^2) (k_U - k_1) \left[\lambda^2 + \frac{\rho k_1 (b_1 - x_0^2) (a_2 c_3 - 2d_2 y_0)}{2y_0 (b_1 + x_0^2) (k_U - k_1)} \right]. \end{aligned} \quad (2.17)$$

Thus, we can get the three roots (three eigenvalues) of $P_1(\lambda)$ as α and $\pm\omega i$, where

$$\begin{aligned} \alpha &= -\frac{2d_2 (k_U - k_1)}{a_2 c_3^2}, \\ \omega_H &= \sqrt{\frac{\rho k_1 (b_1 - x_0^2) (a_2 c_3 - 2d_2 y_0)}{2y_0 (b_1 + x_0^2) (k_U - k_1)}}, \end{aligned} \quad (2.18)$$

satisfying $\alpha < 0$ and $\omega_H > 0$ for $0 < k_1 < k_U$.

In order to make the normal form computation feasible for the Hopf bifurcation, we further set

$$x_0 = \sqrt{X_0}, \quad X_0 > 0, \quad k_1 = k_L + \frac{1}{2}(k_U - k_L), \quad y_0 = \frac{a_2 c_3}{4d_2}, \quad b_1 = x_0^2 + B_1, \quad B_1 > 0. \quad (2.19)$$

Then, we can rewrite k_L , k_U , A_1 , A_2 , A_3 , μ_H , α and ω as

$$\begin{aligned} k_L &= \frac{B_1 \rho^2 c_3^2 a_2 (3B_1 + 4X_0)}{2d_2 [(d_2 + 3\rho)B_1 + 2X_0(d_2 + 2\rho)](2X_0 + B_1)}, \\ k_U &= \frac{c_3^2 \rho B_1 a_2}{2d_2 (2X_0 + B_1)}, \\ A_1 &= \frac{B_1 \rho d_2}{2[(d_2 + 3\rho)B_1 + 2X_0(d_2 + \rho)]}, \\ A_2 &= \frac{(d_2 + 6\rho)B_1 + 2X_0(d_2 + 4\rho)B_1 \rho}{(2X_0 + B_1)^2}, \\ A_3 &= \frac{d_2 \rho^2 B_1^2 [(d_2 + 6\rho)B_1 + 2X_0(d_2 + 4\rho)]}{2[(d_2 + 3\rho)B_1 + 2X_0(d_2 + 2\rho)](2X_0 + B_1)^2}, \\ \alpha &= -\frac{B_1 \rho d_2}{2[(d_2 + 3\rho)B_1 + 2X_0(d_2 + 2\rho)]}, \\ \mu_H &= \frac{[(d_2 + 6\rho)B_1 + 2X_0(d_2 + 4\rho)]B_1}{4(X_0 + B_1)(2X_0 + B_1)}, \\ \omega_H &= \frac{\sqrt{[(d_2 + 6\rho)B_1 + 2X_0(d_2 + 4\rho)]B_1 \rho}}{2X_0 + B_1}, \end{aligned} \quad (2.20)$$

satisfying $A_1 > 0$, $A_2 > 0$, $A_3 > 0$, $\Delta_2 = 0$, $\alpha < 0$, $\mu_H > 0$, $\omega_H > 0$, as expected.

2.3 Existence of three limit cycles around p_0

In this section, we will present our main result. We will apply normal form theory to show that at least three small-amplitude limit cycles can bifurcate from the equilibrium p_0 .

Theorem 2.3.1 *For system (2.6), at least three small-amplitude limit cycles can bifurcate from the equilibrium p_0 .*

Proof In order to study the limit cycle bifurcation around the equilibrium p_0 near the critical point $\mu = \mu_H$, we need to compute the focus values. To achieve this, we use the following transformation,

$$\begin{aligned} x &= x_0 + T_{11}u + T_{12}v + T_{13}w, \\ y &= y_0 + T_{21}u + T_{22}v + T_{23}w, \\ z &= z_0 + T_{31}u + T_{32}v + T_{33}w, \end{aligned} \tag{2.21}$$

where

$$\begin{aligned} T_{11} &= -\frac{8d_2(2X_0 + B_1) \sqrt{X_0}[(d_2 + 3\rho)B_1 + 2X_0(d_2 + 2\rho)]}{c_3^2 a_2 [(d_2 + 7\rho)B_1 + 2X_0(d_2 + 4\rho)] B_1}, \\ T_{12} &= -\frac{8d_2(2X_0 + B_1)^2 \sqrt{X_0}[(d_2 + 3\rho)B_1 + 2X_0(d_2 + 2\rho)] \omega_H}{c_3^2 [(d_2 + 6\rho)B_1 + 2X_0(d_2 + 4\rho)] a_2 [(d_2 + 7\rho)B_1 + 2X_0(d_2 + 4\rho)] B_1}, \\ T_{13} &= \frac{x_0 \rho (-a_2 c_3^2 \rho x_0^2 + a_2 b_1 c_3^2 \rho - 2d_2 k_1 x_0^2 - 2b_1 d_2 k_1) c_3 a_2}{2(a_2 c_3 x_0^2 - 2d_2 x_0^2 y_0 + a_2 b_1 c_3 - 2b_1 d_2 y_0) k_1^2 d_2}, \\ T_{21} &= 0, \\ T_{22} &= \frac{2[(d_2 + 3\rho)B_1 + 2X_0(d_2 + 2\rho)](2X_0 + B_1) \omega_H}{\rho c_3 [(d_2 + 6\rho)B_1 + 2X_0(d_2 + 4\rho)] B_1}, \\ T_{23} &= -\frac{y_0 (-a_2 c_3^2 \rho x_0^2 + a_2 b_1 c_3^2 \rho - 2d_2 k_1 x_0^2 - 2b_1 d_2 k_1)}{(a_2 c_3 x_0^2 - 2d_2 x_0^2 y_0 + a_2 b_1 c_3 - 2b_1 d_2 y_0) c_3 k_1}, \\ T_{31} &= 1, \\ T_{32} &= 0, \\ T_{33} &= 1, \end{aligned} \tag{2.22}$$

to transform system (2.6) to a new system expanded in the form of

$$\begin{aligned} \dot{u} &= v + \sum_{i+j+k=2}^5 a_{ijk} u^i v^j w^k, \\ \dot{v} &= -u + \sum_{i+j+k=2}^5 b_{ijk} u^i v^j w^k, \\ \dot{w} &= c_{001} w_H + \sum_{i+j+k=2}^5 c_{ijk} u^i v^j w^k, \end{aligned} \tag{2.23}$$

where the coefficients a_{ijk} , b_{ijk} and c_{ijk} are expressed in term of the parameters in system (2.6).

Then, using the Maple program in [29], we get the first three focus values as follows:

$$\begin{aligned}
V_1 &= -(B_1d_2 + 3B_1\rho + 2X_0d_2 + 4X_0\rho)^2/[2B_1^3\rho(B_1d_2 + 7B_1\rho + 2X_0d_2 + 8X_0\rho)(4B_1^3d_2^3 \\
&\quad + 49B_1^3d_2^2\rho + 180B_1^3d_2\rho^2 + 216B_1^3\rho^3 + 24B_1^2X_0d_2^3 + 260B_1^2X_0d_2^2\rho + 840B_1^2X_0d_2\rho^2 \\
&\quad + 864B_1^2X_0\rho^3 + 48B_1X_0^2d_2^3 + 452B_1X_0^2d_2^2\rho + 1280B_1X_0^2d_2\rho^2 + 1152B_1X_0^2\rho^3 + 32X_0^3d_2^3 \\
&\quad + 256X_0^3d_2^2\rho + 640X_0^3d_2\rho^2 + 512X_0^3\rho^3)(16B_1^3d_2^3 + 193B_1^3d_2^2\rho + 720B_1^3d_2\rho^2 + 864B_1^3\rho^3 \\
&\quad + 96B_1^2X_0d_2^3 + 1028B_1^2X_0d_2^2\rho + 3360B_1^2X_0d_2\rho^2 + 3456B_1^2X_0\rho^3 + 192B_1X_0^2d_2^3 \\
&\quad + 1796B_1X_0^2d_2^2\rho + 5120B_1X_0^2d_2\rho^2 + 4608B_1X_0^2\rho^3 + 128X_0^3d_2^3 + 1024X_0^3d_2^2\rho \\
&\quad + 2560X_0^3d_2\rho^2 + 2048X_0^3\rho^3)c_3^2]V_{1a}, \\
V_2 &= -2(B_1d_2 + 3B_1\rho + 2X_0d_2 + 4X_0\rho)^4d_2/[9c_3^6a_2^2(36B_1^3d_2^3 + 433B_1^3d_2^2\rho + 1620B_1^3d_2\rho^2 \\
&\quad + 1944B_1^3\rho^3 + 216B_1^2X_0d_2^3 + 2308B_1^2X_0d_2^2\rho + 7560B_1^2X_0d_2\rho^2 + 7776B_1^2X_0\rho^3 \\
&\quad + 432B_1X_0^2d_2^3 + 4036B_1X_0^2d_2^2\rho + 11520B_1X_0^2d_2\rho^2 + 10368B_1X_0^2\rho^3 + 288X_0^3d_2^3 \\
&\quad + 2304X_0^3d_2^2\rho + 5760X_0^3d_2\rho^2 + 4608X_0^3\rho^3)(2X_0 + B_1)(16B_1^3d_2^3 + 193B_1^3d_2^2\rho + 720B_1^3d_2\rho^2 \\
&\quad + 864B_1^3\rho^3 + 96B_1^2X_0d_2^3 + 1028B_1^2X_0d_2^2\rho + 3360B_1^2X_0d_2\rho^2 + 3456B_1^2X_0\rho^3 + 192B_1X_0^2d_2^3 \\
&\quad + 1796B_1X_0^2d_2^2\rho + 5120B_1X_0^2d_2\rho^2 + 4608B_1X_0^2\rho^3 + 128X_0^3d_2^3 + 1024X_0^3d_2^2\rho + 2560X_0^3d_2\rho^2 \\
&\quad + 2048X_0^3\rho^3)^3\rho^3B_1^7(B_1d_2 + 7B_1\rho + 2X_0d_2 + 8X_0\rho)^2(4B_1^3d_2^3 + 49B_1^3d_2^2\rho + 180B_1^3d_2\rho^2 \\
&\quad + 216B_1^3\rho^3 + 24B_1^2X_0d_2^3 + 260B_1^2X_0d_2^2\rho + 840B_1^2X_0d_2\rho^2 + 864B_1^2X_0\rho^3 + 48B_1X_0^2d_2^3 \\
&\quad + 452B_1X_0^2d_2^2\rho + 1280B_1X_0^2d_2\rho^2 + 1152B_1X_0^2\rho^3 + 32X_0^3d_2^3 + 256X_0^3d_2^2\rho + 640X_0^3d_2\rho^2 \\
&\quad + 512X_0^3\rho^3)^3(B_1d_2 + 6B_1\rho + 2X_0d_2 + 8X_0\rho)^2]V_{2a}, \\
V_3 &= -d_2^2(B_1d_2 + 3B_1\rho + 2X_0d_2 + 4X_0\rho)^6/[648(B_1d_2 + 6B_1\rho + 2X_0d_2 + 8X_0\rho)^4B_1^{11}\rho^5(B_1d_2 \\
&\quad + 7B_1\rho + 2X_0d_2 + 8X_0\rho)^3c_3^40a_2^4(64B_1^3d_2^3 + 769B_1^3d_2^2\rho + 2880B_1^3d_2\rho^2 + 3456B_1^3\rho^3 \\
&\quad + 384B_1^2X_0d_2^3 + 4100B_1^2X_0d_2^2\rho + 13440B_1^2X_0d_2\rho^2 + 13824B_1^2X_0\rho^3 + 768B_1X_0^2d_2^3 \\
&\quad + 7172B_1X_0^2d_2^2\rho + 20480B_1X_0^2d_2\rho^2 + 18432B_1X_0^2\rho^3 + 512X_0^3d_2^3 + 4096X_0^3d_2^2\rho \\
&\quad + 10240X_0^3d_2\rho^2 + 8192X_0^3\rho^3)(36B_1^3d_2^3 + 433B_1^3d_2^2\rho + 1620B_1^3d_2\rho^2 + 1944B_1^3\rho^3 \\
&\quad + 216B_1^2X_0d_2^3 + 2308B_1^2X_0d_2^2\rho + 7560B_1^2X_0d_2\rho^2 + 7776B_1^2X_0\rho^3 + 432B_1X_0^2d_2^3 \\
&\quad + 4036B_1X_0^2d_2^2\rho + 11520B_1X_0^2d_2\rho^2 + 10368B_1X_0^2\rho^3 + 288X_0^3d_2^3 + 2304X_0^3d_2^2\rho + 5760X_0^3d_2\rho^2 \\
&\quad + 4608X_0^3\rho^3)^2(2X_0 + B_1)^2(4B_1^3d_2^3 + 49B_1^3d_2^2\rho + 180B_1^3d_2\rho^2 + 216B_1^3\rho^3 + 24B_1^2X_0d_2^3 \\
&\quad + 260B_1^2X_0d_2^2\rho + 840B_1^2X_0d_2\rho^2 + 864B_1^2X_0\rho^3 + 48B_1X_0^2d_2^3 + 452B_1X_0^2d_2^2\rho + 1280B_1X_0^2d_2\rho^2 \\
&\quad + 1152B_1X_0^2\rho^3 + 32X_0^3d_2^3 + 256X_0^3d_2^2\rho + 640X_0^3d_2\rho^2 + 512X_0^3\rho^3)^5(16B_1^3d_2^3 + 193B_1^3d_2^2\rho \\
&\quad + 720B_1^3d_2\rho^2 + 864B_1^3\rho^3 + 96B_1^2X_0d_2^3 + 1028B_1^2X_0d_2^2\rho + 3360B_1^2X_0d_2\rho^2 + 3456B_1^2X_0\rho^3 \\
&\quad + 192B_1X_0^2d_2^3 + 1796B_1X_0^2d_2^2\rho + 5120B_1X_0^2d_2\rho^2 + 4608B_1X_0^2\rho^3 + 128X_0^3d_2^3 + 1024X_0^3d_2^2\rho \\
&\quad + 2560X_0^3d_2\rho^2 + 2048X_0^3\rho^3)^5]V_{3a},
\end{aligned}$$

where V_{1a} , V_{2a} and V_{3a} are polynomials in X_0 , d_2 , ρ and B_1 , and V_{1a} and V_{2a} are listed in Appendix.

From computation, we can choose X_0 as a free parameter to express other parameters as

$$d_2 = D_2 X_0, \quad \rho = R D_2 X_0, \quad B_1 = B X_0.$$

Then, we get

$$V_{1a} = D_2^7 X_0^{16} V_{1b}, \quad V_{2a} = D_2^{26} X_0^{56} V_{2b}, \quad V_{3a} = D_2^{48} X_0^{102} V_{3b},$$

where V_{1b} , V_{2b} and V_{3b} are expressed in term of R and B .

Using the Maple built-in command, we eliminate R from $V_{1b} = V_{2b} = 0$ to obtain

$$\begin{aligned} V_{12b} &= \text{resultant}(V_{1b}, V_{2b}, R) \\ &= -209305557128275993010925074939984178315264B^4 6(B+1)^2(B+2)^{182} \\ &\quad \times (3B+4)^{50}(8+9B)^3(15B+16)^2(23B+24)^2(3B^2+8B+8)F_1F_2^2F_3^2F_4^2F_5, \end{aligned} \quad (2.24)$$

where

$$\begin{aligned} F_1 &= 147B^5 + 874B^4 + 1668B^3 + 1104B^2 + 24B - 128, \\ F_2 &= 9279B^6 + 32016B^5 + 38156B^4 + 10960B^3 - 10700B^2 - 4864B + 2048, \\ F_3 &= 59193B^7 + 227328B^6 - 393560B^5 - 3227552B^4 - 5745904B^3 - 4141440B^2 \\ &\quad - 1167360B - 98304, \\ F_4 &= 265186629B^{14} + 3162608064B^{13} + 18146078748B^{12} + 65973784152B^{11} \\ &\quad + 166528741076B^{10} + 297577658208B^9 + 366510497088B^8 + 283043369216B^7 \\ &\quad + 89715855360B^6 - 57877204992B^5 - 76036567040B^4 - 27416985600B^3 \\ &\quad + 3643146240B^2 + 5555355648B + 1233125376, \end{aligned} \quad (2.25)$$

and F_5 can be found in the Appendix.

Then, we can find seven real positive roots from the polynomial equation $V_{12b} = 0$, however, only one satisfies $V_1 = V_2 = 0$. This solution is given by

$$B = 0.1268297707 \dots, \quad R = 0.235165980 \dots. \quad (2.26)$$

under which $V_1 = V_2 = 0$, $V_3 = -(2.677759596 \dots) \times 10^{10} \frac{D_2^5 X_0^6}{c_3^{10} a_2^4} < 0$.

Further, a simple computation shows that

$$\det \left[\frac{\partial(V_1, V_2)}{\partial(B, R)} \right] = (5.650407050 \dots) \times 10^{11} \frac{D_2^4 X_0^6}{a_2^2 c_3^8} \neq 0.$$

Thus, according to Theorem 1.1.2, two small-amplitude limit cycles can bifurcate from the equilibrium point p_0 in the system (2.6). Finally, a linear small perturbation on μ from μ_H is applied to obtain an additional small-amplitude limit cycle, giving a total of three limit cycles around the equilibrium p_0 .

2.4 Simulation of three limit cycles

In this section, we simulate the three limit cycles bifurcating from the equilibrium p_0 . Since $V_3 < 0$, the outer-most and inner-most limit cycles are stable and the middle one is unstable, and the equilibrium p_0 must be unstable. Note that all the three limit cycles and located on a 2-dimensional invariant manifold near the equilibrium p_0 .

Set $D_2 = 1, X_0 = 1, a_2 = 2, c_3 = 10$. The equilibrium point becomes $p_0 = (1, 5, \frac{50RB(6BR+B+8R+2)}{(2+B)(3BR+B+4R+2)})$. Now, we perturb the parameters B and R as

$$B = B_c - 0.000036455 \dots, \quad R = R_c - 0.000124549 \dots, \quad (2.27)$$

under which the system (2.6) becomes

$$\begin{aligned} \dot{x} &= (0.235041430 \dots)x^3y^2 + (17.62810726 \dots)x^3 - (0.099976908 \dots)x^2y^3 \\ &\quad - (7.498268139 \dots)x^2y + (0.264843112 \dots)xy^2 + (19.86323342 \dots)x, \\ \dot{y} &= (0.101911014 \dots)x^2y^3 + (7.643326115 \dots)x^2y - (0.062388356 \dots)y^3 - 2x^2yz \\ &\quad - (4.679126724 \dots)y - (2.253586630 \dots)yz, \\ \dot{z} &= -x^2y^2z + 20yx^2z - 75x^2z - (1.126793315 \dots)zy^2 + (22.53586630 \dots)yz \\ &\quad - (84.50949863 \dots)z. \end{aligned} \quad (2.28)$$

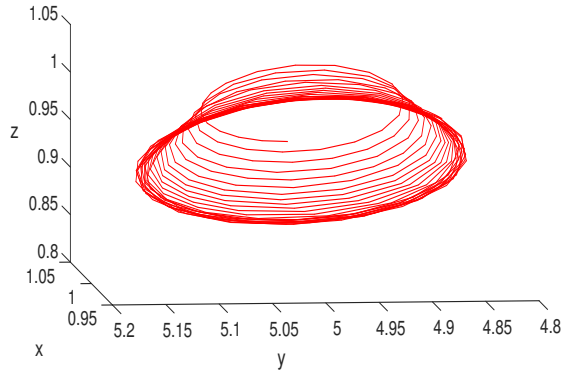


Figure 2.1: Simulation of system (2.28) showing the inner-most stable limit cycle.

2.5 Conclusion and discussion

In this chapter, we have considered a tritrophic food chain model with functional response Holling types III and IV for the predator and superpredator, respectively. We have studied the stability and bifurcation of the positive equilibrium when the prey has linear growth. We have applied center manifold and normal form theory to give a detailed analysis on the Hopf bifurcation.

Moreover, we have investigated the bifurcation of multiple limit cycles, which can cause complex dynamics in biological systems. We have particularly shown that the food chain

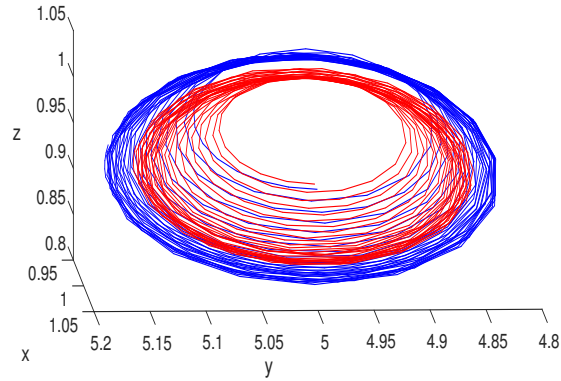


Figure 2.2: Simulation of system (2.28) showing the inner-most stable (in red) and the middle unstable limit cycle (in blue).

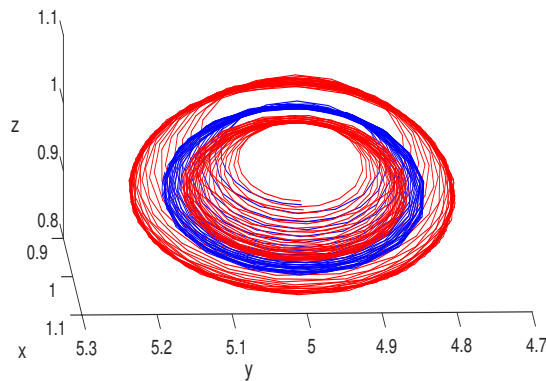


Figure 2.3: Simulation of system (2.28), showing all the limit cycles with inner-most and outer-most ones stable (in red) and middle one unstable (in blue).

model can exhibit at least three limit cycles due to Hopf bifurcation, which may explain how complex dynamical behavior occurs in such food chain systems. The numerical example shows that it is possible to have bistable phenomenon consisting of two stable limit cycles (the inner-most and outer-most ones), restricted to a center manifold. Since periodic and quasi-periodic oscillations are often observed in real biological systems, it is anticipated that the multiple limit cycle bifurcation studied in this chapter may lead to establishing a good methodology for investigating such complex dynamical behaviors. We hope that the method presented in this chapter can be used to study other nonlinear dynamical systems, and promote further research in this field.

Chapter 3

Recurrence Phenomenon in Oscillating Networks

3.1 Introduction

Today organic chemical reaction networks become more and more important in life and play a central role in their origins [38, 52, 53]. Network dynamics regulates cell division [55, 40, 56], circadian rhythms [43], nerve impulses [41] and chemotaxis [50], and provide guidelines for the development of organisms [49]. In chemical reactions, out-of-equilibrium networks have the potential to display emergent network dynamics such as spontaneous pattern formation, bistability and periodic oscillations. However, it has been noted that the principle of organic reaction networks developing complex behaviors is still not completely understood. In [54], a biologically related network organic reaction was developed, which exhibited bistability and oscillations in the concentrations of organic thiols and amides. Oscillations are generated from the interaction between three sub networks: an autocatalytic cycle that produces thiols and amides from thioesters and dialkyl disulfides; a trigger that controls autocatalytic growth; and inhibitory processes that remove activating thiol species that are generated during the autocatalytic cycle. Previous studies proved oscillations and bistability using highly evolved biomolecules or inorganic molecules of questionable biochemical relevance (for example, those used in Belousov-Zhabotinskii-type reactions)[37, 44], while the organic molecules used in [54] are related to metabolism, which is similar to those found in early Earth. The network considered in [54] can be modified to study the influence of molecular structure on the dynamics of reaction networks, and may possibly lead to the design of biomimetic networks and of synthetic self-regulating and evolving chemical systems.

Numerical simulations given in [54] has shown that that space velocities (defined as the ratio of the flow rate and the reactor volume and given in units of per second) in the range 0.0001-0.01/s would produce hysteresis. In order to test the result of simulations, the authors of [54] studied the total concentration of thiols during stepwise changes. In particular, they started from a low flow rate, then rised to a high flow rate, and finally returned to the low flow rate. To activate the autocatalytic pathway, one needs to use high thiol concentrations which are generated through self-amplification [of CSH (cysteamine)], requiring the space velocities to be lowered to 0.0005/s. It has been observed that when the space velocity reaches 0.006/s,

the system transitions will be out of the self-amplifying state. Such limits may explain the self-amplification which requires maleimide to be removed from the CSTR (continuously stirred tank reactor) more rapidly than it is added through the inlet port; while when the termination of self-amplification starts, free thiols should be removed from the CSTR by transporting out from the outlet port more rapidly than they are produced. Noticed from the model prediction, an increase of maleimide concentration reduced the bistable limit flow velocity. This chemical reaction network shows a general process to convert any quadratic autocatalytic system into a bistable switch. In [39], Epstein and Pojman found that bistable systems could generate oscillations in the presence of an inhibition reaction. In the system studied in [54], they choose acrylamide as an inhibitor, and tested this system with acrylamide in batch, which exhibited a oscillation (that is, one peak) in the concentration of free thiols. Moreover NMR (nuclear magnetic resonance) analysis has shown that the oscillation is triggered when the maleimide is removed. With a combination of numerical simulations and experiments in the CSTR under different flow rates, they found the conditions under which the addition of acrylamide can produce sustained oscillations in RSH (organic thiols). To determine how the changes in flow rate affect oscillations, the authors of [54] further examined the influence of flow rate on the stability, period and amplitude of oscillations. It showed that period increases nonlinearly with space velocity, while the amplitude increases linearly.

Recently, the recurrence phenomenon has received great attention. For example, Zhang *et al.* [60] studied the recurrence phenomenon of a newly autoimmune disease model. The newly developed 4-dimensional model exhibits recurrent dynamics, which are preserved in a reduced and rescaled 3-dimensional model as well. They analyzed the dynamics underlying this behavior in both the 4-dimensional and 3-dimensional models, and further proved that the recurrent behavior arises due to Hopf bifurcation. Moreover, some other disease models also show recurrent behavior, which was found in multifocal osteomyelitis [45, 47], eczema [42] and subacute discoid lupus erythematosus [51]. Actually, the subtypes of some diseases are clinically classified based on the patterns of this recurrent behavior [61]. Thus, an improved understanding of recurrence phenomenon in autoimmune disease is important to promoting correct diagnosis, patient management, and treatment decisions. Possibly, the recurrence phenomenon may be used to realistically explain complex dynamics in some real physical systems, and an improved understanding of recurrent dynamics in organic reactions may promote correct classification, management and utilization of energy resources.

To explain the trends in period and amplitude of oscillating networks, and the nature of bifurcations at low and high limiting space velocities, a simple kinetic model has been constructed in [54] to enable qualitative analysis on dynamic behaviors. The model simplifies the autocatalytic thiol network to bimolecular autocatalytic production of thiols from thioester, and considers the concentrations of CSSC (cystamine) and acrylamide ($[CSSC]$ and $[acrylamide]$) as constants:

$$\begin{aligned} \frac{dA}{dt} &= k_1SA - k_2IA - k_3A - k_0A + k_4S, \\ \frac{dI}{dt} &= k_0I_0 - k_0I - k_2IA, \\ \frac{dS}{dt} &= k_0S_0 - k_0S - k_4S - k_1SA, \end{aligned} \tag{3.1}$$

where $A = [\text{RSH}]$, $I = [\text{maleimide}]$, $S = [\text{AlaSEt}]$, I_0 and S_0 are the concentrations of maleimide and AlaSEt fed into the reactor, respectively, $k_i, i = 1, 2, 3, 4$, are rate constants and k_0 is the space velocity. From linear analysis [39] of this model, we find that increasing k_0 from low to high values causes two transitions. First, the system taking the transition from having a stable focus (damped oscillations) to a stable orbit (sustained oscillations) via an Andronov-Hopf bifurcation [48]. Second, the system transits from having a stable orbit to a single stable equilibrium (a stable ‘node’-an equilibrium in which the system, when perturbed, returns directly to the stable state, as opposed to orbiting around it) via a saddle-node or fold bifurcation [48].

In this chapter, we focus on the stability analysis of equilibria. The rest of the chapter is organized as follows. In the next section, we identify the saddle-node and Hopf bifurcations arising from the equilibrium and use simulation to verify the analytical predictions. Further, analysis on the Hopf bifurcation and in particular the post-critical oscillation are given in section 3.3. Numerical simulation to show the recurrence phenomenon is presented in section 3.4, which agrees very well with the experimental results given in [54]. The conclusion and discussion is drawn in Section 3.5

3.2 Stability and bifurcation: linear analysis

In this section, we present a linear analysis for model (3.1) based on the results established for general nonlinear dynamical systems in the previous section. The equilibrium solution of model (3.1) is obtained by simply setting $\dot{A} = \dot{I} = \dot{S} = 0$ and solving the resulting algebraic equations, which yields an equilibrium solution E_1 , given by

$$E_1 = \left(A_1, \frac{I_0 k_0}{A_1 k_2 + k_0}, \frac{S_0 k_0}{A_1 k_1 + k_0 + k_4} \right), \quad (3.2)$$

where A_1 is determined from the equation:

$$\frac{k_1 k_0 S_0 A_1}{k_0 + k_4 + k_1 A_1} - \frac{k_2 k_0 I_0 A_1}{k_0 + k_2 A_1} - (k_0 + k_3) A_1 + \frac{k_4 k_0 S_0}{k_0 + k_4 + k_1 A_1} = 0, \quad (3.3)$$

which is equivalent to:

$$\begin{aligned} & (k_1 k_2 k_3 + k_1 k_2 k_0) A_1^3 + [k_0^2 (k_1 + k_2) + k_0 (k_1 k_2 I_0 + k_2 k_3 + k_2 k_4 + k_1 k_3 - k_1 k_2 S_0) + k_2 k_3 k_4] A_1^2 \\ & + [k_0^3 + k_0^2 (k_2 I_0 + k_3 + k_4 - k_1 S_0) + k_0 (k_2 k_4 I_0 + k_3 k_4 - k_2 k_4 S_0)] A_1 - k_4 k_0^2 S_0 = 0 \end{aligned} \quad (3.4)$$

The data obtained from the experiments [54] for the model are given below,

$$\begin{aligned} S_0 &= 0.05M, & I_0 &= 0.01M, & k_1 &= 0.25s^{-1}M^{-1}, \\ k_2 &= 300s^{-1}M^{-1}, & k_3 &= 0.0035s^{-1}, & k_4 &= 7 \times 10^{-5}s^{-1}, \end{aligned} \quad (3.5)$$

under which system (3.4) becomes

$$\begin{aligned} F(A_1, k_0) &= \left(\frac{21}{80} + 75k_0 \right) A_1^3 + \left(\frac{1201}{4} k_0^2 - \frac{617}{320} k_0 + \frac{147}{2000000} \right) A_1^2 + (k_0^3 \\ &+ \frac{299107}{100000} k_0^2 - \frac{167951}{200000000} k_0) A_1 - \frac{7}{2000000} k_0^2 = 0. \end{aligned} \quad (3.6)$$

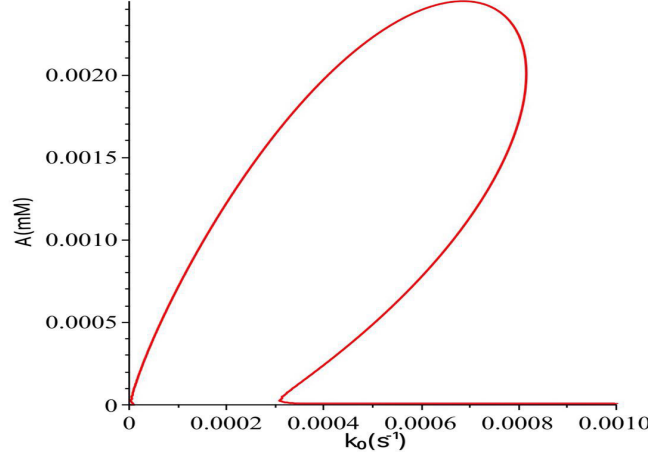


Figure 3.1: The component A_1 of the equilibrium solution E_1 , satisfying $F(A_1, k_0) = 0$.

Note that the rational numbers given in the above equation are obtained by transforming the numbers in digital format for convenience of computation. The graph depicted in Figure 1 shows the component A of the equilibrium solution E_1 , satisfying $F(A_1, k_0) = 0$.

Next, we consider the stability of equilibrium solution E_1 , and give a complete bifurcation classification. Evaluating the Jacobian of (3.1) at E_1 yields a cubic characteristic polynomial, given by

$$P_1(\lambda, A_1, k_0) = \lambda^3 + a_1(A_1, k_0)\lambda^2 + a_2(A_1, k_0)\lambda + a_3(A_1, k_0) = 0, \quad (3.7)$$

where the coefficients $a_1(A_1, k_0)$, $a_2(A_1, k_0)$ and $a_3(A_1, k_0)$, expressed in terms of A_1 and k_0 , are given below:

$$\begin{aligned} a_1(A_1, k_0) &= \frac{1}{(30000000 A_1 + 100000 k_0)(25000 A_1 + 100000 k_0 + 7)} [30000000000 k_0^3 \\ &\quad + (12010000000000 A_1 + 29912800000) k_0^2 + (90375062500000 A_1^2 \\ &\quad - 18440900000 A_1 + 2102499) k_0 + 22518750000000 A_1^3 + 65730000000 A_1^2 \\ &\quad + 749700 A_1], \\ a_2(A_1, k_0) &= \frac{1}{200000000(300A_1 + k_0)(25000A_1 + 100000k_0 + 7)} [60000000000000 k_0^4 \\ &\quad + (30025000000000000 A_1 + 119647000000000) k_0^3 + (361200250000000000 A_1^2 \\ &\quad - 113586100000000 A_1 + 12614896000) k_0^2 + (135112500000000000 A_1^3 \\ &\quad - 15796615625000000 A_1^2 + 8070650000 A_1 + 294343) k_0 + 112500000000000000 A_1^4 \\ &\quad + 1639312500000000 A_1^3 + 450555000000 A_1^2 + 102900 A_1], \\ a_3(A_1, k_0) &= \frac{1}{200000000(300A_1 + k_0)(25000A_1 + 100000k_0 + 7)} [11250000000000000 A_1^4 k_0 \\ &\quad + 9007500000000000000 A_1^3 k_0^2 + 1806001250000000000 A_1^2 k_0^3 + 1201000000000000000 A_1 k_0^4 \\ &\quad + 20000000000000 k_0^5 + 393750000000000 A_1^4 + 3215625000000000 A_1^3 k_0 \\ &\quad - 15922825625000000 A_1^2 k_0^2 - 76284300000000 A_1 k_0^3 + 59822800000000 k_0^4 \\ &\quad + 220500000000 A_1^3 + 892290000000 A_1^2 k_0 + 8041250000 A_1 k_0^2 + 8409898000 k_0^3 \\ &\quad + 30870000 A_1^2 + 205800 A_1 k_0 + 294343 k_0^2]. \end{aligned} \quad (3.8)$$

Based on the characteristic polynomial (3.7), we consider possible bifurcations from E_1 , including both static and dynamical (Hopf) bifurcations. First, we consider static bifurcation, which occurs when $P_1(\lambda, A_1, k_0) = 0$ has zero roots (zero eigenvalues). The simplest case is single zero, i.e. when $a_3(A_1, k_0) = 0$, and A_1 should simultaneously satisfy $F(A_1, k_0) = 0$ (see Eq. (3.6)). Thus, we obtain

$$\begin{aligned} A_{1s}(k_{0s}) = & -[k_{0s}(143903980000000000000000000000000k_{0s}^6 \\ & + 42828804027720000000000000000000k_{0s}^5 - 621327689014719800000000000000k_{0s}^4 \\ & + 268038693917720300000000000k_{0s}^3 + 36314317439488095000000k_{0s}^2 \\ & + 1210694204622124250k_{0s} \\ & + 15045612346947)]/[43164005995000000000000000000000000000k_{0s}^6 \\ & - 130217314646275350000000000000000000k_{0s}^5 \\ & + 29971751440639244750000000000000k_{0s}^4 \\ & - 20878835627000641625000000000k_{0s}^3 - 511166217034919556250000k_{0s}^2 \\ & + 233617980290310525000k_{0s} + 2178822504600000], \end{aligned} \quad (3.9)$$

where k_{0s} is determined from the equation,

$$\begin{aligned} F_2(k_{0s}) = & 1437601000000000000000000000000000000000000000k_{0s}^8 \\ & + 856703108514000000000000000000000000000000000k_{0s}^7 \\ & + 12668328334495684900000000000000000000000000k_{0s}^6 \\ & - 301601761466852029600000000000000000000000k_{0s}^5 \\ & + 29227088739245752225000000000000000k_{0s}^4 \\ & - 795815347914947325000000000k_{0s}^3 \\ & - 377631037207690850937500k_{0s}^2 \\ & + 63258405194198581500k_{0s} + 610426123747209. \end{aligned} \quad (3.10)$$

Solving $F_2(k_{0s}) = 0$ for k_{0s} yields four positive real solutions. Then, substituting the four solutions into $A_{1s}(k_{0s})$ using (3.9), we get four values of $A_{1s}(k_{0s})$, and two of them are positive, which yield two critical values (see the two circles in Figure 2): $(k_{0sn}, A_{1sn}) = (0.000308266 \dots, 0.000026398 \dots)$ and $(0.000815525 \dots, 0.002006192 \dots)$. By verifying the changes of the stability on both sides of the critical points on the curve $F(k_0, A_1) = 0$, we find that the first one defines a saddle-node bifurcation. For example, we select $A_1 = 0.000027$ (above the critical point), the corresponding value of k_0 is equal to $0.000308273 \dots$, under which the eigenvalues defined by equation (3.7) are $0.0000199 \dots, -0.000249107 \dots$ and $-0.112353614 \dots$, implying that the corresponding equilibrium solution is unstable. When we select $A = 0.000025$ (below the critical point), the corresponding k_0 is equal to $0.000308308 \dots$, for which the eigenvalues are $-0.000046078 \dots, -0.000244614 \dots$ and $-0.120143088 \dots$, indicating that the corresponding equilibrium solution is locally asymptotically stable.

Next, we turn to consider Hopf bifurcation which may occur from the equilibrium E_1 . To achieve this, we apply Theorem 2.1 to the equilibrium E_1 , where A_1 satisfies the polynomial equation $F(A_1, k_0) = 0$ in (3.6). Based on the cubic characteristic polynomial $P_1(\lambda, A_1, k_0) = 0$

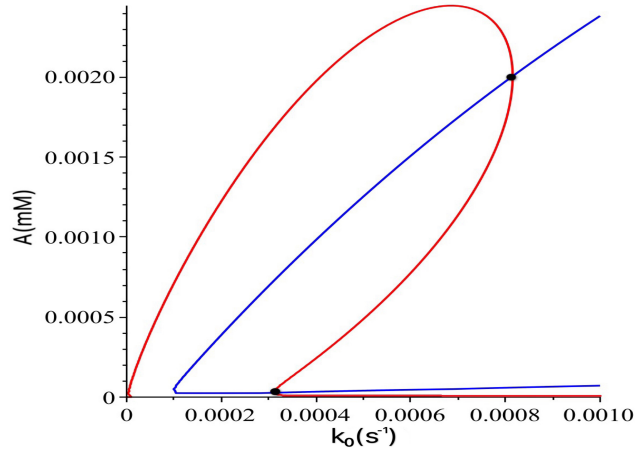


Figure 3.2: The graphs of $a_3(A_1, k_0) = 0$ and $F(A_1, k_0) = 0$.

(see Eq. (3.7)), we apply the formula, $\Delta_2(A_1, k_0) = a_1 a_2 - a_3$, to solve the two polynomial equations, $\Delta_2 = 0$ and $F(A_1, k_0) = 0$, together with the parameter values given in (3.5), yielding three candidates for Hopf critical points: $(k_{0H1}, A_{H1}) = (0.000176806 \dots, 0.001114785 \dots)$, $(0.000254830 \dots, -0.000029768 \dots)$ and $(0.000309121 \dots, 0.000033790 \dots)$. We only consider the biologically meaningful points with two positive entries to get two possible Hopf critical points (k_{0H1}, A_{H1}) and (k_{0H3}, A_{H3}) . For these two sets of solutions, we need to check if the eigenvalues defined by equation (3.7) contain a pair of purely imaginary eigenvalues and a negative eigenvalue. By a simple calculation, we find that the unique Hopf critical point is $(k_{0H}, A_H) = (0.000176806 \dots, 0.001114785 \dots)$, which is shown in Figure 3. Note that at the critical point (k_{0H}, A_H) , other stability conditions given in Theorem 2.1 are still satisfied.

As a matter of fact, by using these given parameter values, we may numerically compute the Jacobian of system (3.1) at the equilibrium E_1 to obtain a purely imaginary pair and one negative real eigenvalues: $\pm 0.001087856i \dots$ and $-0.336194209 \dots$. Therefore, on the equilibrium solution curve defined by $F(k_0, A_1) = 0$ (see Figure 4), the equilibrium E_1 is stable from the origin to the Hopf point (k_{0H}, A_H) , and unstable from (k_{0H}, A_H) to the saddle-node bifurcation point (k_{0sn}, A_{1sn}) , and then returns to stable from the saddle-node bifurcation point, as shown in Figure 3.4.

We have used the MATCONT in Matlab to obtain the numerical bifurcation diagram, as depicted in Figure 3.5, which agrees with that as given in Figure 3.1.

3.3 Normal form of Hopf bifurcation and limit cycles

In this section, we will further study the Hopf bifurcation from the equilibrium E_1 of the system (3.1), and use normal form theory to study stability of the bifurcating limit cycles. Assume that $k_0 = k_{0H} + \mu = 0.000176806 \dots + \mu$, where μ is a small perturbation (bifurcation) parameter.

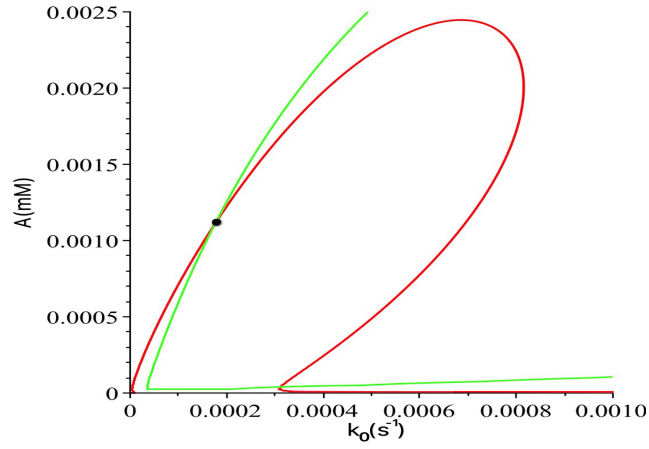


Figure 3.3: The graph of $\Delta_2 = 0$, showing Hopf bifurcation.

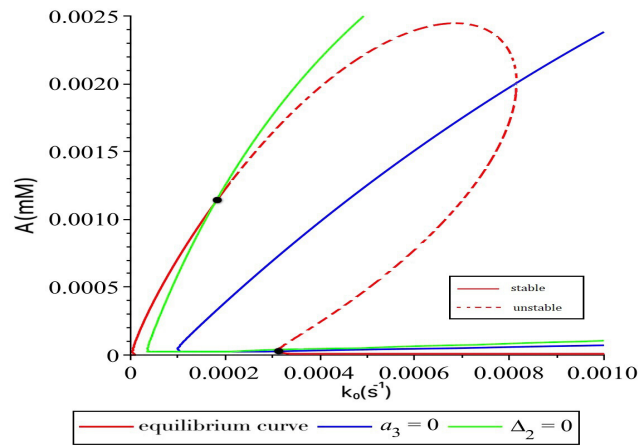


Figure 3.4: Bifurcation diagram

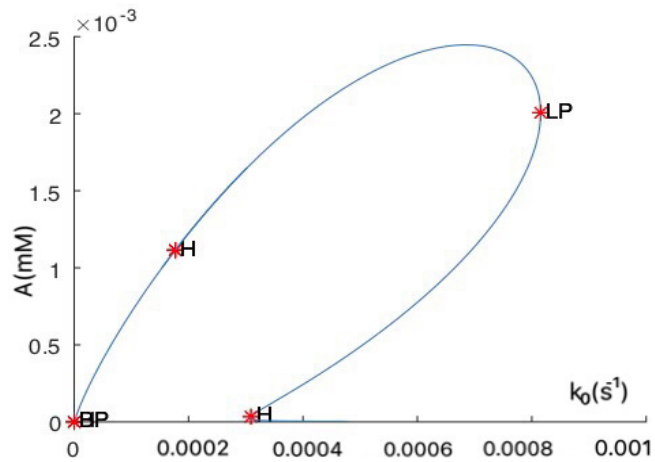


Figure 3.5: Numerical bifurcation diagram obtained by using MATCONT in Matlab, confirming the result shown in Figure 3.1.

Based on the values given in (3.5), we introduce the following transformation,

$$\begin{aligned}
A &= A_1 + x_1 + x_3, \\
I &= -0.004737302 \cdots x_1 + 0.000015401 \cdots x_2 + 1.002113047 \cdots x_3 \\
&\quad + \frac{0.000176806 \cdots + \mu}{100(300A_1 + 0.000176806 \cdots + \mu)}, \\
S &= -1.514185916 \cdots x_1 + 3.134552877 \cdots x_2 + 0.012529174 \cdots x_3 \\
&\quad + \frac{0.000176806 \cdots + \mu}{20(0.25A_1 + 0.000246806 \cdots + \mu)},
\end{aligned} \tag{3.11}$$

into system (3.1) to obtain

$$\frac{dx_i}{dt} = G_i(x_1, x_2, x_3; \mu, A_1), \quad i = 1, 2, 3, \tag{3.12}$$

where

$$\begin{aligned}
G_1(x_1, x_2, x_3; \mu, A_1) &= [-6.685965797 \times 10^{-13}x_1 + 1.270633803 \times 10^{-13}x_2 \\
&\quad + 1.451973290 \times 10^{-15} - 2.174775067 \times 10^{-10}x_1^2 + 4.537921451 \times 10^{-10}x_1x_2 \\
&\quad - 5.827487976 \times 10^{-10}x_1x_3 + 4.537921451 \times 10^{-10}x_3x_2 - 3.652712909 \times 10^{-10}x_3^2 \\
&\quad - 5.038382521 \times 10^{-13}x_3 + (1.642442597 \times 10^{-11} + 0.000004405x_3x_2 \\
&\quad + 0.000004405x_1x_2 - 0.000005657x_1x_3 - 0.000002111x_1^2 - 0.000003545x_3^2 \\
&\quad + 1.246098433 \times 10^{-9}x_1 + 1.233487325 \times 10^{-9}x_2 + 3.427342293 \times 10^{-9}x_3)\mu \\
&\quad + (7.294389852 \times 10^{-10} + 0.000770440x_1x_2 + 0.000770440x_3x_2 - 0.000989380x_1x_3 \\
&\quad - 0.000369229x_1^2 - 0.000620151x_3^2 + 0.000005074x_1 + 2.16179759310^{-7}x_2 \\
&\quad + 0.000005354x_3)A_1 - 0.9953022834A_1^3\mu - 3.984526808A_1^2\mu^2 - 0.0132706971A_1\mu^3 \\
&\quad + (4.64474398910^{-8} + 0.000002911x_2 + 0.0103992451x_3x_2 + 0.0103992451x_1x_2 \\
&\quad - 0.0133544568x_1x_3 - 0.0049837837x_1^2 - 0.0083706731x_3^2 + 0.000026078x_1 \\
&\quad + 0.000035502x_3)\mu^2 + (0.000878680x_2 + 0.035797988x_3 + 0.033677967x_1 \\
&\quad - 1.496381068x_1^2 - 2.513294604x_3^2 + 3.122373365x_1x_2 + 3.122373365x_3x_2 \\
&\quad - 4.009675672x_1x_3 - 0.000002893)A_1\mu + (0.779943388x_3x_2 + 0.779943388x_1x_2 \\
&\quad - 1.001584265x_1x_3 - 0.004135088x_1 + 0.000988827x_2 - 0.004102836x_3 \\
&\quad + 0.3424094672^{-5} - 0.3737837804x_1^2 - 0.6278004841x_3^2)A_1^2 + (3.122373365x_2 \\
&\quad - 2.513294604x_3 - 2.496381068x_1 + 0.0241785817)A_1^2\mu + (-0.0083706731x_3 \\
&\quad + 0.0103992451x_2 - 4.008317117x_1 - 0.0397006230)A_1\mu^2 + (-0.3737837804x_1 \\
&\quad + 0.7799433885x_2 - 0.6278004841x_3 - 0.0036595339)A_1^3 - 0.0133333333x_1\mu^3]/[(A_1 \\
&\quad + 0.000987226 + 4\mu)(A_1 + 5.893552658 \times 10^{-7} + 0.003333333\mu)],
\end{aligned}$$

$$G_2(x_1, x_2, x_3; \mu, A_1) = \{5.046435823 \times 10^{-12}x_1 - 8.222154554 \times 10^{-14}x_2$$

$$\begin{aligned}
& + 7.013669022 \times 10^{-16} - 3.808463387 \times 10^{-11} x_1^2 + 7.375550314 \times 10^{-11} x_1 x_2 \\
& + 4.825811507 \times 10^{-10} x_1 x_3 + 7.375550314 \times 10^{-11} x_3 x_2 + 5.206657845 \times 10^{-10} x_3^2 \\
& + 5.056493269 \times 10^{-12} x_3 - [0.01333333333(-5.950289605 \times 10^{-10} - 0.0000536994 x_3 x_2 \\
& - 0.0000536994 x_1 x_2 - 0.0003513548 x_1 x_3 + 0.0000277284 x_1^2 - 0.0003790832 x_3^2 \\
& - 0.3775567185 \times 10^{-5} x_1 + 1.035004006 \times 10^{-7} x_2 - 0.3782889752 \times 10^{-5} x_3)] \mu \\
& - [0.01333333333(-2.642633124 \times 10^{-8} - 0.0093915594 x_1 x_2 - 0.0093915594 x_3 x_2 \\
& - 0.0614488327 x_1 x_3 + 0.0048494565 x_1^2 - 0.0662982892 x_3^2 + 0.0000183015 x_1 \\
& + 0.0000104640 x_2 + 0.0000169789 x_3)] A_1 - 0.4807747388 A_1^3 \mu - 1.924701537 A_1^2 \mu^2 \\
& - 0.0064103298 A_1 \mu^3 - [0.01333333333(-0.1682711586 \times 10^{-5} + 0.0005649292 x_2 \\
& - 0.1267653433 x_3 x_2 - 0.1267653433 x_1 x_2 - 0.8294237395 x_1 x_3 + 0.0654569690 x_1^2 \\
& - 0.8948807086 x_3^2 - 0.0092468712 x_1 - 0.0092641571 x_3)] \mu^2 \\
& - [0.01333333333(0.1164626449 x_2 - 0.1039722264 x_3 - 0.0983753008 x_1 \\
& + 19.65345496 x_1^2 - 268.6879328 x_3^2 - 38.06129433 x_1 x_2 - 38.06129433 x_3 x_2 \\
& - 249.0344778 x_1 x_3 + 0.000104818)] A_1 \mu - [0.01333333333(-9.507400748 x_3 x_2 \\
& - 9.507400748 x_1 x_2 - 62.20678047 x_1 x_3 + 0.1323386341 x_1 + 0.0012071504 x_2 \\
& + 0.05989444020 x_3 - 0.0001240491 + 4.909272679 x_1^2 - 67.11605314 x_3^2)] A_1^2 \\
& - (0.01333333333(36.93870567 x_2 - 268.6879328 x_3 + 19.65345496 x_1 \\
& - 0.8759488090)) A_1^2 \mu - (0.01333333333(-0.8948807086 x_3 + 300.1232347 x_2 \\
& + 0.06545696905 x_1 + 1.438285911)) A_1 \mu^2 - [0.01333333333(4.909272679 x_1 \\
& - 9.507400748 x_2 - 67.11605314 x_3 + 0.1325786792)] A_1^3 - 0.01333333333 x_2 \mu^3 / [(A_1 \\
& + 0.000987226 + 4\mu)(A_1 + 5.893552658 \times 10^{-7} + 0.003333333\mu)],
\end{aligned}$$

$$\begin{aligned}
G_3(x_1, x_2, x_3; \mu, A_1) = & \{-1.741803333 \times 10^{-9} x_1 + 6.003510305 \times 10^{-16} x_2 \\
& + 8.241160714 \times 10^{-10} x_1^2 - 5.385351495 \times 10^{-13} x_1 x_2 - 1.737257276 \times 10^{-7} x_1 x_3 \\
& - 5.385351495 \times 10^{-13} x_3 x_2 - 1.745498436 \times 10^{-7} x_3^2 + 6.853153162 \times 10^{-18} \\
& - 1.741905912 \times 10^{-9} x_3 - [0.01333333333(-5.814110402 \times 10^{-12} \\
& + 3.920934653 \times 10^{-7} x_3 x_2 + 3.920934653 \times 10^{-7} x_1 x_2 + 0.1264851934 x_1 x_3 \\
& - 0.0006000175 x_1^2 + 0.1270852109 x_3^2 + 0.0012681588 x_1 - 4.371000039 \times 10^{-10} x_2 \\
& + 0.0012682771 x_3)] \mu - [0.01333333333(-2.582153434 \times 10^{-10} + 0.0000685736 x_1 x_2 \\
& + 0.000068573 x_3 x_2 + 22.12113583 x_1 x_3 - 0.1049377304 x_1^2 + 22.22607356 x_3^2 \\
& + 0.0001304019 x_1 - 7.640451461 \times 10^{-8} x_2 + 0.0001566166 x_3)] A_1 - 0.0046977165 A_1^3 \mu \\
& - 0.0188065253 A_1^2 \mu^2 - 0.0000626362 A_1 \mu^3 - (0.01333333333(-1.644200801 \times 10^{-8} \\
& - 0.1031837643 \times 10^{-5} x_2 + 0.0009255932 x_3 x_2 + 0.0009255932 x_1 x_2 \\
& + 298.5865536 x_1 x_3 - 1.416427958 x_1^2 + 300.0029816 x_3^2 + 2.993662281 x_1 \\
& + 2.994262198 x_3)) \mu^2 - [0.01333333333(-0.0003094171 x_2 + 0.9899843300 x_3
\end{aligned}$$

$$\begin{aligned}
& + 0.7352776462x_1 - 425.2824944x_1^2 + 90075.89521x_3^2 + 0.2779093621x_1x_2 \\
& + 0.2779093621x_3x_2 + 89650.61272x_1x_3 + 0.1024198492 \times 10^{-5}]A_1\mu \\
& - [0.0133333333(0.0694194909x_3x_2 + 0.0694194909x_1x_2 + 22393.99152x_1x_3 \\
& - 0.1036671966x_1 - 0.8814161928 \times 10^{-5}x_2 + 22.24056690x_3 - 0.1212101079 \times 10^{-5} \\
& - 106.2320969x_1^2 + 22500.22362x_3^2)]A_1^2 - [0.0133333333(0.2779093621x_2 \\
& + 90150.89521x_3 - 425.2824944x_1 - 0.0085590171)]A_1^2\mu \\
& - [0.0133333333(600.2529816x_3 + 0.0009255932x_2 - 1.416427958x_1 \\
& + 0.0140536908)]A_1\mu^2 - [0.0133333333(-106.2320969x_1 + 0.0694194909x_2 \\
& + 22500.22362x_3 + 0.0012954446)]A_1^3 - 0.0133333333x_3\mu^3\}/[(A_1 + 0.0009872263 \\
& + 4\mu)(A_1 + 5.893552659 \times 10^{-7} + 0.0033333333\mu)].
\end{aligned}$$

Note in the above equations that we have used digits format for convenience. Similarly, with $k_0 = k_{0H} + \mu = 0.000176806 \dots + \mu$, we can rewrite (3.6) as

$$\begin{aligned}
F(\mu, A_1) = & -0.2757604935 \dots A_1^3 - 75 \times A_1^3\mu + 0.0002580192 \dots A_1^2 \\
& + 1.821952649 \dots A_1^2\mu - 300.25A_1^2\mu^2 + 5.496613923 \dots \times 10^{-8}A_1 \\
& - 0.0002180204 \dots A_1\mu - 2.991600420 \dots A_1\mu^2 - A_1\mu^3 \\
& + 1.094119833 \times 10^{-13} + 1.237646058 \dots \times 10^{-9}\mu \\
& + 0.35 \times 10^{-5}\mu^2.
\end{aligned} \tag{3.13}$$

Now, the Jacobian of system (3.12) evaluated at the origin, $x_i = 0$, $i = 1, 2, 3$, at the critical point, $\mu = 0$, $A_1 = 0.001114785 \dots$ (corresponding to the positive equilibrium E_1 for model (3.1)) is in the Jordan canonical form:

$$\begin{bmatrix} 0 & 0.001087856 \dots & 0 \\ -0.001087856 \dots & 0 & 0 \\ 0 & 0 & -0.336194209 \dots \end{bmatrix}. \tag{3.14}$$

To obtain the normal form of Hopf bifurcation, we need to find ν_0 and τ_0 from linear analysis. The following theorem gives formulas for computing ν_0 and τ_0 .

Theorem 3.3.1 [59] *For the two-dimensional linear system,*

$$\begin{pmatrix} \dot{x}_1 \\ \dot{x}_2 \end{pmatrix} = \begin{bmatrix} a_{11}\mu & \omega + a_{12}\mu \\ -\omega + a_{21}\mu & a_{22}\mu \end{bmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}, \tag{3.15}$$

the following hold:

$$\nu_0 = \frac{1}{2}(a_{11} + a_{22}), \quad \tau_0 = \frac{1}{2}(a_{12} - a_{21}). \tag{3.16}$$

Based on the center manifold theory, the system on the center manifold of system (3.12) is

a two-dimensional dynamical system. Then, applying the formula (3.16), we obtain

$$\begin{aligned}
v_0 &= \frac{1}{2} \left(\frac{\partial^2 G_1}{\partial x_1 \partial \mu} + \frac{\partial^2 G_2}{\partial x_2 \partial \mu} \right) \Big|_{x_i=0, \mu=0} \\
&= \frac{1}{2} \left[\left(\frac{\partial(\frac{\partial G_1}{\partial x_1})}{\partial \mu} + \frac{\partial(\frac{\partial G_1}{\partial x_1})}{\partial A_1} \frac{\partial A_1}{\partial \mu} \right) + \left(\frac{\partial(\frac{\partial G_2}{\partial x_2})}{\partial \mu} + \frac{\partial(\frac{\partial G_2}{\partial x_2})}{\partial A_1} \frac{\partial A_1}{\partial \mu} \right) \right] \Big|_{x_i=0, \mu=0} \\
&= \frac{1}{2} \left[\left(\frac{\partial(\frac{\partial G_1}{\partial x_1})}{\partial \mu} + \frac{\partial(\frac{\partial G_1}{\partial x_1})}{\partial A_1} \frac{\partial F(\mu, A_1)}{\partial \mu} \Big|_{A_1} \right) + \left(\frac{\partial(\frac{\partial G_2}{\partial x_2})}{\partial \mu} + \frac{\partial(\frac{\partial G_2}{\partial x_2})}{\partial A_1} \frac{\partial F(\mu, A_1)}{\partial \mu} \Big|_{A_1} \right) \right] \Big|_{x_i=0, \mu=0} \\
&= 1.455701498 \dots, \\
\tau_0 &= \frac{1}{2} \left(\frac{\partial^2 G_1}{\partial x_2 \partial \mu} - \frac{\partial^2 G_2}{\partial x_1 \partial \mu} \right) \Big|_{x_i=0, \mu=0} \\
&= \frac{1}{2} \left[\left(\frac{\partial(\frac{\partial G_1}{\partial x_2})}{\partial \mu} + \frac{\partial(\frac{\partial G_1}{\partial x_2})}{\partial A_1} \frac{\partial A_1}{\partial \mu} \right) - \left(\frac{\partial(\frac{\partial G_2}{\partial x_1})}{\partial \mu} + \frac{\partial(\frac{\partial G_2}{\partial x_1})}{\partial A_1} \frac{\partial A_1}{\partial \mu} \right) \right] \Big|_{x_i=0, \mu=0} \\
&= \frac{1}{2} \left[\left(\frac{\partial(\frac{\partial G_1}{\partial x_2})}{\partial \mu} + \frac{\partial(\frac{\partial G_1}{\partial x_2})}{\partial A_1} \frac{\partial F(\mu, A_1)}{\partial \mu} \Big|_{A_1} \right) - \left(\frac{\partial(\frac{\partial G_2}{\partial x_1})}{\partial \mu} + \frac{\partial(\frac{\partial G_2}{\partial x_1})}{\partial A_1} \frac{\partial F(\mu, A_1)}{\partial \mu} \Big|_{A_1} \right) \right] \Big|_{x_i=0, \mu=0} \\
&= 1.538917076 \dots.
\end{aligned} \tag{3.17}$$

Next, substituting $\mu = 0$, and $A_1 = A_H = 0.001114785$ into system (3.12), and then applying the Maple program [58] to the resulting system yields

$$v_1 = 36.64582372 \dots, \quad \tau_1 = -54130.35015 \dots. \tag{3.18}$$

Therefore, the normal form associated with this Hopf bifurcation, up to third-order terms, is given by

$$\begin{aligned}
\dot{r} &= r(v_0 \mu + v_1 r^2) \\
&= r(1.455701498 \dots \mu + 36.64582372 \dots r^2), \\
\dot{\theta} &= w_c + \tau_0 \mu + \tau_1 r^2 \\
&= 0.001087856 \dots + 1.538917076 \dots \mu - 54130.35015 \dots r^2.
\end{aligned} \tag{3.19}$$

The steady-state solutions of Eq. (3.19) are determined from $\dot{r} = \dot{\theta} = 0$, yielding

$$\bar{r} = 0, \quad \bar{r}^2 \approx -0.039723530 \dots \mu. \tag{3.20}$$

The equilibrium $\bar{r} = 0$ represents the equilibrium E_1 of model (3.2). A linear analysis on the first differential equation of (3.19) shows that $\frac{d}{dr}(\frac{dr}{dt})|_{\bar{r}=0} = v_0 \mu$, and thus $\bar{r} = 0$ (ie. the equilibrium E_1) is stable (unstable) for $\mu < 0$ (> 0), as expected. When μ is increased from negative to cross zero, a Hopf bifurcation occurs and the amplitude of the bifurcating limit cycles is approximated by the nonzero steady state solution,

$$\bar{r} = 0.1993076279 \dots \sqrt{-\mu} \quad (\mu < 0). \tag{3.21}$$

Since $\frac{d}{dr}(\frac{dr}{dt})|_{(3.21)} = 2v_1 \bar{r}^2 = -2v_0 \mu > 0$ ($\mu < 0, v_0 > 0, v_1 > 0$), the Hopf bifurcation is subcritical and so the bifurcating limit cycles are unstable. Equation (3.21) gives the approximate amplitude of the bifurcating limit cycles, while the phase of the motion is determined by

$\theta = \omega t$, where ω is given by

$$\omega = \left. \frac{d\theta}{dt} \right|_{(3.21)} = 0.001087856 \cdots + 2151.787535 \cdots \mu. \quad (3.22)$$

3.4 Simulations

In this section, we present simulation to demonstrate the behavior changes of solutions, showing a good agreement with the experimental results reported in [54].

Based on the given parameter values in (3.5), the system (3.1) can be rewritten as

$$\begin{aligned} \frac{dA}{dt} &= 0.25SA - 300IA - 0.0035A - k_0A + 0.00007S, \\ \frac{dI}{dt} &= 0.01k_0 - Ik_0 - 300IA, \\ \frac{dS}{dt} &= -0.25SA - k_0S - 0.00007S + 0.05k_0. \end{aligned} \quad (3.23)$$

We use the ode45 package in Matlab to simulate the above system to obtain the results, as shown in Figure 3.6.

It is seen from Figure 3.6 that the solutions of A are oscillating when the values of k_0 are chosen between k_{0H} and k_{0sn} . The period of oscillation increases with the increase of k_0 , as shown in Figure 3.7. This shows the interesting recurrence phenomenon, which has been also studied by Zhang *et al* for a recurrent autoimmune disease model [60]. From a biological point of view, the subtypes of some diseases are classified based on the patterns of this recurrent behavior [61]. Therefore, an improved understanding of recurrence phenomenon in autoimmune disease is crucial to promoting correct diagnosis, patient management, and treatment decisions. For the recurrence phenomenon studied in this chapter, it can be used to realistically explain complex dynamics in organic reactions and promote correct classification, management and utilization of energy resources.

By simulation, we also find that the stable region before the Hopf critical point as shown in Figure 3.4 (i.e. for $k_0 \in (0, k_{0H})$) can be divided into two parts: globally asymptotic stable and locally asymptotic stable. The approximate value of the dividing point can be obtained as follows: Recall $k_{0H} = 0.000176806$, we choose $k_0 = 0.00014466350$ and two initial points $(A, I, S) = (1, 1, 1)$ and $(0.001, 0.000005, 0.016)$ for simulation and obtain the results as shown in Figures ?? and 3.9, respectively. It is seen that the trajectory starting from the first initial point converges a large stable limit cycle, while that starting from the second critical point converges to the equilibrium E_1 . We also choose $k_0 = 0.00014466348$ and the initial point $(A, I, S) = (1, 1, 1)$ to obtain the result depicted in Figure ?. It is shown that the trajectory eventually converges to the equilibrium E_1 even from a far away initial point, showing that the E_1 is globally asymptotically stable for this value of k_0 . Thus, the approximate dividing point for globally asymptotic stability and locally asymptotic stability is $k_0 \approx 0.00014466348$.

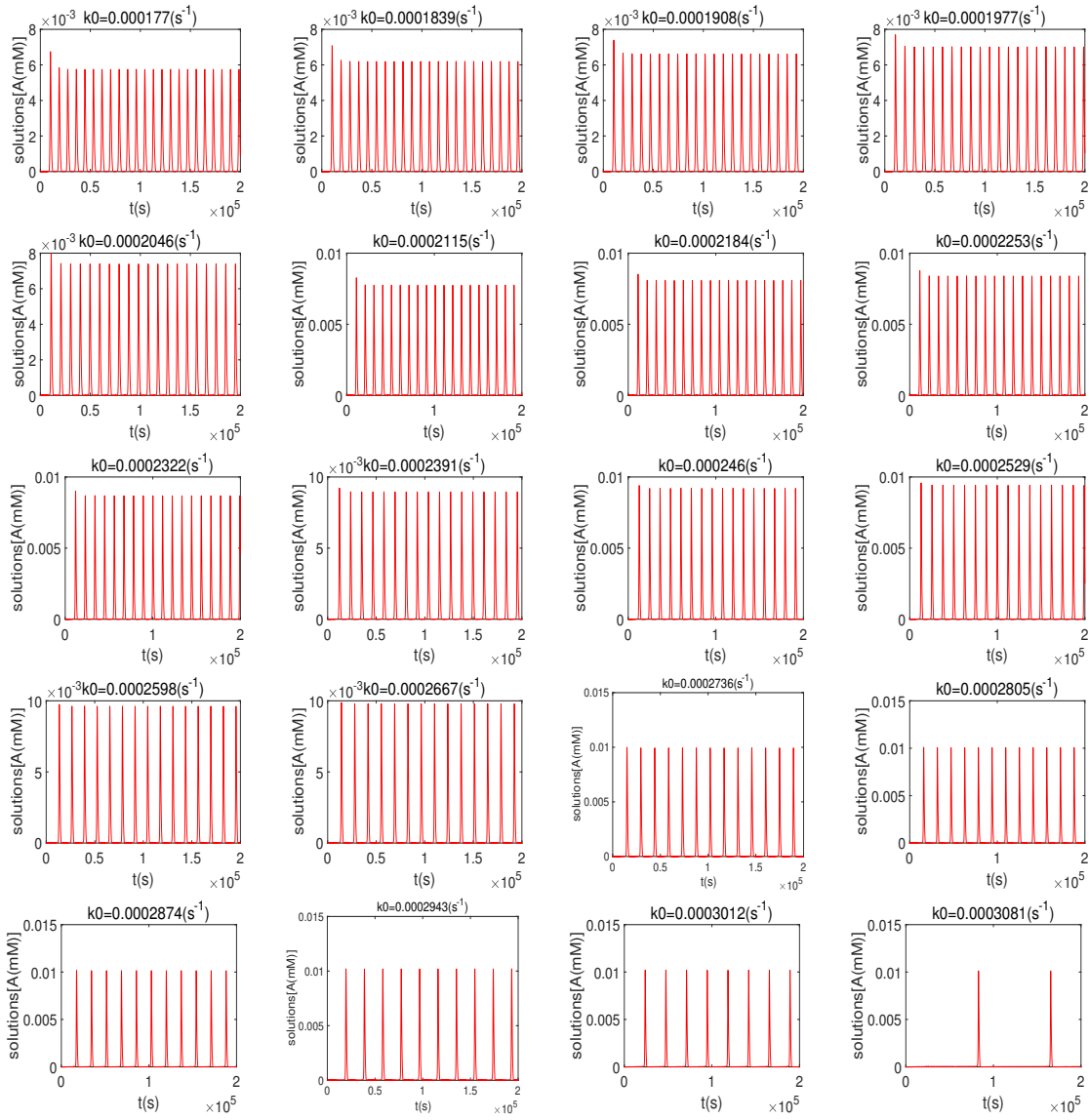


Figure 3.6: Simulated component A of system (3.23) for $k_0 = k_{0H} + 0.0000069j$, $j = 1, 2, \dots, 20$.

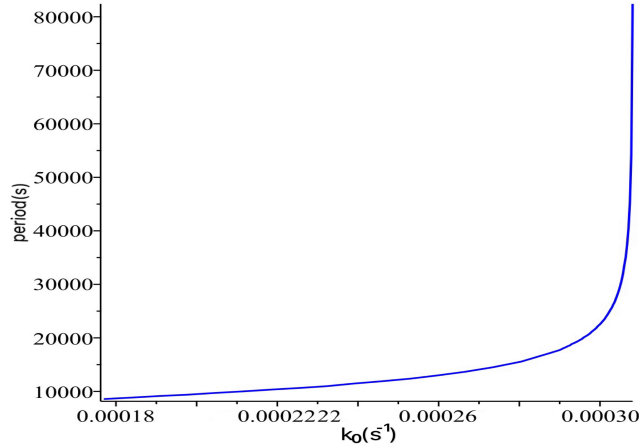


Figure 3.7: The period of oscillation with respect to k_0 .

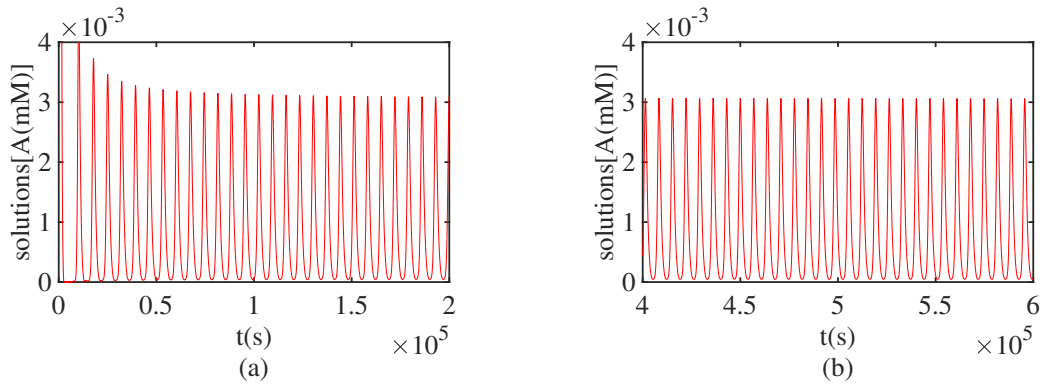


Figure 3.8: Simulated trajectory of system (3.23), starting from $t = 0$ and ended at $t = 6 \times 10^6$, converging to a large stable limit cycle starting from the initial point $(1, 1, 1)$ for $k_0 = 0.00014466350$: (a) showing time history for $t \in (0, 2 \times 10^5)$; and (b) showing time history for $t \in (4 \times 10^5, 6 \times 10^5)$.

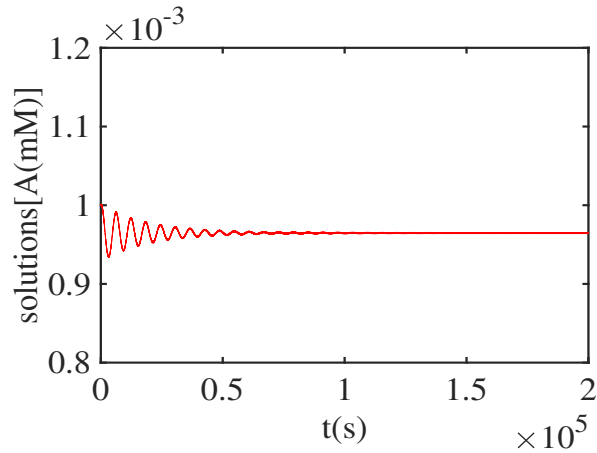


Figure 3.9: Simulated trajectory of system (3.23), converging to the equilibrium E_1 starting from the initial point $(0.001, 0.000005, 0.016)$ for $k_0 = 0.00014466350$.

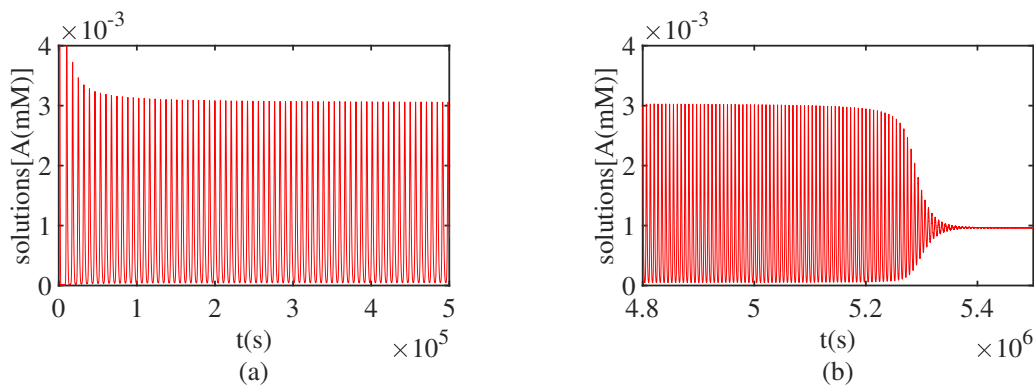


Figure 3.10: Simulated trajectory of system (3.23), starting from $t = 0$ and ended at $t = 6 \times 10^6$, converging to the equilibrium E_1 starting from the initial point $(1, 1, 1)$ for $k_0 = 0.00014466348$: (a) showing time history for $t \in (0, 5 \times 10^5)$; and (b) showing time history for $t \in (4.8 \times 10^6, 5.5 \times 10^6)$.

3.5 Conclusion and discussion

In this chapter, we have analyzed the stability and bifurcation in a kinetic model, which was constructed to enable qualitative analysis of dynamic behaviors in oscillating networks of biologically relevant organic reactions. In particular, a Hopf bifurcation is identified to be subcritical, and recurrence phenomenon is induced from the Hopf bifurcation for a pretty large interval of parameter. Simulations are given to verify the theoretical predictions and to show a very good agreement. The recurrence phenomenon studied in this chapter for a kinetic model which characterizes oscillating networks of biologically relevant organic reactions may be one of the sources of generating complex dynamics in biological systems or even more generally in real physical systems. It is anticipated that the method developed in this chapter can be applied to study other nonlinear dynamical systems, and promote further development in this field.

Chapter 4

Conclusion and Future work

4.1 Conclusion

In this thesis, we have applied nonlinear dynamical system theory to study two practical biological models: a tritrophic food chain model with Holling functional response types III and IV for the predator and superpredator, respectively and an oscillating networks model of biologically relevant organic reactions. In particular, we have used stability and bifurcation theory to investigate the dynamical behavior arising from Hopf bifurcation and multiple limit cycle bifurcation, which may explain how complex dynamical behavior occurs in such systems. Simulations are given to verify the theoretical predictions.

For the tritrophic food chain model studied in Chapter 2, we focus on the stability and bifurcation of the positive equilibrium when the prey has linear growth. Center manifold theory and normal form theory are applied to analyze Hopf bifurcation. Moreover, bifurcation of multiple limit cycles is explored to show that the food chain model can exhibit at least three limit cycles due to Hopf bifurcation, which may explain the complex dynamical behavior occurring in such food chain systems. The multiple cycle bifurcation, confirmed by simulation, indicates that a new bistable phenomenon consisting of two stable oscillations (the inner-most and outer-most limit cycles), can occur in such a food chain model. Since periodic and quasi-periodic oscillations are often observed in practical biological systems, it is anticipated that the multiple limit cycle bifurcation studied in this thesis can establish a good method for investigating such complex dynamical behaviors.

For the oscillating networks model studied in Chapter 3, a Hopf bifurcation is identified to be subcritical, and recurrence phenomenon is induced from the Hopf bifurcation for a pretty large interval of a parameter. Simulations are given to verify the theoretical predictions and to show a very good agreement. The recurrence phenomenon studied in this thesis may explain how complex dynamics occurs in biological systems or even more generally in real physical systems. It is expected that the method developed in this thesis can be applied to consider other nonlinear dynamical systems and promote further development in this field.

4.2 Future work

There are some interesting but also challenging problems that are worth to study further.

In Chapter 2, we obtain at least three limit cycles in the food chain model due to Hopf bifurcation. However, this result is based on the assumption that the prey has a linear growth, which is a unbounded function. More realistically, the linear growth should be modified as a bounded function, for example, the logistic equation. Certainly, studying such a nonlinear growth function is much more challenging, but exhibit more interesting results. Also, to make the complex algebraic computation manageable, we have set fixed values for some parameters. It would be interesting to see what the maximal number of limit cycles can be achieved if all parameters are chosen free.

In Chapter 3, we study the recurrence phenomenon in the oscillating networks model, and use the method of normal forms to analytically determine the Hopf critical point, and show that the Hopf bifurcation is subcritical by using just one bifurcation parameter. If we choose more parameters, say two parameters, as bifurcation parameters, can we analytically determine the generalized Hopf bifurcation? Also, in this thesis, we use numerical simulation to show the critical point which divides the interval of the parameter corresponding to the stable equilibrium into two parts: one is locally asymptotically stable and the other is globally asymptotically stable. Thus, as a future work, we will try to use an analytical approach such as Lyapunov function method to give a rigorous mathematical proof and find the algebraic expression to determine this critical point.

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Appendix A

In Section 2.2 of Chapter 2, the V_{1a} and V_{2a} are given below.

$$\begin{aligned}
 V_{1a} = & 190B_1^9 d_2^7 + 5823B_1^8 d_2^6 \rho + 74616B_1^7 d_2^5 \rho^2 + 516841B_1^6 d_2^4 \rho^3 + 2082330B_1^5 d_2^3 \rho^4 + 4855896B_1^4 d_2^2 \rho^5 + 6029856B_1^3 d_2 \rho^6 + 3048192B_1^2 \rho^7 + 2660B_1^8 X_0 d_2^7 + 78636B_1^8 X_0 d_2^6 \rho + 972132B_1^8 X_0 d_2^5 \rho^2 + 6499616B_1^8 X_0 d_2^4 \rho^3 \\
 & + 25307088B_1^8 X_0 d_2^3 \rho^4 + 57179952B_1^8 X_0 d_2^2 \rho^5 + 69149376B_1^8 X_0 d_2 \rho^6 + 34380288B_1^8 X_0 \rho^7 + 15960B_1^7 X_0^2 d_2^7 + 455172B_1^7 X_0^2 d_2^6 \rho + 5428668B_1^7 X_0^2 d_2^5 \rho^2 + 35023680B_1^7 X_0^2 d_2^4 \rho^3 + 131680092B_1^7 X_0^2 d_2^3 \rho^4 \\
 & + 287756400B_1^7 X_0^2 d_2^2 \rho^5 + 337626432B_1^7 X_0^2 d_2 \rho^6 + 163759104B_1^7 X_0^2 \rho^7 + 53200B_1^6 X_0^3 d_2^7 + 1465344B_1^6 X_0^3 d_2^6 \rho + 16871464B_1^6 X_0^3 d_2^5 \rho^2 + 105038400B_1^6 X_0^3 d_2^4 \rho^3 + 381078184B_1^6 X_0^3 d_2^3 \rho^4 + 804123776B_1^6 X_0^3 d_2^2 \rho^5 \\
 & + 912658304B_1^6 X_0^3 d_2 \rho^6 + 429576192B_1^6 X_0^3 \rho^7 + 106400B_1^5 X_0^4 d_2^7 + 2839440B_1^5 X_0^4 d_2^6 \rho + 31619552B_1^5 X_0^4 d_2^5 \rho^2 + 190070544B_1^5 X_0^4 d_2^4 \rho^3 + 664935376B_1^5 X_0^4 d_2^3 \rho^4 + 1352318144B_1^5 X_0^4 d_2^2 \rho^5 + 1480145152B_1^5 X_0^4 d_2 \rho^6 \\
 & + 672995328B_1^5 X_0^4 \rho^7 + 127680B_1^4 X_0^5 d_2^7 + 3327936B_1^4 X_0^5 d_2^6 \rho + 35998592B_1^4 X_0^5 d_2^5 \rho^2 + 209153920B_1^4 X_0^5 d_2^4 \rho^3 + 704389664B_1^4 X_0^5 d_2^3 \rho^4 + 1375463936B_1^4 X_0^5 d_2^2 \rho^5 + 1443665408B_1^4 X_0^5 d_2 \rho^6 + 629407744B_1^4 X_0^5 \rho^7 \\
 & + 85120B_1^3 X_0^6 d_2^7 + 2215872B_1^3 X_0^6 d_2^6 \rho + 23511744B_1^3 X_0^6 d_2^5 \rho^2 + 132067456B_1^3 X_0^6 d_2^4 \rho^3 + 425126784B_1^3 X_0^6 d_2^3 \rho^4 + 786673152B_1^3 X_0^6 d_2^2 \rho^5 + 777416704B_1^3 X_0^6 d_2 \rho^6 + 317521920B_1^3 X_0^6 \rho^7 + 24320B_1^2 X_0^7 d_2^7 \\
 & + 689664B_1^2 X_0^7 d_2^6 \rho + 7351936B_1^2 X_0^7 d_2^5 \rho^2 + 39342592B_1^2 X_0^7 d_2^4 \rho^3 + 115571456B_1^2 X_0^7 d_2^3 \rho^4 + 187174912B_1^2 X_0^7 d_2^2 \rho^5 + 154066944B_1^2 X_0^7 d_2 \rho^6 + 48758784B_1^2 X_0^7 \rho^7 + 43008B_1 X_0^8 d_2^6 \rho + 483328B_1 X_0^8 d_2^5 \rho^2 \\
 & + 1412096B_1 X_0^8 d_2^4 \rho^3 - 2496512B_1 X_0^8 d_2^3 \rho^4 - 20799488B_1 X_0^8 d_2^2 \rho^5 - 38469632B_1 X_0^8 d_2 \rho^6 - 23592960B_1 X_0^8 \rho^7 - 65536X_0^9 d_2^5 \rho^2 - 917504X_0^9 d_2^4 \rho^3 - 4980736X_0^9 d_2^3 \rho^4 - 13107200X_0^9 d_2^2 \rho^5 - 16777216X_0^9 d_2 \rho^6 \\
 & - 8388608X_0^9 \rho^7,
 \end{aligned}$$

$$\begin{aligned}
 V_{2a} = & 1566767862220559410419204096X_0^{30} \rho^{26} + 1615491072B_1^{30} d_2^{26} + 5616915145497151241453568B_1^{30} \rho^{26} - 51493574661926498662041845235712B_1^{30} X_0^{27} d_2^6 \rho^{20} \\
 & - 27971434658404737495577309216768B_1^{30} X_0^{27} d_2^5 \rho^{21} - 6660479065380721153124423696384B_1^{30} X_0^{27} d_2^4 \rho^{22} + 3499605027152561581515314561024B_1^{30} X_0^{27} d_2^3 \rho^{23} \\
 & + 4025658451720501600221954834432B_1^{30} X_0^{27} d_2^2 \rho^{24} + 1619394882390787724957901127680B_1^{30} X_0^{27} d_2 \rho^{25} - 478313946361626624B_1^{30} X_0^{27} d_2^4 \rho^2 - 35513029308513779712B_1^{30} X_0^{28} d_2^3 \rho^3 \\
 & - 1264667219894558785536B_1^{30} X_0^{28} d_2^2 \rho^4 - 28487775409239018700800B_1^{30} X_0^{28} d_2 \rho^5 - 452543913381432697815040B_1^{30} X_0^{28} \rho^6 - 536600948223057293685552B_1^{30} X_0^{29} \rho^7 \\
 & - 49113900594231696745824256B_1^{30} X_0^{28} d_2^8 \rho^8 - 354158016711274130007130112B_1^{30} X_0^{28} d_2^7 \rho^9 - 2034763617195911230259200000B_1^{30} X_0^{28} d_2^6 \rho^{10} - 9341207982479964524943245312B_1^{30} X_0^{28} d_2^5 \rho^{11} \\
 & - 34002684911068372093030629376B_1^{30} X_0^{28} d_2^4 \rho^{12} - 95520546964793629896939143168B_1^{30} X_0^{28} d_2^3 \rho^{13} - 191147050919283962656426295296B_1^{30} X_0^{28} d_2^2 \rho^{14} - 189185372437994969079209787392B_1^{30} X_0^{28} d_2 \rho^{15} \\
 & + 351455553358327094241413562368B_1^{30} X_0^{28} d_2^8 \rho^{16} + 223790189895860148459645359040B_1^{30} X_0^{28} d_2^7 \rho^{17} + 6190483300810719699247478865920B_1^{30} X_0^{28} d_2^6 \rho^{18} \\
 & + 11811632821143043137592140759040B_1^{30} X_0^{28} d_2^5 \rho^{19} + 1689626921252722531747683893248B_1^{30} X_0^{28} d_2^4 \rho^{20} + 18468082500266070356576796934144B_1^{30} X_0^{28} d_2^3 \rho^{21} \\
 & + 1531102183930330060868987912192B_1^{30} X_0^{28} d_2^2 \rho^{22} + 9362195266082360040017914494976B_1^{30} X_0^{28} d_2 \rho^{23} + 3993281674537398031306828283904B_1^{30} X_0^{28} d_2^2 \rho^{24} \\
 & + 1062982802402942553927758905344B_1^{30} X_0^{28} d_2 \rho^{25} - 296393150476320768B_1 X_0^{29} d_2^3 \rho^3 - 17236401673853730816B_1 X_0^{29} d_2^2 \rho^4 - 441383233148537536512B_1 X_0^{29} d_2 \rho^5 \\
 & - 6276260491537378443264B_1 X_0^{29} \rho^6 - 46478572699320651350016B_1 X_0^{29} d_2^9 \rho^7 + 23339916890796617367552B_1 X_0^{29} d_2^8 \rho^8 + 5095746646859631921463296B_1 X_0^{29} d_2^7 \rho^9 \\
 & + 70878133203522963017564160B_1 X_0^{29} d_2^6 \rho^{10} + 610870659090303834409402368B_1 X_0^{29} d_2^5 \rho^{11} + 3874971782820400278433431552B_1 X_0^{29} d_2^4 \rho^{12} + 19202512912878866273579040768B_1 X_0^{29} d_2^3 \rho^{13} \\
 & + 76478463262845275391878234112B_1 X_0^{29} d_2^2 \rho^{14} + 248522867683632458898402705408B_1 X_0^{29} d_2 \rho^{15} + 664056354842142804057501204480B_1 X_0^{29} \rho^{16} \\
 & + 1463012460280402356107539906560B_1 X_0^{29} d_2^9 \rho^{17} + 2654038698987177867057762926592B_1 X_0^{29} d_2^8 \rho^{18} + 3943336193681313519067226701824B_1 X_0^{29} d_2^7 \rho^{19} \\
 & + 4751697548206931438690377924608B_1 X_0^{29} d_2^6 \rho^{20} + 4571912680230561391877717753856B_1 X_0^{29} d_2^5 \rho^{21} + 3429831522985365858215666909184B_1 X_0^{29} d_2^4 \rho^{22} \\
 & + 193332273919627056975043362816B_1 X_0^{29} d_2^3 \rho^{23} + 770268710461531085821993549824B_1 X_0^{29} d_2^2 \rho^{24} + 193393827868209102850155872256B_1 X_0^{29} d_2 \rho^{25} \\
 & - 3115142450923633789958360342528B_1^5 X_0^{25} d_2^12 \rho^{14} - 137903484571095428228470167044096B_1^5 X_0^{25} d_2^11 \rho^{15} - 413010997572062864341078743449600B_1^5 X_0^{25} d_2^10 \rho^{16} \\
 & - 945010117522963114195309798883328B_1^5 X_0^{25} d_2^9 \rho^{17} - 1714571463347991579063666130026496B_1^5 X_0^{25} d_2^8 \rho^{18} - 2494313501467179283894785347158016B_1^5 X_0^{25} d_2^7 \rho^{19} \\
 & - 290439274843571660706835084397728B_1^5 X_0^{25} d_2^6 \rho^{20} - 2676352796714457972412647682867200B_1^5 X_0^{25} d_2^5 \rho^{21} - 1910119684964937806903419317780480B_1^5 X_0^{25} d_2^4 \rho^{22}
 \end{aligned}$$

Appendix B

In Section 2.3 of Chapter 2, F_5 is given by

$$\begin{aligned} F_5 = & -864464377694645416623129992344153559007022296693513484920422400B + 2228306636658271597680217190712124929833066993086157821238033736794112B^9 \\ & - 40435209964788672146644072100858576391561470115673355682305802240B^3 - 8918435998193445262141304707525582575088268563207977047666196480B^2 \\ & + 2833668187910231954767839263180657180541636809081398759513714065408B^5 + 78718308342022918287936146803681132485676509344598352818037850112B^4 \\ & + 27081297340361231405196066604128902110172584960204378361661197647872B^6 + 174087484365990852717439671855048944628683714503171788350866864472064B^7 \\ & + 798659496595526480275430414068083769643346262472645628861740042158080B^8 - 852744691736691109416296752563291608072603295836565421132433510629376B^{10} \\ & - 49199497352029688521240172293846721419180371919411141607100881543223936144113664B^{28} - 16147183674470087554218532691689097007161921517412184941680970441195738825228288B^{27} \\ & - 131405270820585046639393043952480754451383602714317248134622775701516890153156608B^{29} - 4304961477745220764118281630398404713078606597759412885681244910201214091657216B^{26} \\ & - 691392610024376260623143828455472386550042593996705703013962739848616752447488B^{25} - 317492713766703952829346944132422019590734236155172839211379021777884314513440768B^{31} \\ & + 133239266481636432023330830377276717523086636610410083280565869074438099566592B^{24} + 187464463292809544282197747635910544370359334476415709113367241070354368561152B^{23} \\ & + 107958976668820913879275680087326706132925098484172366971593007037049613582336B^{22} + 46612618781269434279626994261138858794741358277175328648141259923815053393920B^{21} \\ & + 16494827270600767238354142611397787650055480300946358362589298392919909072896B^{20} + 4818349368201861877824035055288737817622233233957955371827966800623612985344B^{19} \\ & + 110859568348120500859621483523440401211602514487234920480124940199535837184B^{18} + 165669841975284358430462960032793240728806162451056288354272815736978145280B^{17} \\ & - 4832384744940670989357217144056634736674917660314855438032018724442079232B^{16} - 14178377202552699290952826200991320221928521549329002584615928618582802432B^{15} \\ & - 6068390752867003242669510150983134361855175544158376829920884340994080768B^{14} - 174897187780955504538723924655233737877046302000247022248310659291807744B^{13} \\ & - 37436109303659530323772645293537928820157513185550423110354763488690176B^{12} - 53106130597903514386047931702617243249438598624499369291523039395053568B^{11} \\ & - 34313945632736272058442969453574860833977262463190895375155200 - 33683119304032183110184323317919313893520717898668783216904818332349136497893441536B^{46} \\ & - 17003144062760968660378327971680603042297257407408497731219251030899999434650681344B^{47} - 134957276746875374923740385526185669316527203034155340751941671021525279793217536B^{48} \\ & + 14598890496414185672815357588603844868395540369528038737624096019537196853839790080B^{49} + 25424557460646419148144180225350840615902048737132715932645573075791321948655452160B^{50} \\ & + 31474737963311881579881757559731529639809699796442780369269232486327042788219158528B^{51} + 32873453628273140083345243605651374606435678446495047563671113485125527175811825664B^{52} \\ & + 30546159339109793682256860679103923049408985544494515968285366876963144727938465792B^{53} + 2585112344367004287038634740049852437432901691811192170171770593704842582510534656B^{54} \\ & + 20177113058915606384468292494734631280216959459146300939875379474618849998451769344B^{55} + 1463667154214617724399895699198075086710844885539449434620662948387567111505969152B^{56} \\ & + 9921138618776562537984320957278331701159948281439215925119770231634777125626576896B^{57} + 6310320766191126860970727551161443717011112652601244561387596833164429511173865472B^{58} \\ & + 3780233358783349505927533651321978985679402273456129965748655094265079298189688832B^{59} + 2140322894056250862109839779098251242812183270191712458734361124653797398508732416B^{60} \\ & + 1149245991122357815944901422666152674603625056567297516394939707028866435395878912B^{61} + 587155069352855427238307672185496171300384390401429571418058545893085484175851520B^{62} \\ & + 286305189953955179443254051407672522644422391479631134638669293790606627158622208B^{63} + 133594410393301385725454277620591695253095671894615595022191321750371784920662016B^{64} \\ & + 59773636951182552650757868176629574034267681878494188791146472074744794349305856B^{65} + 25677040000419505167533313221126178157135865410136068517703108022651829481373696B^{66} \\ & + 1059450281139796543829525540378709881249172522528791828913137507428106835066880B^{67} + 4196733970864559766834478064870957861353132426914563568994861684921869113671680B^{68} \\ & + 159369491822918834842145955500708457236757596830019867308761287375394770209968B^{69} + 578701469294295591246827381793060381798577336547355021534568801525564069355520B^{70} \\ & + 200191557319770776421689775503577188357998172315669561498340562971883901743104B^{71} + 65658766542693861484359458767644475310768417586505388593791370222847605429248B^{72} \\ & + 20304229537682847837317954520997667919386328220424826875768975758404783750144B^{73} + 5886902644112089761620872545778248355121788188868511223978983602535475382272B^{74} \\ & + 1592818627034952058685318652214702491762873415568845081553651877294462686208B^{75} + 401241465543680213387790306398757347271232587480278829553889448387702697728B^{76} \\ & + 94249923916521150078631218433850868235096101060610524854527623145144260096B^{77} + 20779989489319877399703583527515752404274744627420873836464639501307364608B^{78} \end{aligned}$$

$$\begin{aligned}
& + 4345297599775069282697579532388400651195712670826494946595220215542599680B^{79} + 868972384463904100851813025901258804307166316085191317833898103884890816B^{80} \\
& + 165484192416576952892901312705393490193724491190309149387567938234737024B^{81} + 29245075587337576633344008537713123120888688274749905671834797032187232B^{82} \\
& + 4555663712743241880421362741450860233110581772191842840074454087427232B^{83} + 571203288451571386296560176966060474242703259416798380702889700896704B^{84} \\
& + 45319613426612752343825810807691253162714659912018743506866830950320B^{85} - 1166794620597851651132049664252200430087126021140256853680082067840B^{86} \\
& - 1167381368576163646122125939493350946776752691699180733944948876112B^{87} - 232014361115239982403914227205551240816761671666820553619417342976B^{88} \\
& - 29089711529355303661726972081845878836559016936740276694197256084B^{89} - 2531005177185608266508542071673123140278795495815090933305932166B^{90} \\
& - 149549367622987447906965545183008044019692794618873264044429134B^{91} - 5388560723782331297633859785815789431262103166195127966521279B^{91} \\
& - 84326158219881805836473602514305641213212565918588218889317B^{93} + 359098678279423005492281073288668612343391930044438789855B^{94} \\
& - 705270480874162918169608110073368268522537624966304359348574139956490396827123712B^{31} - 1453958760790569308791949958366380197063623226292517763245785721961171315719143424B^{32} \\
& - 2797996262562109015457342459943542965547840278377491465733471147728298223465398272B^{33} - 5044974575917371484501132736820586236904525763486455461910071644523550372989501440B^{34} \\
& - 8543409870289718450699464386071673866841751490524878712398611467681143253981200384B^{35} - 13608617423245523405894914150642309702400480048230350832936036026665374854036848640B^{36} \\
& - 20405997303863177725693194521993698607009852985321509564527723749485208239467397120B^{37} - 28810242368459463269971368614587250624125571885153881901444790768153139965797072896B^{38} \\
& - 38280805555684489034710760396940203846702171434690372106253958276636584037761155072B^{39} - 47808392031978545468308470698705868203390102357918540121152716534999523869698555904B^{40} \\
& - 55983682169042299585838324922562174124498351621236948599502049551986015611813625856B^{41} - 61212354610447227687052064722571085382706601186933989786117763996122484650761256960B^{42} \\
& - 62053562539165251376337717718395036211556223836300620038119531132553698274487304192B^{43} - 57606292059355173319533379830506677784159720091834317708244075016902418159785476096B^{44} \\
& - 47830058126634418936613575278542918103861716825094407287265778119890736613787959296B^{45}.
\end{aligned}$$

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