# Predator-Prey Models with Discrete Time Delay

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Predator-Prey Models with Discrete Time Delay

AUTHOR:

Guihong Fan, B.Sc (Yantai Normal University),M.S. (Yunnan University, P.R.China),M.Sc. (McMaster University)

SUPERVISOR:

Dr. G.S.K. Wolkowicz

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### Abstract

Our goal in this thesis is to study the dynamics of the classical predator-prey model and the predator-prey model in the chemostat when a discrete delay is introduced to model the time between the capture of the prey and its conversion to biomass. In both models we use Holling type I response functions so that no oscillatory behavior is possible in the associated system when there is no delay. In both models, we prove that as the parameter modelling the delay is varied Hopf bifurcation can occur. However, we show that there seem to be differences in the possible sequences of bifurcations. Numerical simulations demonstrate that in the classical predator-prey model period doubling bifurcation can occur, possibly leading to chaos while that is not observed in the chemostat model for the parameters we use.

For a delay differential equation, a prerequisite for Hopf bifurcation is the existence of a pair of pure imaginary eigenvalues for the characteristic equation associated with the linerization of the system. In this case, the characteristic equation is a transcendental equation with delay dependent coefficients. For our models, we develop two different methods to show how to find values of the bifurcation parameter at which pure imaginary eigenvalues occur. The method used for the classical predator-prey model was developed first. However, it was necessary to develop a more robust, less complicated method to analyze the predator-prey model in the chemostat with a discrete delay. The latter method was then generalized so that it could be applied to any second order transcendental equation with delay dependent coefficients.

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### Chapter 1

### Introduction

In this thesis, we consider two predator-prey models with discrete time delay. One is the classical Gause type predator-prey model and the other is the resource based chemostat model. We choose Holling type I response functions so that no nontrivial oscillating solutions are possible in the absence of delay. The delay is introduced to model the time between the capture of the prey and its conversion to viable biomass. In this chapter, we give a brief literature review related to predator-prey models. Then we introduce the models that will be considered, first without and then with delay. We conclude this chapter by reviewing the results on solutions of transcendental equations with delay dependent coefficients. Analysis of such equations constitutes a major part of our contribution to the study of these models.

#### 1.1 Predator-Prey Models

The classical Lotka-Volterra predator-prey model ([39], [52]) is one of the simplest mathematical models to incorporate interactions between species, and it serves as a basis for many models used today to analyze population dynamics (see Chapter 6 in [15], Chapter 11 in [25], and Chapter 3 in [42]). Although this model is a milestone in the history of mathematical modelling, its inadequacy cannot be neglected. The phase plane is a center and hence the model predicts that the population sizes oscillate and that the amplitude of the oscillations depends on the initial conditions. This phenomenon does not seem to occur in real ecosystems.

One of the unrealistic assumptions of this model is that prey reproduce exponentially in the absence of predation. Various modifications have been introduced, see Gause, Smaragdova, and Witt [19], Rosenzweig [44], and Schoener [47]. Among them, Gause et al. [19] proposed the so called Gause type predator-prey model when they analyzed the interaction between Paramecium and Didinium. The classical Gause type predator-prey model incorporates population regulation (also termed as overcrowding or intraspecific competition) by replacing the exponential growth term with a logistic growth term for the prey population in the absence of predation. Ever since, models of this type (discrete, continuous or integral) with different forms of functional response describing predator growth dependency on prey density have been studied by ecologists, biologists, and mathematicians, see Armstrong[2]-[3], Hassell and May [23], Hassell [24], Hsu, Hwang, and Kuang [32], Kuang and Freedman [36], Rosenzweig [45]-[46], Sugie, Kohno, and Miyazakiand [49].

The first mathematical description of functional responses dates back to Holling

[27], [28], and [29]. Holling described the changes in organism's (predator's) feeding rates as a function of the changes on the density of food (prey population) and called this the functional response. He proposed three forms of response functions, Holling type I, II, and III. The Holling type I function takes the form mx, The Holling type II function is a saturating function of the form  $\frac{mx}{a+x}$ , and is particularly relevant for nonlearning predators. This form is also called Michaelis-Menten when used in enzyme kinetics. Parameter m is called the maximum specific growth rate and a is called the half saturation constant since it is the concentration at which the half maximal growth rate  $\frac{m}{2}$  is reached. The Holling type III function  $\frac{mx}{(a+x)(b+x)}$  is S-shaped. It is most useful for predators that show a certain type of learning ability. When the prey population is below a threshold density, predators have difficulty capturing the prey. Above that threshold predators tend to increase their feeding rate as the prey density increases until a saturation level is met. Holling type response functions have become the most often used functional forms used in models of population dynamics.

Oscillation in population size has often been observed in natural ecosystems. After Lotka and Volterra, many modelers have tried to derive models that account for these oscillations. They are particularly interested in the existence of stable periodic solutions. Biologists and ecologists attempt to find more realistic models that can capture the observed oscillations in experiments or in natural ecosystems (see Armstrong [2]-[3], Hassell and May [24]). In this area, mathematicians try to understand the qualitative properties of the models. They are interested in the local and global stability of equilibrium solutions. See for example, Cheng, Hsu, and Lin [11], Hsu, Hubbelld, and Waltman [31], Hsu, Hwang, and Kuang [32], Kuang and Freedman [36], May [40], Sugie, Kohno, and Miyazaki [49]. They also often try to determine necessary and sufficient conditions that guarantee the existence of periodic solutions.

Hsu et al. [31] investigated the dynamics of a Gause type predator-prey model with Holling type II response function  $\frac{mx}{a+x}$ . They showed that either the predators die out and the prey population approaches its carrying capacity, or the interior equilibrium is globally asymptotically stable, or there is a periodic orbit which is stable if it is unique. If there is more than one periodic orbit, the outer one is stable from the outside and the inner one is stable from the inside. They conjectured that the periodic orbit is unique. The conjecture was later proved by Cheng [10]. Ding [14] studied the model further and gave a classification of the dynamics in the case of response function  $\frac{x^n}{a+x^n}$  for both n = 1 and 2. He proved that when a periodic orbit exists it is unique. Sugie et al. [49] considered this model with response functions allowing n to be any real positive number and obtained necessary and sufficient conditions under which the system has exactly one stable limit cycle. Kuang and Freedman [36] considered a more generalized predator-prey model of Gause type and derived criteria for the uniqueness of limit cycles which includes the results of Cheng [10].

The Gause type predator-prey model with the Holling type I response function is given by

$$\begin{cases} \dot{x}(t) = rx(t)\left(1 - \frac{x(t)}{K}\right) - my(t)x(t), \\ \dot{y}(t) = -sy(t) + Ymy(t)x(t), \end{cases}$$
(1.1.1)

where x(t) denotes the density of the prey population and y(t) the density of predators. Parameters r, K, s, Y, and m are positive constants denoting the intrinsic growth rate and the carrying capacity of the prey, the death rate of the predator in the absence of prey, the yield constant, and the maximal growth rate of the predator, respectively. It is known that for this model either the predator population becomes extinct and the prey population approaches its carrying capacity, or the predator population and the prey population coexist and their density approaches a positive equilibrium that is an asymptotically stable spiral. The Dulac criterion is used to eliminate the possibility of any nontrivial periodic solution. The Poincaré-Bendixson Theorem is used to prove that the positive equilibrium is globally asymptotically stable when it exists. This system has no nontrivial periodic solution. For a detailed analysis, refer to Chapter 6 and 8 in reference [15].

We are interested to study how delay affects the dynamics of this model. In particular, we wish to determine whether delay can induce periodic solutions. We include a time delay in (1.1.1) to model the time between the capture of the prey and its conversion to viable biomass and obtain the following system:

$$\begin{cases} \dot{x}(t) = rx(t) \left( 1 - \frac{x(t)}{K} \right) - y(t)x(t), \\ \dot{y}(t) = -sy(t) + Ye^{-s\tau}my(t-\tau)x(t-\tau). \end{cases}$$
(1.1.2)

Here the term  $e^{-s\tau}y(t-\tau)$  represents the density of the predator population at time t, that captured prey at time  $t-\tau$  and survived the  $\tau$  units of time required to process the captured prey. The reason we chose the Gause type predator-prey model with Holling type I response function instead of a more realistic response function is that we are guaranteed that there is no intrinsic periodicity without delay, and and so it is possible to isolate the effect of the delay. If the delay can produce oscillating behavior in this model, then it is very likely that it can also induce oscillatory behavior in a model with more detailed response functions. The way we incorporate delay in this

system was first proposed by Freedman, So, and Waltman [18] when they modelled a single species in the chemostat feeding on a growth-limiting nutrient. See also Ellermeyer [16], Wang and Wolkowicz [53], Xia and Wolkowicz [56], Xia, Wolkowicz, and Wang [57]. Other researchers obtained a similar model when they considered a structured population model. One such model was studied by Gourley and Kuang [21]. They considered a two-stage predator-prey ecosystem, where they assumed that juvenile predators take  $\tau$  units of time to mature. If the juveniles suffer the same mortality rate as adult predators, their model reduces to the model (1.1.2). Cooke, Elderkin, and Huang [12] also obtained the same model when they considered inactive juvenile predators in their predator-prey model. We improve the existing results concerning the dynamics of (1.1.2) by extending the analytical results and giving less complicated criteria that are easier to apply.

In Chapter 2, we show that model (1.1.2) can have up to three equilibria. We analyzed the stability of each equilibrium and obtained some analytical results about the Hopf bifurcation of the interior equilibrium as the delay  $\tau$  varies. Combining the analytical results with the numerical simulations, we confirmed that a stable periodic solution bifurcates from the interior equilibrium as the time delay increases from zero. As the time delay increases further the periodic solution eventually disappears through a secondary Hopf bifurcation. Numerically, we determine there is a parameter range for the parameter  $\tau$  where more complicated dynamics including a series of period doubling occurs, possibly leading to chaotic dynamics. This appears to be a new result.

#### 1.2 The Predator-Prey Model in the Chemostat

In Chapter 3, we studies the chemostat version of the predator-prey model. This scenario has attracted the attention of many investigators (see [7], [8], [34], [50]) mainly motivated by the feasibility to test the mathematical predictions in a laboratory environment. The chemostat, also known as a Continuous Stir Tank Reactor (CSTR) in the engineering literature, is a basic piece of laboratory apparatus used for the continuous culture of microorganisms. It has potential for such process as wastewater decomposition and water purification. Some ecologists consider it a lake in a laboratory. It consists of three vessels, the feed bottle which contains fresh medium with all the necessary nutrients, the growth chamber where the microorganisms interact, and the collection vessel. The fresh medium from the feed bottle is continuously added to the growth chamber. The growth chamber is well stirred and its contents are then removed to the collection vessel at a rate that maintains constant volume. For a detailed description of the importance of the chemostat and its application in biology and ecology, one can refer to [30] and [48].

The following system describes a food chain in the chemostat where a predator population feeds on a prey population of microorganisms which in turn consumes a nonreproducing nutrient that is assumed to be growth limiting at low concentrations.

$$\begin{cases} \dot{s}(t) = (s^{0} - s(t))D_{0} - \frac{x(t)f(s(t))}{\eta}, \\ \dot{x}(t) = x(t)\left(-D + f(s(t))\right) - \frac{y(t)g(x(t))}{\xi}, \\ \dot{y}(t) = -\Delta y(t) + y(t)g(x(t)). \end{cases}$$
(1.2.3)

Here s(t) represents the concentration of the nutrient, x(t) the density of the prey population, and y(t) the density of the predator population. Parameter  $s^0$  denotes the input nutrient concentration,  $D_0$  the dilution rate,  $\eta$  (or  $\xi$ ) the growth yield constant, and D (or  $\Delta$ ) a sum of the natural death rate and the dilution rate of the prey (or predator) population, respectively. Here f(s) denotes the functional response of the prey population on the nutrient and g(x) denotes the predators functional response on the prey.

Butler, Hsu, and Waltman [7] considered the coexistence of two competing predators feeding on a single prey population growing in the chemostat. As a subsystem of their model, they studied the global stability of system (1.2.3) with both f(s) and g(x) taking the form of Holling type II. They proved that under certain conditions the interior equilibrium is globally asymptotically stable with respect to the interior of the positive cone. If one particular condition is reversed, they proved there is at least one limit cycle and conjectured that the limit cycle is unique and would be a global attractor with respect to the non-critical orbits in the open positive octant. This conjecture was partially solved by Kuang [34]. Kuang showed that there is a range of parameters that guarantees the uniqueness of the limit cycle of this system and roughly located the position of the limit cycle. But he was unable to give an explicit estimate of the parameter range.

Bulter and Wolkowicz [8] studied predator mediated coexistence in the chemostat assuming  $D_0 = D = \Delta$ . Model (1.2.3) was studied as a submodel. For general monotone response functions, Bulter and Wolkowicz showed that (1.2.3) is uniformly persistent if the sum of the break even concentrations of substrate and prey is less than the input rate of the nutrient  $s^0$ . However they showed that it is necessary to specify the form of the response functions to discuss the global dynamics of the model. If f(s) is modelled by Holling type I or II and g(x) by Holling type I, Bulter and Wolkowicz proved that (1.2.3) could have three potential equilibrium points and that there is a transfer of global stability from one equilibrium point to another as different parameters are varied making conditions favorable enough for a new population to survive. In this case, there are no periodic solutions. However, even if f(s)is given by Holling type I, if g(x) is given by Holling type II, they showed that a Hopf bifurcation can occur in (1.2.3), and numerical results indicated that the bifurcating periodic solution is asymptotically stable.

We include a time delay in (1.2.3) as we did in the predator-prey model and require that both f(s) and g(x) are modelled by the simplest form for the response functions, Holling type I so that (1.2.4) has no nontrivial periodic solutions without delay. With delay modelling the time required for the predator to process the prey after it has been captured, the model is given by

$$\begin{cases} \dot{s}(t) = (s^{0} - s(t))D_{0} - \frac{x(t)f(s(t))}{\eta}, \\ \dot{x}(t) = x(t)\left(-D + f(s(t))\right) - \frac{y(t)g(x(t))}{\xi}, \\ \dot{y}(t) = -\Delta y(t) + e^{-\Delta\tau}y(t-\tau)g(x(t-\tau)). \end{cases}$$
(1.2.4)

We are interested whether delay can induce oscillatory behavior in this system.

In Chapter 3 we analyze the stability of each equilibrium and prove that the coexistence equilibrium can undergo Hopf bifurcations. Numerical simulations appear to show that (1.2.4) can have a stable periodic solution bifurcating from the coexistence equilibrium as the delay parameter increases from zero. This periodic orbit can then disappear through a secondary Hopf bifurcation as the delay parameter increases further.

# 1.3 2<sup>nd</sup> Order Transcendental Equations with Delay Dependent Coefficients

To study stability switches of models with delay, we consider the roots of the characteristic equation. In this case we consider the stability of the coexistence equilibrium, and so evaluate the characteristic equation given by

$$P(\lambda) = \lambda^2 + p(\tau)\lambda + (q(\tau)\lambda + c(\tau))e^{-\lambda\tau} + \alpha(\tau) = 0.$$
(1.3.5)

A necessary condition for Hopf bifurcation is that the characteristic equation has a pair of pure imaginary eigenvalues. However, since (1.3.5) involves a transcendental term and also its coefficients depend on delay, it is difficult to find the actual values of the parameter modeling the delay, at which pure imaginary roots occur. For coefficients with special form, there are some results, see [54], [57] and [58]. In [5], Beretta and Kuang consider a general equation of the form

$$P_n(\lambda,\tau) + Q_m(\lambda,\tau)e^{-\lambda\tau} = 0, \qquad (1.3.6)$$

where  $n > m \ge 0$  and

$$P_n(\lambda,\tau) = \sum_{k=0}^n p_k(\tau)\lambda^k, \qquad Q_m(\lambda,\tau) = \sum_{k=0}^m q_k(\tau)\lambda^k.$$

Coefficients  $q_k(\tau)$  and  $p_k(\tau)$  are continuously differentiable functions for  $\tau \ge 0$ . Equation (1.3.5) is a special case of (1.3.6) when n = 2 and m = 1. Beretta and Kuang provide a systematic method for finding pure imaginary roots of (1.3.6). Although their method is constructive, it relies heavily on numerical techniques.

In Chapter 4, we present sufficient conditions that guarantee the existence of pure imaginary roots for (1.3.5). Also a procedure is proposed to find the delay values

at which the pure imaginary roots occur. The method also depends on numerical techniques, but extra care is taken to define all functions involved explicitly, which endows the method with some advantages in applications. The method is applied to a single patch model in Brauer, van den Driessche, and Wang [6], where they consider a patchy environment disease model and assume that the host has a period of immunity of fixed length  $\tau$  after recovery from the disease. For (1.3.5) in the case of constant coefficients, a considerable amount of work has been done, and the interested reader is referred to [9], [13], and [33] and the references therein.

The remainder of this thesis is organized as follows. In Chapter 2, we consider the delayed Gause type predator-prey model. In Chapter 3, we consider the analogous model for predator-prey interaction with delay in the chemostat. In Chapter 4, we generalize the method given in Chapter 3 used to find pure imaginary roots of the characteristic equation so that it can be applied to any second order transcendental equation with delay dependent coefficients. This method can be used to study Hopf bifurcations of delay differential equations for characteristic equations that are second order transcendental equations of the form (1.3.5).

#### Chapter 2

# A Gause Type Predator-Prey Model with Delay

#### 2.1 Model Considered

In this chapter, we are interested in a predator-prey model with discrete time delay. Let x(t) denote the density of the prey population and y(t) the density of the predator. The model is given by

$$\begin{cases} \dot{x}(t) = rx(t) \left(1 - \frac{x(t)}{K}\right) - y(t)f(x(t)), \\ \dot{y}(t) = -sy(t) + Y e^{-s\tau} y(t-\tau)f(x(t-\tau)), \end{cases}$$
(2.1.1)

where r, K, s and Y are positive constants and  $\tau$  is a nonnegative constant. In the absence of the predator population, it is assumed that the prey population grows logistically with intrinsic growth rate r and carrying capacity K. In the absence of the prey population, the predator population declines exponentially at rate s. The function f(x) denotes the response function of predators to the prey density. We consider the simplest choice for the response function, Holling type I, i.e. f(x) = mx, where m > 0, so that the model has no periodic orbits if delay is ignored.

It is assumed that the process of conversion of the prey, once caught, to predator biomass takes  $\tau$  units of time. Therefore  $e^{-s\tau}y(t-\tau)$  represents the density of the predator population at time t, that captured prey at time  $t - \tau$  and survived the  $\tau$  units of time required to process the captured prey. Parameter Y is a growth yield constant.

For any integer  $n \ge 1$ , define  $\mathbb{R}^n_+ = \{(x_1, x_2, \dots, x_n) \in \mathbb{R}^n | x_i \ge 0, 1 \le i \le n\}$ and denote its interior by  $\operatorname{Int} \mathbb{R}^n_+ = \{(x_1, x_2, \dots, x_n) \in \mathbb{R}^n | x_i > 0, 1 \le i \le n\}$ . For  $\tau > 0$ , let  $\mathbb{C}([-\tau, 0], \mathbb{R}^2)$  denote the space of continuous functions mapping the interval  $[-\tau, 0]$  into  $\mathbb{R}^2$  with the uniform norm, i.e. if  $\phi \in \mathbb{C}([-\tau, 0], \mathbb{R}^2)$ ,  $\|\phi\| = \sup_{\theta \in [-\tau, 0]} |\phi(\theta)|$ , where  $|\cdot|$  is any norm in  $\mathbb{R}^2$ . Let  $\mathbb{C}^2_+ = \mathbb{C}([-\tau, 0], \operatorname{Int} \mathbb{R}^2_+)$ . If  $\sigma > 0$ and  $\phi : [-\tau, \sigma) \to \operatorname{Int} \mathbb{R}^2_+$ , define  $\phi_t(\theta) = \phi(t + \theta)$  for  $t \in [0, \sigma)$  and  $\theta \in [-\tau, 0]$ . Then if  $\phi$  is continuous on  $[-\tau, \sigma)$ , then  $\phi_t \in \mathbb{C}^2_+$ . For system (2.1.1), we consider any initial data in  $\operatorname{Int} C^2_+$ .

### 2.2 Scaling of the Model and Basic Properties of Solutions

We introduce the following change of variables in order to simplify model (2.1.1):

$$\begin{split} \breve{t} &= rt, \qquad \breve{x}(\breve{t}) = x(t)/K, \qquad \breve{y}(\breve{t}) = my(t)/r, \\ \breve{\tau} &= r\tau, \qquad \breve{s} = \frac{s}{r}, \qquad \qquad \breve{Y} = YKm/r. \end{split}$$
(2.2.2)

A direct calculation, using (2.1.1) gives:

$$\begin{split} \frac{d\breve{x}}{d\breve{t}} &= \frac{1}{Kr} \frac{dx}{dt} \\ &= \frac{1}{Kr} \left[ rx(t) \left( 1 - \frac{x(t)}{K} \right) - my(t)x(t) \right] \\ &= \frac{x(t)}{K} \left( 1 - \frac{x(t)}{K} \right) - \frac{my(t)}{r} \frac{x(t)}{K} \\ &= \breve{x}(\breve{t})(1 - \breve{x}(\breve{t})) - \breve{y}(\breve{t})\breve{x}(\breve{t}), \end{split}$$

and

$$\begin{split} \frac{d\breve{y}}{d\breve{t}} &= \frac{m}{r^2} \frac{dy}{dt} = \frac{m}{r^2} \left[ -sy(t) + Y e^{-s\tau} my(t-\tau) x(t-\tau) \right] \\ &= -\frac{s}{r} \frac{my(t)}{r} + \frac{YKm}{r} \exp\left\{ -\frac{s}{r} r\tau \right\} \frac{my(t-\tau)}{r} \frac{x(t-\tau)}{K} \\ &= -\breve{s}\breve{y}(\breve{t}) + \breve{Y} e^{-\breve{s}\breve{\tau}}\breve{y}(\breve{t}-\breve{\tau})\breve{x}(\breve{t}-\breve{\tau}). \end{split}$$

To simplify the notation, we drop the 's and study the equivalent scaled version of model (2.1.1):

$$\begin{cases} \dot{x}(t) = x(t)(1 - x(t)) - y(t)x(t), \\ \dot{y}(t) = -sy(t) + Ye^{-s\tau}y(t - \tau)x(t - \tau). \end{cases}$$
(2.2.3)

Let  $\tau = 0$  in (2.2.3). To have biological significance, an equilibrium point of (2.2.3) is only assumed to exist provided all of its components are nonnegative. In this case, the model has been well studied (see [15]). If Y < s, the model has two equilibria (0,0) and (1,0). Equilibrium (0,0) is a saddle point and (1,0) is globally asymptotically stable with respect to the positive cone. When Y = s, equilibrium points (1,0) and  $(\frac{s}{Y}, 1 - \frac{s}{Y})$  coalesce and are globally attracting. If Y > s, there is one more equilibrium point  $(\frac{s}{Y}, 1 - \frac{s}{Y})$ . Equilibrium point (0,0) remains a saddle point, equilibrium point (1,0) becomes a saddle point, and equilibrium point  $(\frac{s}{Y}, 1 - \frac{s}{Y})$  is globally asymptotically stable. Therefore system (2.1.1) with response function modeled by Holling type I has no periodic solutions. If the response function is

allowed to be Holling type II, it is possible that (2.1.1) has periodic solutions (see [31]). But in this thesis, we restrict ourselves to the simplest case, the Holling type I response function in order to see whether delay can destabilize model (2.1.1) by means of a Hopf bifurcation resulting in periodic solutions. If delay can destabilize the simplest model, it is likely that delay can destabilize a model with more detailed response functions.

**Lemma 2.1.** Solutions of (2.2.3) with initial data  $C_+^2$  exist on  $[0, \sigma)$ , for some  $\sigma > 0$ , and are unique and positive for  $0 < t < \sigma$ .

**Proof.** Since the right hand side of (2.2.3) is smooth, by Theorem 2.1 and 2.3 in Hale and Verduyn Lunel [22], solutions of (2.2.3) with such initial data exist on  $0 < t < \sigma$  for some  $\sigma > 0$ , and are unique. Suppose (x(t), y(t)) is a solution of (2.2.3) for  $t \in [0, \sigma)$ . Without loss of generality, assume that  $[0, \sigma)$  is the maximum interval of the solution and  $\sigma = \infty$  if the solution exists for any t > 0. Integrating the equation

$$\dot{x}(t) = x(t) (1 - x(t)) - y(t)x(t)$$

gives

$$x(t) = \phi_1(0) \exp\left(\int_0^t (1 - x(t) - y(t)) ds\right) > 0, \qquad t \in [0, \sigma).$$

Hence the prey population density x(t) is positive for any  $t \in [0, \sigma)$ .

To prove the predator population density y(t) > 0 for any  $t \in [0, \sigma)$ , use the method of contradiction. Suppose there exists  $\hat{t} \in [0, \sigma)$  such that

$$y(\hat{t}) = 0$$
, and  $y(t) > 0$  for any  $t \in [-\tau, \hat{t})$ .

Then  $\dot{y}(\hat{t}) \leq 0$ . From the second equation of the system (2.2.3), we have

$$\dot{y}(\hat{t}) = -sy(\hat{t}) + Ye^{-s\tau}y(\hat{t}-\tau)x(\hat{t}-\tau) = Ye^{-s\tau}y(\hat{t}-\tau)x(\hat{t}-\tau) > 0,$$

a contradiction. Hence y(t) > 0 for all  $t \in [0, \sigma)$ .

**Lemma 2.2.** The solutions of (2.2.3) are bounded for  $t \ge 0$ . In addition  $\limsup_{t\to\infty} x(t) \le 1$ .

**Proof.** From the first equation of (2.2.3)

$$\dot{x}(t) = x(t)(1 - x(t)) - y(t)x(t) \leq x(t)(1 - x(t)).$$

Consider  $\dot{z}(t) = z(t) (1 - z(t))$ , this is the well known logistic equation.

Given 
$$\epsilon_0 > 0$$
,  $\exists T > 0$  s.t.  $|z(t)| < 1 + \epsilon_0$  for  $\forall t \ge T$ .

By Theorem A.4 in **Appendix A**,  $x(t) \leq z(t)$  and so  $0 < x(t) < 1 + \epsilon_0$  for all  $t \ge T$ .

To prove y(t) is bounded, we define

$$w(t) = Y e^{-s\tau} x(t-\tau) + y(t).$$
(2.2.4)

Then

$$\begin{split} \dot{w}(t) &= Y e^{-s\tau} \frac{dx(t-\tau)}{dt} + \frac{dy(t)}{dt} \\ &= -sy(t) + Y e^{-s\tau} x(t-\tau) \left(1 - x(t-\tau)\right) \\ &= -sw(t) + sY e^{-s\tau} x(t-\tau) + Y e^{-s\tau} x(t-\tau) \left(1 - x(t-\tau)\right) \\ &= -sw(t) + Y e^{-s\tau} x(t-\tau) \left(s + 1 - x(t-\tau)\right) \\ &\leq -sw(t) + \frac{1}{4} Y e^{-s\tau} (s+1)^2, \\ (x(t-\tau) - 2(s+1))^2 \geq 0. \end{split}$$

and since  $(x(t - \tau) - 2(s + 1))^2 \ge 0$ ,

$$x(t-\tau)(s+1-x(t-\tau)) \leq \frac{(s+1)^2}{4}.$$

Therefore, by Theorem A.4,  $w(t) \leq z(t)$ , where  $z(t) = z(0)e^{-st} + \frac{1}{4s}Ye^{-s\tau}(s+1)^2(1-e^{-st})$  is the solution of the initial value problem

$$\dot{z}(t) = -sz(t) + \frac{1}{4}Ye^{-s\tau}(s+1)^2, \qquad z(0) = w(0).$$

Consequently  $w(t) \leq w(0) + \frac{1}{4s} Y e^{-s\tau} (s+1)^2$ . By (2.2.4),

$$Ye^{-s\tau}x(t-\tau) + y(t) = w(t) \le w(0) + \frac{1}{4s}Ye^{-s\tau}(s+1)^2$$
  
$$\le \left(Ye^{-s\tau}x(-\tau) + y(0)\right) + \frac{1}{4s}Ye^{-s\tau}(s+1)^2.$$

Therefore y(t) is bounded.

#### 2.3 Equilibria and their Stabilities

For the sake of biological realism, we only consider equilibria with nonnegative components. Model (2.2.3) can have three equilibria  $E_0 = (0,0), E_1 = (1,0)$  and

$$E_{+} = (x_{+}(\tau), y_{+}(\tau)) = (\frac{s}{Y}e^{s\tau}, 1 - \frac{s}{Y}e^{s\tau}).$$
(2.3.5)

Note, therefore, that  $E_+$  exists and is distinct from  $E_1$  if and only if  $0 \leq \tau < \tau_c$ , where

$$\tau_c = \frac{1}{s} \ln\left(\frac{Y}{s}\right). \tag{2.3.6}$$

We call  $E_+$  the coexistence equilibrium.

To analyze the local stability of each equilibrium, we use the linearization technique for differential equations with discrete delays (see Hale and Verduyn Lunel [22]). The linearization of system (2.2.3) about any one of the three equilibria  $E_0$ ,  $E_1$  and  $E_+$ , denoted as  $(x^*, y^*)$  is given by

$$\begin{bmatrix} \dot{x}(t) \\ \dot{y}(t) \end{bmatrix} = \begin{bmatrix} 1 - 2x^{\star} - y^{\star} & -x^{\star} \\ 0 & -s \end{bmatrix} \begin{bmatrix} x(t) \\ y(t) \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ Ye^{-s\tau}y^{\star} & Ye^{-s\tau}x^{\star} \end{bmatrix} \begin{bmatrix} x(t-\tau) \\ y(t-\tau) \\ (2.3.7) \end{bmatrix},$$

The characteristic equation  $P(\lambda)$  is given by det A = 0, where

$$A = \begin{bmatrix} 1 - 2x^{\star} - y^{\star} - \lambda & -x^{\star} \\ Y e^{-(s+\lambda)\tau} y^{\star} & -s + Y e^{-(s+\lambda)\tau} x^{\star} - \lambda \end{bmatrix}.$$

Therefore

$$P(\lambda) = (\lambda + s)(\lambda + y^{\star} - (1 - 2x^{\star})) + Ye^{-(s+\lambda)\tau}x^{\star}(1 - 2x^{\star}) - \lambda Ye^{-(s+\lambda)\tau}x^{\star} = 0.$$

The stability of each equilibrium can be determined by studying the roots of  $P(\lambda) = 0$ .

**Theorem 2.3.** Consider (2.2.3). Equilibrium  $E_0$  is a saddle point.

**Proof.** Evaluating the characteristic equation  $P(\lambda)$  at the equilibrium  $E_0$  gives

$$P(\lambda)|_{E_0} = (\lambda + s)(\lambda - 1) = 0.$$

Then  $P(\lambda)$  has two real roots  $\lambda = -s$  and  $\lambda = 1$ . Therefore, the equilibrium  $E_0$  is a saddle point.

**Theorem 2.4.** Consider (2.2.3). Equilibrium  $E_1$  is unstable if  $0 \leq \tau < \tau_c$  and globally asymptotically stable if  $\tau > \tau_c$ .

**Proof.** The characteristic equation evaluated at  $E_1$  is given by

$$P(\lambda)|_{E_1} = (\lambda + 1)(\lambda + s - Ye^{-(s+\lambda)\tau}) = 0.$$

One of the roots of the characteristic equation is  $\lambda = -1$ . The other roots satisfy

$$(\lambda + s)e^{(\lambda + s)\tau} = Y. \tag{2.3.8}$$

For any fixed  $0 \leq \tau < \tau_c$ , we show that there is a positive real root. The left hand side of (2.3.8) is a monotone increasing function in  $\lambda$  for any fixed  $\tau$ . It takes the value  $se^{s\tau}$  at  $\lambda = 0$  and tends to positive infinity as  $\lambda \to +\infty$ . Since  $0 \leq \tau < \tau_c$ ,  $se^{s\tau} < Y$ . By the Intermediate Value Theorem, there exists a unique  $\lambda(\tau) > 0$  such that equation (2.3.8) holds and so  $P(\lambda)|_{E_1} = 0$  has at least one positive root  $\lambda(\tau)$ . Hence  $E_1$  is unstable for  $0 \leq \tau < \tau_c$ .

Now, we prove  $E_1$  is globally asymptotically stable if  $\tau > \tau_c$ . Since  $\tau > \tau_c$ , then  $Ye^{-s\tau} < s$ . If  $\epsilon_0 = \frac{1}{2} \left( \frac{s}{Y} e^{s\tau} - 1 \right) > 0$ , by Lemma 2.2, there exists a T > 0 such that  $x(t) < 1 + \epsilon_0$  for all t > T. Therefore

$$Ye^{-s\tau}x(t-\tau) < Ye^{-s\tau}\left(1 + \frac{1}{2}\left(\frac{s}{Y}e^{s\tau} - 1\right)\right)$$
$$= \frac{1}{2}Ye^{-s\tau} + \frac{s}{2} < s.$$

Therefore the second equation of (2.2.3) can be written

$$\dot{y}(t) = -sy(t) + b(t)y(t-\tau),$$

where  $b(t) = Ye^{-s\tau}x(t-\tau) < s$ . Choose  $\alpha = s/2$  in Lemma A.1 in Appendix A. Since  $4(s-s/2)s/2 = s^2 > b^2(t), y(t) \to 0$  as  $t \to \infty$ . Hence, for any  $\epsilon > 0$ , there exists  $T_1$  such that  $0 < y(t) < \epsilon$  for  $t > T_1$ . From the first equation of (2.2.3),

$$x(t) (1 - x(t) - \epsilon) < \dot{x}(t) < x(t) (1 - x(t)).$$

Note that  $1 - \epsilon$  and 1 are globally asymptotically stable equilibria of equation  $\dot{z}(t) = z(t)(1 - z(t) - \epsilon)$  and  $\dot{z}(t) = z(t)(1 - z(t))$ , respectively where  $\epsilon > 0$  is arbitrary. By Theorem A.4, for any solution x(t) of (2.2.3),  $x(t) \to 1$  as  $t \to \infty$ . Therefore  $E_1$  is globally asymptotically stable. Thus we have proved that if  $\tau > \tau_c$ , there are only two equilibria:  $E_0$ , a saddle, and  $E_1$ , a globally asymptotically stable equilibrium. However if  $0 \leq \tau < \tau_c$ , both  $E_0$  and  $E_1$  are unstable and the coexistence equilibrium  $E_+$  also exists, since

$$y_+(\tau) = 1 - \frac{se^{s\tau}}{Y} > 0.$$

In what follows, we investigate the local stability of  $E_+$ . Evaluating the characteristic equation  $P(\lambda)$  at  $E_+$  gives

$$P(\lambda)|_{E_+} = \lambda^2 + \lambda s \left(1 + \frac{e^{s\tau}}{Y}\right) + \frac{s^2}{Y} e^{s\tau} + e^{-\lambda\tau} s \left(-\lambda + \left(1 - \frac{2se^{s\tau}}{Y}\right)\right) = 0.$$

Denoting the coefficients of  $P(\lambda)|_{E_+}$  as

$$p(\tau) = s\left(1 + \frac{e^{s\tau}}{Y}\right), \quad q = -s, \quad c(\tau) = s\left(1 - 2\frac{se^{s\tau}}{Y}\right) \quad \text{and} \quad \alpha(\tau) = \frac{s^2 e^{s\tau}}{Y},$$
$$P(\lambda)|_{E_+} = \lambda^2 + p(\tau)\lambda + (q\lambda + c(\tau))e^{-\lambda\tau} + \alpha(\tau) = 0. \tag{2.3.9}$$

First assume that  $\tau = 0$ . Then (2.3.9) reduces to

$$\lambda^{2} + (p(0) + q)\lambda + (\alpha(0) + c(0)) = 0.$$

Since  $\alpha(0) + c(0) = s\left(1 - \frac{s}{Y}\right) = s \cdot y_{+}(0) > 0$  and  $p(0) + q = \frac{se^{s\tau}}{Y} > 0$ , by the Routh-Hurwicz criterion, all roots of (2.3.9) have negative real part. Hence  $E_{+}$  is locally asymptotically stable.

Now assume that  $\tau > 0$ .  $P(0)|_{E_+} = \alpha(\tau) + c(\tau) = s \ y_+(\tau) > 0$ , and so  $\lambda = 0$ is not a root of  $P(\lambda)|_{E_+} = 0$ .

**Lemma 2.5.** As  $\tau$  increases from zero, roots of (2.3.9) with positive real part can only appear if roots with negative real part cross the imaginary axis as  $\tau$  increases.

**Proof.** In Theorem 1.4 (see p.66) of Kuang [35], taking n = 2 and  $g(\lambda, \tau) = p(\tau)\lambda + (q\lambda + c(\tau))e^{-\lambda\tau} + \alpha(\tau)$  gives

$$\lim \sup_{\mathrm{Re}\lambda > 0, |\lambda| \to \infty} |\lambda^{-2}g(\lambda, \tau)| \to 0.$$

No root of (2.3.9) with positive real part can enter from infinity as  $\tau$  increases from 0. Hence roots with positive real part can only appear by crossing the imaginary axis.

Suppose that 
$$\lambda = i\omega$$
 ( $\omega > 0$ ) is a root of  $P(\lambda)|_{E_+} = 0$ , where  $i = \sqrt{-1}$ . Then

$$P(i\omega)|_{E_{+}} = -\omega^{2} + ip(\tau)\omega + (iq\omega + c(\tau))e^{-i\omega\tau} + \alpha(\tau) = 0.$$
 (2.3.10)

Using Euler's identity  $e^{i\theta} = \cos\theta + i\sin\theta$ ,

$$-\omega^2 + \alpha(\tau) + q\omega\sin(\omega\tau) + c(\tau)\cos(\omega\tau) + i\left(p(\tau)\omega + q\omega\cos(\omega\tau) - c(\tau)\sin(\omega\tau)\right) = 0.$$

Separating the real and imaginary parts,

$$\begin{cases} c(\tau)\cos(\omega\tau) + q\omega\sin(\omega\tau) = \omega^2 - \alpha(\tau), \\ c(\tau)\sin(\omega\tau) - q\omega\cos(\omega\tau) = p(\tau)\omega. \end{cases}$$
(2.3.11)

Solving for  $\cos(\omega \tau)$  and  $\sin(\omega \tau)$  gives

$$\begin{cases} \sin(\omega\tau) = \frac{c(\tau)(p(\tau)\omega) + q\omega(\omega^2 - \alpha(\tau))}{c(\tau)^2 + q^2\omega^2}, \\ \cos(\omega\tau) = \frac{c(\tau)(\omega^2 - \alpha(\tau)) + q\omega(-p(\tau)\omega)}{c(\tau)^2 + q^2\omega^2}. \end{cases}$$
(2.3.12)

Recalling that  $\sin^2(\omega \tau) + \cos^2(\omega \tau) = 1$ , squaring both sides of equations (2.3.11), adding them, and rearranging gives

$$\omega^4 + (p(\tau)^2 - q^2 - 2\alpha(\tau))\omega^2 + \alpha(\tau)^2 - c(\tau)^2 = 0.$$
 (2.3.13)

Define

$$\tau^* = \frac{1}{s} \ln\left(\frac{Y}{3s}\right). \tag{2.3.14}$$

Therefore  $\frac{se^{s\tau^*}}{Y} = \frac{1}{3}$ .

**Lemma 2.6.** Assume that  $\tau \in [0, \tau^*)$ , or equivalently  $x_+(\tau) \in (0, \frac{1}{3})$ . Then (2.3.13) has one positive root  $\omega_+(\tau)$  given by

$$\omega_{+}(\tau) = \sqrt{\frac{1}{2} \left( -\left(\frac{se^{s\tau}}{Y}\right)^{2} + \sqrt{\left(\frac{se^{s\tau}}{Y}\right)^{4} + s^{2} \left(12\frac{s^{2}e^{2s\tau}}{Y^{2}} - 16\frac{se^{s\tau}}{Y} + 4\right)} \right)}.$$
 (2.3.15)

Also  $\omega_+(\tau^*) = 0$  and if  $\tau > \tau^*$ , then (2.3.13) has no positive root.

**Proof.** Solving for  $\omega^2$  in (2.3.13),

$$\omega_{\pm}^{2} = \frac{1}{2} \left( q^{2} - p^{2}(\tau) + 2\alpha(\tau) \pm \sqrt{(q^{2} - p^{2}(\tau) + 2\alpha(\tau))^{2} - 4(\alpha^{2}(\tau) - c^{2}(\tau))} \right).$$
(2.3.16)

The quantity

$$q^{2} - p^{2}(\tau) + 2\alpha(\tau) = s^{2} - s^{2} \left(1 + \frac{e^{s\tau}}{Y}\right)^{2} + 2\frac{s^{2}e^{s\tau}}{Y} = -\left(\frac{se^{s\tau}}{Y}\right)^{2} < 0.$$

Therefore  $\omega_{-}^{2}$  is either complex or negative for any  $\tau$ . But  $\omega_{+}$  is positive if

$$\begin{aligned} (\alpha^{2}(\tau) - c^{2}(\tau)) &= s^{2} \left( \frac{s^{2} e^{2s\tau}}{Y^{2}} - 1 + 4 \frac{s e^{s\tau}}{Y} - 4 \frac{s^{2} e^{2s\tau}}{Y^{2}} \right) \\ &= s^{2} \left( 4 \frac{s e^{s\tau}}{Y} - 1 - 3 \frac{s^{2} e^{2s\tau}}{Y^{2}} \right) \\ &= -3s^{2} \left( \frac{s e^{s\tau}}{Y} - \frac{1}{3} \right) \left( \frac{s e^{s\tau}}{Y} - 1 \right) \\ &< 0. \end{aligned}$$

This is the case if

$$\frac{se^{s\tau}}{Y} < \frac{1}{3}$$
 or  $\frac{se^{s\tau}}{Y} > 1$ 

However,  $E_+$  only exists when  $x_+(\tau) = \frac{se^{s\tau}}{Y} < 1$ . Therefore, we only consider  $\frac{se^{s\tau}}{Y} < \frac{1}{3}$ . This implies that  $\tau < \tau^*$  or equivalently  $x_+(\tau) < \frac{1}{3}$ . Hence, for  $\tau \in [0, \tau^*)$ , a root with  $\omega_+(\tau) > 0$  exists and is defined explicitly by (2.3.15). If  $\tau > \tau^*$ , then  $\omega_+(\tau)$  is complex.

Consider (2.3.12) and note that  $p(\tau) = s + x_+(\tau)$ , q = -s,  $c(\tau) = s(1 - 2x_+(\tau))$  and  $\alpha(\tau) = sx_+(\tau)$ . Therefore,

$$\begin{aligned} \sin(\omega\tau) &= \omega \frac{c(\tau)p(\tau) + q(\omega^2 - \alpha(\tau))}{c(\tau)^2 + q^2\omega^2} \\ &= \omega \frac{s(1 - 2x_+(\tau))(s + x_+(\tau)) + (-s)(\omega^2 - sx_+(\tau))}{s^2\left((1 - 2x_+(\tau))^2 + \omega^2\right)} \\ &= \omega \frac{(1 - 2x_+(\tau))(s + x_+(\tau)) - (\omega^2 - sx_+(\tau))}{s\left((1 - 2x_+(\tau))^2 + \omega^2\right)} \\ &= \frac{\omega}{s} \left(\frac{s + x_+(\tau) - 2sx_+(\tau) - 2(x_+(\tau))^2 - \omega^2 + sx_+(\tau)}{(1 - 2x_+(\tau))^2 + \omega^2}\right) \\ &= \frac{\omega}{s} \left(\frac{s + x_+(\tau) - sx_+(\tau) - 2(x_+(\tau))^2 - \omega^2}{(1 - 2x_+(\tau))^2 + \omega^2}\right).\end{aligned}$$

and

$$\begin{aligned} \cos(\omega\tau) &= \frac{\omega^2 (c(\tau) - qp(\tau)) - c(\tau)\alpha(\tau)}{c(\tau)^2 + q^2 \omega^2} \\ &= \frac{\omega^2 [s(1 - 2x_+(\tau)) + s(s + x_+(\tau))] - s(1 - 2x_+(\tau))sx_+(\tau)}{s^2 \left((1 - 2x_+(\tau))^2 + \omega^2\right)} \\ &= \frac{\omega^2 (1 + s - x_+(\tau)) - (1 - 2x_+(\tau))sx_+(\tau)}{s \left((1 - 2x_+(\tau))^2 + \omega^2\right)}. \end{aligned}$$

Denote the function on the right hand side of  $\sin(\omega \tau)$  and  $\cos(\omega \tau)$ , respectively by

$$h_1(\omega,\tau) = \frac{\omega}{s} \left( \frac{s + x_+(\tau) - sx_+(\tau) - 2(x_+(\tau))^2 - \omega^2}{(1 - 2x_+(\tau))^2 + \omega^2} \right).$$
(2.3.17)

and

$$h_2(\omega,\tau) = \frac{\omega^2(1+s-x_+(\tau)) - (1-2x_+(\tau))sx_+(\tau)}{s\left((1-2x_+(\tau))^2 + \omega^2\right)}.$$
 (2.3.18)

**Lemma 2.7.** Assume  $\tau \in [0, \tau^*)$  so that  $0 < x_+(\tau) < \frac{1}{3}$ . Define  $l(\tau) = \sqrt{s(1 - 2x_+(\tau))}$ . Then there exists a unique  $\bar{\omega}(\tau) \in [0, l(\tau))$  satisfying  $\sin(\arccos(h_2(\bar{\omega}(\tau), \tau))) = h_1(\bar{\omega}(\tau), \tau)$ . In fact  $\bar{\omega}(\tau) = \omega_+(\tau)$ . Let

$$\theta(\tau) = \arccos(h_2(\omega_+(\tau), \tau)). \tag{2.3.19}$$

There exists  $\epsilon > 0$  such that  $\epsilon \leqslant \theta(\tau) \leqslant \pi$  and  $\theta(\tau)$  satisfies

$$\begin{cases} \sin(\theta(\tau) + 2k\pi) = h_1(\omega_+(\tau), \tau), \\ \cos(\theta(\tau) + 2k\pi) = h_2(\omega_+(\tau), \tau). \end{cases} \quad k = 0, 1, 2, \cdots \qquad (2.3.20)$$

**Proof.** Fix  $\tau \in [0, \tau^*)$ . Recall that  $x_+(\tau) = \frac{se^{s\tau}}{Y}$ . It follows that  $0 < x_+(\tau) < \frac{1}{3}$ . For  $\omega > 0$ 

$$\begin{aligned} \frac{\partial h_2(\omega,\tau)}{\partial \omega} &= \frac{2\omega(1+s-x_+(\tau))s\left[(1-2x_+(\tau))^2+\omega^2\right]}{s^2\left[(1-2x_+(\tau))^2+\omega^2\right]^2} \\ &- \frac{\left[\omega^2(1+s-x_+(\tau))-(1-2x_+(\tau))sx_+(\tau)\right](2\omega s)}{s^2\left[(1-2x_+(\tau))^2+\omega^2\right]^2} \\ &= 2\omega s(1-2x_+(\tau))\frac{(1+s-x_+(\tau))(1-2x_+)+sx_+(\tau)}{s^2\left[(1-2x_+(\tau))^2+\omega^2\right]^2} > 0. \end{aligned}$$

Therefore  $h_2(\omega, \tau)$  is monotonically increasing in  $\omega$  and

$$\lim_{\omega \to +\infty} h_2(\omega, \tau) = \frac{1 + s - x_+(\tau)}{s} > 1.$$

Also

$$h_2(0,\tau) = -\frac{(1-2x_+(\tau))sx_+(\tau)}{s(1-2x_+(\tau))^2} = \frac{1}{2-\frac{1}{x_+(\tau)}} = \frac{x_+(\tau)}{2x_+(\tau)-1}$$

Thus for  $\tau \in [0, \tau^*)$ ,  $-1 < h_2(0, \tau) < 0$  and for  $\tau = \tau^*$ ,  $x_+(\tau^*) = \frac{1}{3}$  and

$$h_2(0,\tau^*) = -1.$$
 (2.3.21)

Solving for l so that  $h_2(l,\tau) = 1$  gives  $l(\tau) = \sqrt{s(1-2x_+(\tau))}$ . Therefore, for  $\tau \in [0,\tau^*)$  and  $\omega \in [0,l(\tau)]$ , we have  $-1 < h_2(\omega,\tau) \leq 1$ , and for  $l(\tau) \in [\sqrt{\frac{s}{3}},\sqrt{s}]$ ,  $x_+(\tau) \in [0,\frac{1}{3}]$ .

For any fixed  $\tau \in [0, \tau^*]$  and  $\omega \in [0, l(\tau)]$ , consider the function

$$\Gamma(\omega,\tau) = \sin(\arccos(h_2(\omega,\tau))) - h_1(\omega,\tau).$$

Then

$$\Gamma(0,\tau) = \begin{cases} \sin(\arccos(h_2(0,\tau))) - 0 > 0, & \text{for} \quad 0 < \tau < \tau^*, \\ 0, & \text{for} \quad \tau = \tau^*. \end{cases}$$
(2.3.22)

Also

$$\Gamma(l(\tau),\tau) = \sin(\arccos(h_2(l(\tau),\tau))) - h_1(l(\tau),\tau) = -h_1(l(\tau),\tau) < 0,$$

since

$$h_1(l(\tau),\tau) = \left(\frac{\sqrt{s(1-2x_+(\tau))}}{s}\right) \frac{s+x_+(\tau)-sx_+(\tau)-2x_+^2(\tau)-s(1-2x_+(\tau))}{(1-2x_+(\tau))^2+s(1-2x_+(\tau))}$$
$$= \left(\frac{\sqrt{s(1-2x_+(\tau))}}{s}\right) \frac{x_+(\tau)(1+s-2x_+(\tau))}{(1-2x_+(\tau))^2+s(1-2x_+(\tau))} > 0.$$

By the Mean Value Theorem, for any fixed  $\tau \in [0, \tau^*)$ , there exists at least one  $\bar{\omega}(\tau) \in (0, l(\tau))$  such that  $\Gamma(\bar{\omega}(\tau), \tau) = 0$ . In addition,

 $-1 < h_2(\bar{\omega}(\tau), \tau) < 1$  for any  $\tau \in [0, \tau^*).$ 

For  $\tau = \tau^*$ ,  $x_+(\tau^*) = \frac{1}{3}$ . By (2.3.22),  $\Gamma(0, \tau^*) = 0$ . Thus  $\bar{\omega}(\tau^*) = 0$ . By (2.3.21),  $h_2(\bar{\omega}(\tau^*), \tau^*) = -1$ . If there is another zero  $\hat{\omega}$  such that  $\Gamma(\hat{\omega}, \tau^*) = 0$ , then  $\hat{\omega} \neq l(\tau^*)$ , since  $\Gamma(l(\tau^*), \tau^*) < 0$ . Therefore  $0 < \hat{\omega} < l(\tau^*)$ . And so  $-1 < h_2(\hat{\omega}(\tau^*), \tau^*) < 1$ . In summary

$$\begin{cases} -1 < h_2(\bar{\omega}(\tau), \tau) < 1, & \tau \in [0, \tau^*), \text{ or } \tau = \tau^* \text{ but } \bar{\omega}(\tau^*) \neq 0, \\ h_2(\bar{\omega}(\tau^*), \tau^*) = -1, & \tau = \tau^* \text{ and } \bar{\omega}(\tau^*) = 0. \end{cases}$$
(2.3.23)

In what follows, we want to prove that for any fixed  $\tau \in [0, \tau^*]$ , there is a unique  $\bar{\omega}(\tau)$  such that  $\Gamma(\bar{\omega}(\tau), \tau) = 0$  by considering the partial derivative of  $\Gamma(\omega, \tau)$ with respect to  $\omega$  or  $\tau$  at the point  $(\bar{\omega}(\tau), \tau)$ . To do that, we need to evaluate the partial derivatives of  $h_1(\omega, \tau)$  and  $h_2(\omega, \tau)$  with respect to both  $\omega$  and  $\tau$ .

The partial derivatives of the function  $h_1(\omega, \tau)$  with respect to  $\omega$  evaluated at the point  $(\overline{\omega}(\tau), \tau)$  are given by

$$\begin{split} & \frac{\partial h_1(\omega,\tau)}{\partial \omega} \bigg|_{(\overline{\omega}(\tau),\tau)} \\ &= \frac{s - 5sx_+(\tau) + 8sx_+^2(\tau) - s\omega^2 + x_+(\tau) - 6x_+^2(\tau) + 12x_+^3(\tau) + 11x_+(\tau)\omega^2}{s(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2} \bigg|_{(\overline{\omega}(\tau),\tau)} \\ &+ \frac{sx_+(\tau)\omega^2 - 4sx_+^3(\tau) - 8x_+^4(\tau) - 10x_+^2(\tau)\omega^2 - 3\omega^2 - \omega^4}{s(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2} \bigg|_{(\overline{\omega}(\tau),\tau)} \\ &= \frac{s - 5sx_+(\tau) + 8sx_+^2(\tau) - s\overline{\omega}^2(\tau) + x_+(\tau) - 6x_+^2(\tau) + 12x_+^3(\tau) + 11x_+(\tau)\overline{\omega}^2(\tau)}{s(1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))^2} \\ &+ \frac{sx_+(\tau)\overline{\omega}^2(\tau) - 4sx_+^3(\tau) - 8x_+^4(\tau) - 10x_+^2(\tau)\overline{\omega}^2(\tau) - 3\overline{\omega}^2(\tau) - \overline{\omega}^4(\tau)}{s(1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))^2} \end{split}$$

and

$$\begin{split} & \frac{\partial h_1(\omega,\tau)}{\partial \tau} \Big|_{(\overline{\omega}(\tau),\tau)} = \frac{\partial h_1(\omega,\tau)}{\partial x_+} \frac{dx_+}{d\tau} \Big|_{(\overline{\omega}(\tau),\tau)} \\ &= \frac{\omega(1-4x_++4x_+^2-3\omega^2+3s-8sx_++4sx_+^2-s\omega^2+4x_+\omega^2)}{s\left(1-4x_++4x_+^2+\omega^2\right)^2} \cdot sx_+ \Big|_{(\overline{\omega}(\tau),\tau)} \\ &= \frac{\overline{\omega}(\tau)x_+(\tau) \left(1-4x_+(\tau)+4x_+^2(\tau)-3\overline{\omega}^2(\tau)\right)}{\left(1-4x_+(\tau)+4x_+^2(\tau)+\overline{\omega}^2(\tau)\right)^2} \\ &+ \frac{3s-8sx_+(\tau)+4sx_+^2(\tau)-s\overline{\omega}^2(\tau)+4x_+(\tau)\overline{\omega}^2(\tau)\right)}{\left(1-4x_+(\tau)+4x_+^2(\tau)+\overline{\omega}^2(\tau)\right)^2}. \end{split}$$

Similarly, the partial derivatives of the function  $h_2(\omega, \tau)$  with respect to  $\omega$  at the

point  $(\overline{\omega}(\tau), \tau)$  are given by

$$\frac{\partial h_2(\omega,\tau)}{\partial \omega}\Big|_{(\overline{\omega}(\tau),\tau)} = \frac{2\omega(1-5x_+(\tau)+8x_+^2(\tau)+s-3sx_+(\tau)+2sx_+^2(\tau)-4x_+^3(\tau))}{s\left(1-4x_+(\tau)+4x_+^2(\tau)+\omega^2\right)^2}\Big|_{(\overline{\omega}(\tau),\tau)} = \frac{2\overline{\omega}(\tau)(1-5x_+(\tau)+8x_+^2(\tau)+s-3sx_+(\tau)+2sx_+^2(\tau)-4x_+^3(\tau))}{s\left(1-4x_+(\tau)+4x_+^2(\tau)+\overline{\omega}^2(\tau)\right)^2}$$

and

$$\begin{split} \left. \frac{\partial h_2(\omega,\tau)}{\partial \tau} \right|_{(\overline{\omega}(\tau),\tau)} &= \left. \frac{\partial h_2(\omega,\tau)}{\partial x_+} \frac{dx_+}{d\tau} \right|_{(\overline{\omega}(\tau),\tau)} \\ &= \left( \frac{3\omega^2 - 8x_+(\tau)\omega^2 + 4x_+^2(\tau)\omega^2 - \omega^4 + 4sx_+(\tau)}{s(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2} \right. \\ &+ \left. \frac{-4sx_+^2(\tau) - 4sx_+(\tau)\omega^2 - s + 3s\omega^2}{s(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2} \right) \cdot sx_+(\tau) \right|_{(\overline{\omega}(\tau),\tau)} \\ &= \frac{x_+(\tau) \left( 3\overline{\omega}^2(\tau) - 8x_+(\tau)\overline{\omega}^2(\tau) + 4x_+^2(\tau)\overline{\omega}^2(\tau) - \overline{\omega}^4(\tau) + 4sx_+(\tau) \right)}{(1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))^2} \\ &+ \frac{-4sx_+^2(\tau) - 4sx_+(\tau)\overline{\omega}^2(\tau) - s + 3s\overline{\omega}^2(\tau)}{(1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))^2}. \end{split}$$

For  $\tau = \tau^*$  and  $\bar{\omega}(\tau^*) = 0$ ,

$$\begin{split} \frac{\partial \Gamma(\omega,\tau)}{\partial \omega} \bigg|_{\tau=\tau^*,\overline{\omega}(\tau^*)=0} &= \left( \cos(\arccos(h_2(\omega,\tau))) \frac{-1}{\sqrt{1-h_2^2}} \frac{\partial h_2}{\partial \omega} - \frac{\partial h_1}{\partial \omega} \right) \bigg|_{\tau=\tau^*,\overline{\omega}(\tau^*)=0} \\ &= \frac{-h_2(\omega,\tau^*)}{\sqrt{1-h_2^2(\omega,\tau^*)}} \frac{\partial h_2(\omega,\tau^*)}{\partial \omega} - \frac{\partial h_1(\omega,\tau^*)}{\partial \omega} \\ &= \frac{s(\frac{1}{9}+\omega^2)}{\omega\sqrt{(\frac{2s}{9}-\frac{2\omega^2}{3})(\frac{2}{3}+2s)}} \left( \frac{4\omega(3+9s)}{s(1+9\omega^2)^2} \right) - \frac{\frac{1}{81}+\frac{2s}{27}-\frac{4}{9}\omega^2-\frac{2s}{3}\omega^2-\omega^4}{s(\frac{1}{9}+\omega^2)^2} \\ &= \frac{4(3+9s)}{9\sqrt{\frac{2s}{9}(\frac{2}{3}+2s)}} - \frac{6s+1}{s} = \frac{2+6s}{\sqrt{s(\frac{1}{3}+s)}} - \frac{6s+1}{s} \\ &= \frac{2s+6s^2-(6s+1)\sqrt{s(\frac{1}{3}+s)}}{s\sqrt{s(\frac{1}{3}+s)}} \\ &= \frac{\sqrt{36s^4+24s^3+4s^2}-\sqrt{36s^4+24s^3+5s^2+\frac{1}{3}s}}{s\sqrt{s(\frac{1}{3}+s)}} < 0, \end{split}$$

since s > 0.

Before considering the partial derivatives of  $\Gamma(\omega, \tau)$  at the point  $(\bar{\omega}(\tau), \tau)$  with  $\tau \in [0, \tau^*)$ , or  $\tau = \tau^*$ , but  $\bar{\omega}(\tau^*) \neq 0$ , we require some preliminary calculations. Since  $\Gamma(\bar{\omega}(\tau), \tau) = 0$  and  $\sin(\arccos(h_2(\bar{\omega}(\tau), \tau))) = \sqrt{1 - h_2^2(\bar{\omega}(\tau), \tau)}$ , it follows that

$$\sqrt{1 - h_2^2(\overline{\omega}(\tau), \tau)} = h_1(\overline{\omega}(\tau), \tau).$$
(2.3.24)

Therefore  $h_1^2(\overline{\omega}(\tau), \tau) + h_2^2(\overline{\omega}(\tau), \tau) = 1$ . By (2.3.17) and (2.3.18)

$$\begin{split} h_2^2(\omega,\tau) + h_1^2(\omega,\tau) \\ &= \frac{\omega^2}{s^2} \left( \frac{s + x_+(\tau) - sx_+(\tau) - 2(x_+(\tau))^2 - \omega^2}{(1 - 2x_+(\tau))^2 + \omega^2} \right)^2 \\ &+ \left( \frac{\omega^2(1 + s - x_+(\tau)) - (1 - 2x_+(\tau))sx_+(\tau)}{s((1 - 2x_+(\tau))^2 + \omega^2)} \right)^2 \\ &= \frac{\omega^2 s^2 + \omega^2 x_+^2(\tau) + s^2 \omega^2 x_+^2(\tau) + 4\omega^2 x_+^4(\tau) + \omega^6 - 4x_+(\tau) s^2 \omega^2}{(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2 s^2} \\ &+ \frac{4x_+^2(\tau)\omega^4 - 4x_+^3(\tau)\omega^2 + \omega^4 + \omega^4 s^2 + \omega^4 x_+^2(\tau) + s^2 x_+^2(\tau)}{(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2 s^2} \\ &+ \frac{4s^2 x_+^4(\tau) + 4s^2 x_+^2(\tau)\omega^2 - 4s^2 x_+^3(\tau) - 4x_+(\tau)\omega^4}{(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2 s^2} \\ &= \frac{(x_+^2(\tau) + \omega^2)(s^2 + \omega^2)(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2 s^2}{(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2 s^2} \\ &= \frac{(x_+^2(\tau) + \omega^2)(s^2 + \omega^2)}{(1 - 4x_+(\tau) + 4x_+^2(\tau) + \omega^2)^2 s^2}. \end{split}$$

Therefore

$$\frac{(x_+^2(\tau) + \overline{\omega}^2(\tau))(s^2 + \overline{\omega}^2(\tau))}{(1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))s^2} = 1.$$
(2.3.25)

The partial derivative of  $\Gamma(\omega, \tau)$  with respect to  $\omega$  at the point  $(\bar{\omega}(\tau), \tau)$  with  $\tau \in$ 

 $[0, \tau^*)$ , or  $\tau = \tau^*$ , but  $\overline{\omega}(\tau^*) \neq 0$  is given by

$$\begin{aligned} \frac{\partial \Gamma(\omega,\tau)}{\partial \omega} \Big|_{(\overline{\omega}(\tau),\tau)} &= \left( \cos(\arccos(h_2(\omega,\tau))) \frac{-1}{\sqrt{1-h_2^2}} \frac{\partial h_2}{\partial \omega} - \frac{\partial h_1}{\partial \omega} \right) \Big|_{(\overline{\omega}(\tau),\tau)} \\ &= \left( \frac{-1}{\sqrt{1-h_2^2}} h_2 \frac{\partial h_2}{\partial \omega} - \frac{\partial h_1}{\partial \omega} \right) \Big|_{(\overline{\omega}(\tau),\tau)}. \end{aligned}$$

By (2.3.24)

$$\begin{split} \frac{\partial \Gamma(\omega,\tau)}{\partial \omega} \bigg|_{(\overline{\omega}(\tau),\tau)} &= \frac{-1}{\sqrt{1-h_2^2}} \left( h_2 \frac{\partial h_2}{\partial \omega} + h_1 \frac{\partial h_1}{\partial \omega} \right) \bigg|_{(\overline{\omega}(\tau),\tau)} \\ &= \frac{-\overline{\omega}(\tau)}{\sqrt{1-h_2^2(\overline{\omega}(\tau),\tau)}} \left( \frac{\overline{\omega}^4(\tau) + 8\overline{\omega}^2(\tau)x_+^2(\tau) + 2\overline{\omega}^2(\tau) - 8\overline{\omega}^2(\tau)x_+(\tau) + x_+^2(\tau)}{s^2(1-4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))^2} \right) \\ &\quad + \frac{4x_+^4(\tau) + s^2 - 4s^2x_+(\tau) + 3s^2x_+^2(\tau) - 4x_+^3(\tau)}{s^2(1-4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))^2} \right) \\ &= \frac{-\overline{\omega}(\tau)}{\sqrt{1-h_2^2(\overline{\omega}(\tau),\tau)}} \left( \frac{(s^2 + x_+^2(\tau) + 2\overline{\omega}^2(\tau))(1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))}{s^2(1-4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))^2} \right) \\ &= \frac{-\overline{\omega}(\tau)}{\sqrt{1-h_2^2(\overline{\omega}(\tau),\tau)}} \left( \frac{s^2 + x_+^2(\tau) + 2\overline{\omega}^2(\tau)}{s^2(1-4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))^2} \right) \\ &= \frac{-\overline{\omega}(\tau)}{\sqrt{1-h_2^2(\overline{\omega}(\tau),\tau)}} \left( \frac{s^2 + x_+^2(\tau) + 2\overline{\omega}^2(\tau)}{s^2(1-4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))} - \frac{(\overline{\omega}^2(\tau) + x_+^2(\tau))(s^2 + \overline{\omega}^2(\tau))}{s^2(1-4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))} \right) . \end{split}$$

From (2.3.25),

$$\begin{aligned} \frac{\partial \Gamma(\omega,\tau)}{\partial \omega} \bigg|_{(\overline{\omega}(\tau),\tau)} &= \frac{-\overline{\omega}(\tau)}{\sqrt{1 - h_2^2(\overline{\omega}(\tau),\tau)}} \left( \frac{s^2 + x_+^2(\tau) + 2\overline{\omega}^2(\tau)}{s^2(1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))} - \frac{1}{1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau)} \right) \\ &= \frac{-1}{\sqrt{1 - h_2^2(\overline{\omega}(\tau),\tau)}} \left( \frac{\overline{\omega}(\tau)(x_+^2(\tau) + 2\overline{\omega}^2(\tau))}{s^2(1 - 4x_+(\tau) + 4x_+^2(\tau) + \overline{\omega}^2(\tau))} \right) < 0. \end{aligned}$$

The partial derivative of the function  $\Gamma(\omega, \tau)$  with respect to  $\tau$  at the point  $(\overline{\omega}(\tau), \tau)$ 

for  $\tau \in [0, \tau^*)$ , or  $\tau = \tau^*$ , but  $\overline{\omega}(\tau^*) \neq 0$  is

$$\begin{aligned} \frac{\partial \Gamma(\omega,\tau)}{\partial \tau} \Big|_{(\overline{\omega}(\tau),\tau)} &= \left( \cos(\arccos(h_2(\omega,\tau))) \frac{-1}{\sqrt{1-h_2^2}} \frac{\partial h_2}{\partial \tau} - \frac{\partial h_1}{\partial \tau} \right) \Big|_{(\overline{\omega}(\tau),\tau)} \\ &= \left( \frac{-1}{\sqrt{1-h_2^2}} h_2 \frac{\partial h_2}{\partial \tau} - \frac{\partial h_1}{\partial \tau} \right) \Big|_{(\overline{\omega}(\tau),\tau)}. \end{aligned}$$

By (2.3.24)

$$\begin{split} \frac{\partial\Gamma(\omega,\tau)}{\partial\tau}\bigg|_{(\overline{\omega}(\tau),\tau)} &= \frac{-1}{\sqrt{1-h_2^2}} \left(h_2\frac{\partial h_2}{\partial\tau} + h_1\frac{\partial h_1}{\partial\tau}\right)\bigg|_{(\overline{\omega}(\tau),\tau)} \\ &= \frac{-sx_+(\tau)}{\sqrt{1-h_2^2(\overline{\omega}(\tau),\tau)}} \left(\frac{2\overline{\omega}^4(\tau) - 3\overline{\omega}^4(\tau)x_+(\tau) - 2\overline{\omega}^2(\tau)x_+^2(\tau)}{s^2(1-4x_+(\tau)+4x_+^2(\tau)+\overline{\omega}^2(\tau))^2} \right. \\ &+ \frac{-3s^2x_+(\tau)\overline{\omega}^2(\tau) + x_+(\tau)\overline{\omega}^2(\tau) + 2s^2\overline{\omega}^2(\tau) - 2s^2x_+^2(\tau) + s^2x_+(\tau)}{s^2(1-4x_+(\tau)+4x_+^2(\tau)+\overline{\omega}^2(\tau))^2}\right) \\ &= \frac{sx_+(\tau)(s^2 + \overline{\omega}^2(\tau))}{\sqrt{1-h_2^2(\overline{\omega}(\tau),\tau)}} \left(\frac{2\overline{\omega}^2(\tau) - 3\overline{\omega}^2(\tau)x_+(\tau) - 2x_+^2(\tau) + x_+(\tau)}{s^2(1-4x_+(\tau)+4x_+^2(\tau)+\overline{\omega}^2(\tau))^2}\right). \end{split}$$

From (2.3.25),

$$\begin{split} &\frac{\partial\Gamma(\omega,\tau)}{\partial\tau}\bigg|_{(\overline{\omega}(\tau),\tau)} \\ &= \frac{-1}{\sqrt{1-h_2^2(\overline{\omega}(\tau),\tau)}} \left(\frac{sx_+(\tau)(2\overline{\omega}^2(\tau)-3\overline{\omega}^2(\tau)x_+(\tau)-2x_+^2(\tau)+x_+(\tau)}{(x_+^2(\tau)+\overline{\omega}^2(\tau))(1-4x_+(\tau)+4x_+^2(\tau)+\overline{\omega}^2(\tau))}\right) \\ &= \frac{s^2x_+(\tau)}{(\overline{\omega}^2(\tau)+x_+^2(\tau))\sqrt{s-3sx_+(\tau)+2sx_+^2(\tau)+\overline{\omega}^2(\tau)(x_+(\tau)-1)}} \\ &\times \frac{\overline{\omega}^2(\tau)(2-3x_+(\tau))+x_+(\tau)(1-2x_+(\tau))}{\sqrt{s-5sx_+(\tau)+6sx_+^2(\tau)+\overline{\omega}^2(\tau)(2s+x_+(\tau)-1)}} < 0. \end{split}$$

Therefore for any  $\bar{\omega}(\tau)$  with  $\tau \in [0, \tau^*]$ ,

$$\frac{\partial \Gamma(\omega, \tau)}{\partial \omega} \bigg|_{(\overline{\omega}(\tau), \tau)} < 0.$$
(2.3.26)

For any fixed  $\tau \in [0, \tau^*]$ , assume that  $\bar{\omega}_1(\tau) < \bar{\omega}_2(\tau)$  are two different consecutive zeros of  $\Gamma(\omega, \tau)$ . We have either

$$\Gamma(\omega, \tau) > 0$$
 for  $\bar{\omega}_1(\tau) < \omega < \bar{\omega}_2(\tau),$ 

or

$$\Gamma(\omega,\tau) < 0$$
 for  $\bar{\omega}_1(\tau) < \omega < \bar{\omega}_2(\tau)$ .

In either case, derivatives of  $\Gamma(\omega, \tau)$  at  $\bar{\omega}_1(\tau)$  and  $\bar{\omega}_2(\tau)$  should have opposite signs, which contradicts (2.3.26). Hence, there is a unique  $\bar{\omega}(\tau)$  for any  $\tau \in [0, \tau^*]$ . In addition, by Theorem A.5 in **Appendix A**,  $\bar{\omega}(\tau)$  is continuous on  $[0, \tau^*]$  and differentiable on  $[0, \tau^*)$  with

$$\frac{\partial \bar{\omega}(\tau)}{\partial \tau} = -\frac{\frac{\partial \Gamma(\omega,\tau)}{\partial \tau}}{\frac{\partial \Gamma(\omega,\tau)}{\partial \omega}} \bigg|_{(\bar{\omega}(\tau),\tau)} < 0.$$

From (2.3.25)

$$\overline{\omega}^4(\tau) + x_+^2(\tau)\overline{\omega}^2(\tau) - s^2(1 - 4x_+(\tau) + 3x_+^2(\tau)) = 0.$$

Since  $\overline{\omega}(\tau) \ge 0$ ,

$$\overline{\omega}(\tau) = \sqrt{\frac{1}{2}(-x_{+}^{2}(\tau) + \sqrt{x_{+}^{4}(\tau) + s^{2}(1 - 4x_{+}(\tau) + 3x_{+}^{2}(\tau))})}.$$

Noting that  $x_+(\tau) = \frac{se^{s\tau}}{Y}$  and (2.3.15), it follows that  $\bar{\omega}(\tau) = \omega_+(\tau)$ . Therefore

$$\Gamma(\omega_+(\tau),\tau) = \sin(\arccos(h_2(\omega_+(\tau),\tau))) - h_1(\omega_+(\tau),\tau).$$

Defining  $\theta(\tau) = \arccos(h_2(\omega_+(\tau), \tau))$  for  $\tau \in [0, \tau^*]$ . Then  $\theta(\tau)$  is continuous and satisfies (2.3.20). By (2.3.23) and  $\omega_+(\tau) = \overline{\omega}(\tau)$ ,  $0 < \theta(\tau) < \pi$  for  $\tau \in [0, \tau^*)$ . Also  $\omega_+(\tau^*) = \overline{\omega}(\tau^*) = 0$ . By (2.3.21)

$$\theta(\tau^*) = \arccos(h_2(\omega_+(\tau^*), \tau^*)) = \arccos(h_2(0, \tau^*) = \arccos(-1) = \pi.$$

Therefore  $0 < \theta(\tau) \leq \pi$  for any  $\tau \in [0, \tau^*]$ . Since  $\theta(\tau)$  is continuous on the closed interval  $[0, \tau^*]$ , there exists  $\epsilon > 0$  such that  $\epsilon \leq \theta(\tau) \leq \pi$ .

**Theorem 2.8.** Consider system (2.2.3). Assume that  $\tau \in [0, \tau^*]$  (where  $\tau^*$  was defined by (2.3.14)). If there exists an integer  $n \ge 0$  such that  $\theta(\tau) + 2n\pi$  intersects  $\tau \omega_+(\tau)$  at some  $\tau_n \in (0, \tau^*)$ , then the characteristic equation (2.3.9) has a pair of pure imaginary eigenvalues  $\lambda = \pm i\omega_+(\tau_n)$ . Thus system (2.2.3) undergoes a Hopf bifurcation at  $\tau = \tau_n$  provided that  $\frac{d\operatorname{Re}(\lambda(\tau))}{d\tau}\Big|_{\tau=\tau_n} \ne 0$ .

**Proof.** Assume that  $\tau \in [0, \tau^*]$ . By Lemma 2.6,  $\omega_+(\tau) \ge 0$  with equality holding at  $\tau = \tau^*$ . By Lemma 2.7, there exists  $\epsilon > 0$  and  $\theta(\tau)$  such that  $\epsilon \le \theta(\tau) \le \pi$ and  $\theta(\tau)$  satisfies (2.3.20). Suppose there exists an integer  $n \ge 0$  such that  $\theta(\tau) + 2n\pi$ intersects  $\tau \omega_+(\tau)$  at some  $\tau_n \in (0, \tau^*)$ . Then  $(\tau_n, \omega_+(\tau_n))$  is a solution of (2.3.12), and therefore the characteristic equation (2.3.9) of (2.3.7) at  $E_+$  has a pair of pure imaginary eigenvalues  $\lambda = \pm i\omega_+(\tau_n)$ , and no other root of (2.3.9) is an integral multiple of  $\pm i\omega_+(\tau_n)$ .

In what follows we will verify the requirements of the Hopf Bifurcation Theorem (see Theorem A.2 in **Appendix A**) for the linearized equation (2.3.7) of (2.2.3) at  $E_+$ .

In (A.0.3), choosing the bifurcating parameter  $\alpha = \tau$ ,

$$D(\alpha, x_t) = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} x(t) \\ y(t) \end{bmatrix},$$

and

$$L(\alpha, x_t) = \begin{bmatrix} 1 - 2x^* - y^* & -x^* \\ 0 & -s \end{bmatrix} \begin{bmatrix} x(t) \\ y(t) \end{bmatrix} + \begin{bmatrix} 0 & 0 \\ Ye^{-s\tau}y^* & Ye^{-s\tau}x^* \end{bmatrix} \begin{bmatrix} x(t-\tau) \\ y(t-\tau) \end{bmatrix},$$

(A.0.3) reduces to equation (2.3.7). Taking a to be any positive real number and

 $b = \frac{1}{2}$ , then hypothesis  $(S_1)$  in the Hopf Bifurcation Theorem holds since

$$\left|\det\left[\sum_{k=0}^{\infty} A_k(\alpha) e^{-\lambda r_k(\alpha)}\right]\right| = \left|\det\left[\begin{array}{cc} 1 & 0\\ 0 & 1 \end{array}\right]\right| = 1 \geqslant \frac{1}{2},$$

and

$$\left|\det\left[\sum_{k=0}^{\infty} A_k(\alpha)e^{-\lambda r_k(\alpha)} + \int_{-1}^{0} A(\alpha, \ \theta)e^{\lambda\theta} \mathrm{d}\theta\right]\right| = \left|\det\left[\begin{array}{cc} 1 & 0\\ 0 & 1 \end{array}\right]\right| = 1 \ge \frac{1}{2}$$

for all  $\tau \in \mathbb{R}$  and  $|\operatorname{Re}\lambda| < a$ .

Since the characteristic equation (2.3.9) has a pair of pure imaginary eigenvalues  $\lambda = \pm i\omega_+(\tau_n)$  and no other root of (2.3.9) is an integral multiple of  $\pm i\omega_+(\tau_n)$ , hypothesis (S<sub>2</sub>) holds. Then (2.2.3) undergoes a Hopf bifurcation at  $E_+$  when  $\tau = \tau_n$  provided  $\operatorname{Re} \frac{d\lambda(\tau)}{d\tau}\Big|_{\tau=\tau_n} \neq 0$ .

**Theorem 2.9.** Consider system (2.2.3) with  $\tau \in [0, \tau^*]$ . Assume that there exists  $N \ge 0$  such that  $(2N+1)\pi < \max_{\tau \in [0,\tau^*]} \tau \omega_+(\tau) \le (2N+3)\pi$ .

- 1. For  $0 \leq n \leq N$ ,  $\theta(\tau) + 2n\pi$  and  $\tau \omega_+(\tau)$  have at least two intersections in  $(0, \tau^*)$ denoted as  $\tau_n^1$  and  $\tau_n^2$ . Hence (2.2.3) undergoes a Hopf bifurcation at  $\tau = \tau_n^j$ provided  $\frac{\mathrm{d}\mathrm{Re}(\lambda(\tau))}{\mathrm{d}\tau}\Big|_{\tau=\tau_n^j} \neq 0$ .
- 2. For n = N + 1, one of the following holds.
  - i) Function  $\theta(\tau) + 2n\pi$  and  $\tau \omega_+(\tau)$  have no intersection in  $(0, \tau^*)$ .
  - ii)  $\theta(\tau) + 2n\pi$  and  $\tau\omega_{+}(\tau)$  have an intersection denoted as  $\tau_{n}^{j}$ , where  $j \ge 1$ , and thus (2.2.3) undergoes a Hopf bifurcation at  $\tau = \tau_{n}^{j}$  provided  $\frac{\mathrm{d}\mathrm{Re}(\lambda(\tau))}{\mathrm{d}\tau}\Big|_{\tau=\tau_{n}^{j}} \neq 0.$

3. For  $n \ge N+2$ ,  $\theta(\tau) + 2n\pi$  and  $\tau \omega_+(\tau)$  have no intersection in  $(0, \tau^*)$ .

Further, if  $\tilde{\tau}$  is the smallest delay such that (2.3.9) has a pair of pure imaginary eigenvalues, then the coexistence equilibrium  $E_+$  is asymptotically stable for  $0 \leq \tau < \tilde{\tau}$ .

**Proof.** Fix  $\tau \in [0, \tau^*]$ . By Lemma 2.6,  $\omega_+(\tau) \ge 0$  with equality holding at  $\tau = \tau^*$ . By Lemma 2.7, there exists  $\epsilon > 0$  and  $\theta(\tau)$  such that  $\epsilon \le \theta(\tau) \le \pi$ , and  $\theta(\tau)$  satisfies (2.3.20).

**1.** For  $0 \le n \le N$ . Since  $\omega_+(\tau^*) = 0$ ,  $\tau \omega_+(\tau) = 0$  for  $\tau = 0$  and  $\tau = \tau^*$ , and  $\omega(\tau)$  is positive for  $\tau \in (0, \tau^*)$ . Therefore  $\min_{\tau \in [0, \tau^*]} \tau \omega_+(\tau) = 0$ . Since  $\epsilon \le \theta(\tau) \le \pi$ , we have

$$\epsilon + 2n\pi \leqslant \theta(\tau) + 2n\pi \leqslant \pi + 2n\pi.$$

Assume that there exists  $N \ge 0$  such that  $(2N+1)\pi < \max_{\tau \in [0,\tau^*]} \tau \omega_+(\tau) \le (2N+3)\pi$ . Then

$$\min_{\tau \in [0,\tau^*]} \tau \omega_+(\tau) < \theta(\tau) + 2n\pi < \max_{\tau \in [0,\tau^*]} \tau \omega_+(\tau).$$

By the Mean Value Theorem,  $\tau \omega_+(\tau)$  intersects  $\theta(\tau) + 2n\pi$  at least twice. Denote these intersection points  $\tau_n^j$ , j = 1, 2. By Theorem 2.8, (2.2.3) undergoes a Hopf bifurcation at  $\tau = \tau_n^j$  provided  $\frac{d\operatorname{Re}(\lambda(\tau))}{d\tau}\Big|_{\tau=\tau_n^j} \neq 0$ .

2. For n = N+1,  $\theta(\tau) + 2n\pi$  and  $\tau \omega_+(\tau)$  may or may not have an intersection. If  $\theta(\tau) + 2n\pi$  and  $\tau \omega_+(\tau)$  have an intersection  $\tau_n^j$ , by Theorem 2.8 the conclusion follows.

**3.** For any  $n \ge N+2$ , since

$$\theta(\tau) + 2n\pi \ge \epsilon + 2n\pi \ge \epsilon + 2(N+2)\pi > (2N+4)\pi > \max_{\tau \in [0,\tau^*]} \tau \omega_+(\tau),$$

 $\theta(\tau) + 2k\pi$  and  $\tau\omega_+(\tau)$  have no intersection.

Assume that  $\tilde{\tau}$  is the smallest delay such that the characteristic equation (2.3.9) has a pair of pure imaginary eigenvalues. Since 0 is not a root of (2.3.9), and Lemma 2.5 assures no roots of (2.3.9) with positive real part can enter from infinity as  $\tau$  increases from 0, it follows that all eigenvalues of  $E_+$  have negative real parts for  $\tau \in [0, \tilde{\tau})$ . Therefore  $E_+$  is asymptotically stable for  $\tau \in [0, \tilde{\tau})$ .

**Corollary 2.10.** Consider system (2.2.3) with  $\tau \in [0, \tau^*]$ . If there exists  $N \ge 0$  such that  $\frac{1}{s} \ln\left(\frac{Y}{6s}\right) \sqrt{-\frac{1}{72} + \frac{1}{2}\sqrt{\frac{1}{64} + \frac{13}{3}s^2}} > (2N+1)\pi$ , then for  $0 \le n \le N$ ,  $\theta(\tau) + 2n\pi$  and  $\tau\omega_+(\tau)$  have at least two intersections in  $(0, \tau^*)$  denoted by  $\tau_n^1$  and  $\tau_n^2$ . Hence (2.2.3) undergoes a Hopf bifurcation at  $\tau = \tau_n^j$  provided  $\frac{\mathrm{dRe}(\lambda(\tau))}{\mathrm{d}\tau}\Big|_{\tau=\tau_n^j} \neq 0$ .

**Proof.** Let  $\tau = \frac{1}{s} \ln\left(\frac{Y}{6s}\right)$ . Then  $\tau \omega_+(\tau) = \frac{1}{s} \ln\left(\frac{Y}{6s}\right) \sqrt{-\frac{1}{72} + \frac{1}{2}\sqrt{\frac{1}{6^4} + \frac{13}{3}s^2}}$ . Hence  $\max_{\tau \in [0, \tau^*]} \tau \omega_+(\tau) > \frac{1}{s} \ln\left(\frac{Y}{6s}\right) \sqrt{-\frac{1}{72} + \frac{1}{2}\sqrt{\frac{1}{6^4} + \frac{13}{3}s^2}} > (2N+1)\pi$ . By Theorem 2.9, for  $0 \leq n \leq N$ , the conclusion follows.

As in Kuang [5], we define

$$S_k(\tau) = \tau - \frac{\theta(\tau) + 2k\pi}{\omega_+(\tau)},$$

where k is a nonnegative integer. Then any zero of  $S_k(\tau)$  corresponds to an intersection of  $\theta(\tau) + 2k\pi$  with  $\tau\omega_+(\tau)$  and vice verse. From (4.10) (see p.1157 of Beretta and Kuang [5]), we have the relation

$$\operatorname{sign}\left\{\frac{\mathrm{d}\operatorname{Re}(\lambda(\tau))}{\mathrm{d}\tau}\right\}$$
$$=\operatorname{sign}\left\{\left(q^{2}-p^{2}(\tau)+2\alpha^{2}(\tau)\right)^{2}-4\left(\alpha^{2}(\tau)-c^{2}(\tau)\right)\right\}\operatorname{sign}\left\{\frac{\mathrm{d}S_{k}(\tau)}{\mathrm{d}\tau}\right\} \qquad (2.3.27)$$
$$=\operatorname{sign}\left\{\frac{\mathrm{d}S_{k}(\tau)}{\mathrm{d}\tau}\right\}.$$

Assume that Theorem 2.9 holds. The characteristic equation (2.3.9) has a pair of pure imaginary eigenvalues  $\lambda = \pm i\omega_+(\tau_n^j)$  at  $\tau_n^j$  for  $0 \le n \le N$  and j = 1, 2, and this pair of imaginary roots cross the imaginary axis from left to right if

$$\operatorname{sign}\left\{\frac{\mathrm{d}S_k(\tau)}{\mathrm{d}\tau}\Big|_{\tau=\tau_n^i}\right\} > 0,$$

and from right to left if it is less than zero (see Figure 2.1 (Right)), where

$$\begin{split} & \operatorname{sign} \left\{ \frac{\mathrm{d}S_k(\tau)}{\mathrm{d}\tau} \Big|_{\tau = \tau_n^i} \right\} \\ &= \omega_+^2(\tau) \left[ \omega_+^2(\tau) q^2 + c^2(\tau) + p'(\tau) \left( \alpha(\tau) - \omega_+(\tau) \right) + qc'(\tau) - p(\tau)c'(\tau) \right) \right] \\ &+ \omega_+(\tau) \omega_+'(\tau) \left[ \tau(\omega_+^2 q^2 + c^2(\tau)) - qc(\tau) + p(\tau) \left( \alpha(\tau) - \omega_+^2 \right) \right) + 2\omega_+^2 p(\tau) \right] . \end{split}$$

## 2.4 Numerical Simulations

In this section, we present some numerical results to illustrate the analytical results obtained in the former section, mainly those of Theorem 2.9. In carrying out our numerical simulations, we use the package DDE23 in MATLAB. We employ the non-scaled model (2.1.1) with f(x) = mx. Within this section  $\tau^*$ ,  $\tau_c$ ,  $\omega_+(\tau)$ , and  $\theta(\tau)$  are calculated in terms of the non-scaled parameters. We fix all parameters m = 1, r = 10, Y = 0.2, s = 0.2 except for  $\tau$  and K. We divide our numerical analysis into two parts corresponding to two different choices of K. The first set of figures (Figures 2.1-2.13) is for K = 30 chosen to illustrate cases 1., 2.i), and 3. of Theorem 2.9. The second set of figures (Figures 2.14-2.22) is for K = 50 chosen to demonstrate cases 1., 2.ii), and 3. of the theorem.

For the choice of K = 30,  $\tau_c = \frac{1}{s} \ln \left(\frac{YK}{s}\right) \approx 17.00$  and  $\tau^* = \frac{1}{s} \ln \left(\frac{YK}{3s}\right) \approx 11.51$ , we see in Figure 2.1 (Left), for n = 0, function  $\theta(\tau)$  intersects  $\tau \omega_+(\tau)$  exactly twice

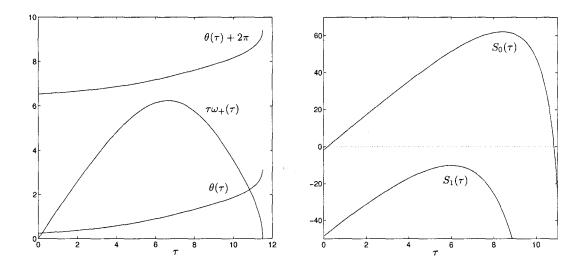


Figure 2.1: (Left) Intersections of  $\theta(\tau) + 2k\pi$  (k = 0, 1) and  $\tau \omega_+(\tau)$ .  $\tau \omega_+(\tau)$  intersects  $\theta(\tau)$  twice. (Right)  $S_0(\tau)$  has two zeros.

at  $\tau_0^1 = 0.15$  and  $\tau_0^2 = 10.81$ . By (2.3.27), instead of  $\frac{d\operatorname{Re}(\lambda(\tau))}{d\tau}\Big|_{\tau=\tau_0^j} \neq 0$ , one can check if sign  $\left\{\frac{dS_0(\tau)}{d\tau}\right\}\Big|_{\tau=\tau_0^j} \neq 0$ , where j = 1, 2. Figure 2.1 (Right) shows that sign  $\left\{\frac{dS_0(\tau)}{d\tau}\right\}\Big|_{\tau=0.15} = 1$  and sign  $\left\{\frac{dS_0(\tau)}{d\tau}\right\}\Big|_{\tau=10.81} = -1$ . For n = 1,  $\theta(\tau) + 2\pi$  has no intersection with  $\tau\omega_+(\tau)$ . For n > 2, there is no intersection and  $\theta(\tau) + 2k\pi$  (not plotted in the figure) lies above  $\theta(\tau) + 2\pi$ . This confirms our findings in Theorem 2.9. 1., 2.i), and 3. with N = 0.

To demonstrate the occurrence of Hopf bifurcations at  $\tau_0^1$  or  $\tau_0^2$ , we chose the initial data x(t) = 1.6 and y(t) = 0.4 for  $t \in [-\tau, 0]$ . For a small delay, the coexistence equilibrium  $E_+$  is stable (see Figure (2.2) with  $\tau = 0.1$ ). However, when  $\tau$  increases beyond  $\tau_0^1$ ,  $E_+$  becomes unstable, since a Hopf bifurcation occurs at  $\tau_0^1$ . There is a stable periodic orbit surrounding  $E_+$  (see Figure 2.3 and 2.4 for  $\tau = 0.2$ ). Increasing  $\tau$  to 7, the periodic solution changes its shape slightly and develops a kink (see Figure

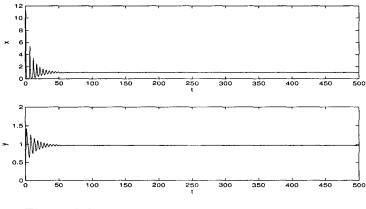


Figure 2.2: Equilibrium  $E_+$  is stable when  $\tau$  is small.

2.6). From Figure 2.5, it appears that a period doubling bifurcation occurs for some  $\tau$  between 0.2 and 7. As  $\tau$  continues to increase, it seems that the original periodic solution develops more kinks and loses its periodic feature (see Figures 2.7 and 2.8). In fact, when  $\tau = 9$ , we calculated the largest Lyapunov exponent and it was equal to 0.12. Since it is positive, this seems to indicate that the system is chaotic. Increasing  $\tau$  even further, say  $\tau = 10$ , kinks on the orbit disappear and the solution is once again attracted to a periodic solution (see Figures 2.9 and 2.10). Taking  $\tau = 12$ , the periodic orbit disappears and the coexistence equilibrium  $E_+$  regains its stability and remains stable until  $\tau = 17$  (see Figure 2.11). For  $\tau > 17$ ,  $E_+$  disappears since the predator component  $y_+(\tau)$  becomes negative, and  $E_1$  is globally asymptotically stable.

We also used MATLAB to plot a bifurcation diagram as a function of  $\tau$  (see Figure (2.12)). Along the vertical axis, the local maximum and minimum values of the density of the predator on the attracting solution are plotted (ignoring the initial transient solution). At  $\tau \approx 5.2$ , a period doubling bifurcation appears. Around  $\tau = 7.8$ , it is necessary to blow up the figure in order to see the detail, since the

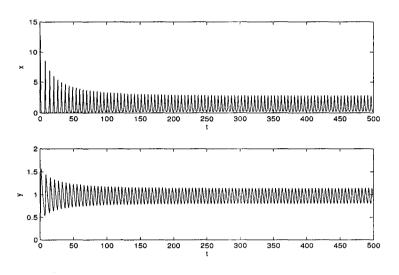


Figure 2.3: Time series of a solution that converges to a periodic solution for  $\tau = 0.2$ .

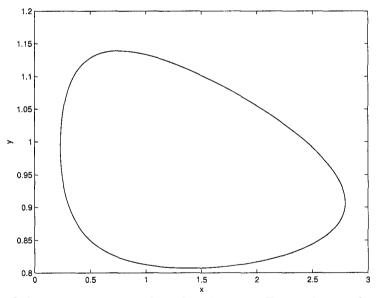


Figure 2.4: The stable periodic orbit shown in Figure 2.3 in phase space for  $\tau = 0.2$ .

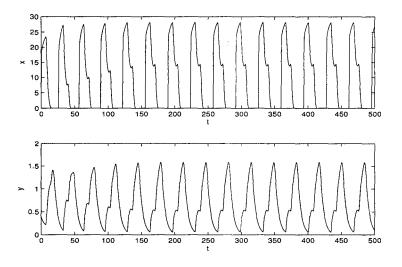


Figure 2.5: Time series of a solution when  $\tau = 7$ .

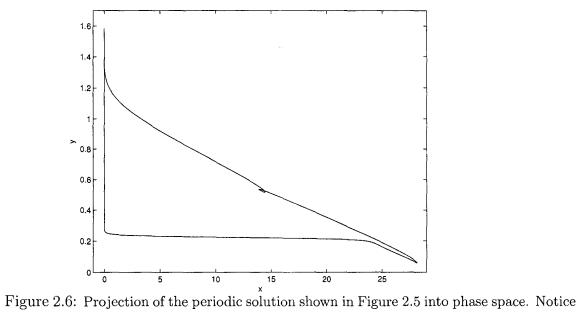


Figure 2.6: Projection of the periodic solution shown in Figure 2.5 into phase space. Notice the kinks.

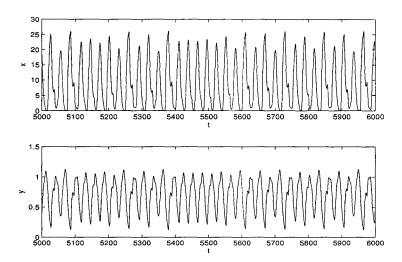


Figure 2.7: Time series of a solution that no longer appears to be periodic, for  $\tau = 9$ .

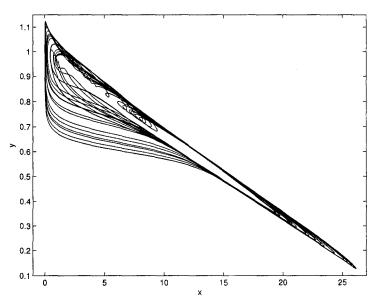


Figure 2.8: Projection of the solution in Figure 2.7 into phase space. The solution no longer appears to be periodic. The largest Lyapunov exponent is positive indicating that the system is chaotic

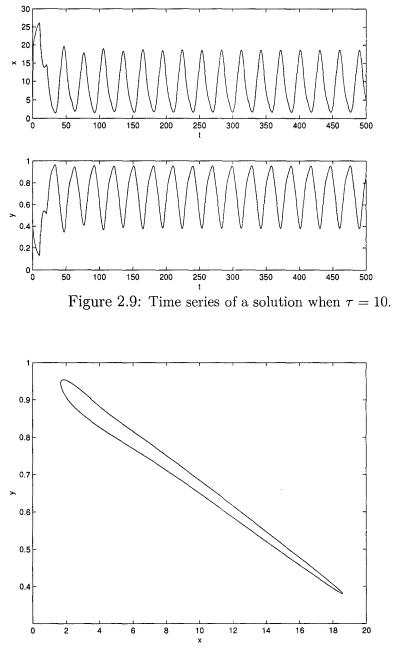


Figure 2.10: The stable periodic solution from Figure 2.9 in phase space when  $\tau = 10$ .

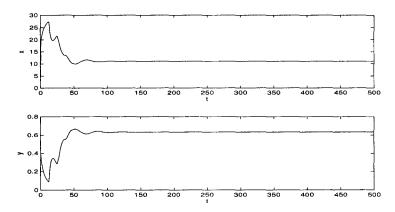


Figure 2.11: Equilibrium  $E_+$  regains stability when  $\tau$  is larger than  $\tau_0^2$ .

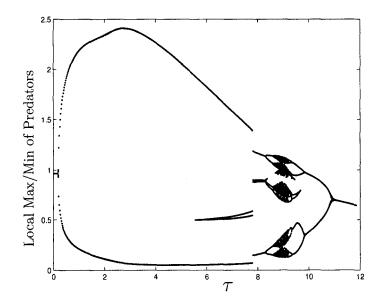


Figure 2.12: Bifurcation diagram. For more detail for  $\tau \in (7.798, 7.803)$ , see Figure 2.13.

curves around this area change quickly as  $\tau$  varies and our mesh size for  $\tau$  was relatively large. This blow up is given in Figure 2.13.

For K = 50,  $\tau_c \approx 19.56$  and  $\tau^* \approx 14.06$ . In Figure 2.14 (Left),  $\theta(\tau)$  and  $\tau \omega_+(\tau)$  have two intersections,  $\tau_0^1 \approx 0.12$  and  $\tau_0^2 \approx 13.55$ . From Figure 2.14

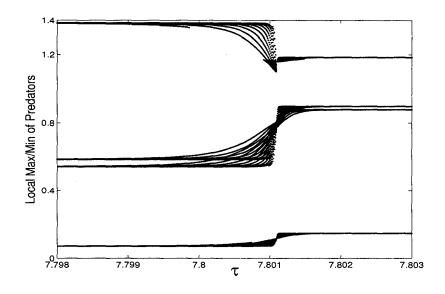


Figure 2.13: Blow up of the bifurcation diagram in Figure 2.12 for  $\tau \in (7.798, 7.803)$ .

(Right), sign  $\left\{\frac{dS_0(\tau)}{d\tau}\Big|_{\tau_0^1}\right\} = 1$  and sign  $\left\{\frac{dS_0(\tau)}{d\tau}\Big|_{\tau_0^2}\right\} = -1$ . For n = 1,  $\theta(\tau) + 2\pi$  intersects  $\tau\omega_+(\tau)$  twice at  $\tau_1^1 \approx 5.4$  with sign  $\left\{\frac{dS_1(\tau)}{d\tau}\Big|_{\tau_1^1}\right\} = 1$ , and  $\tau_1^2 \approx 10.6$  with sign  $\left\{\frac{dS_1(\tau)}{d\tau}\Big|_{\tau_1^2}\right\} = -1$ . This illustrates cases 1., 2.ii), and 3. in Theorem 2.9. We use constant initial data x(t) = 1.6 and y(t) = 0.4 for  $t \in [-\tau, 0]$  to show that Hopf bifurcations occur. Figure 2.15-2.22 show how the dynamics of system (2.1.1) change when  $\tau$  increases from zero to 13.7. The coexistence equilibrium  $E_+$  is stable for small delays. Increasing  $\tau = 0.14 > \tau_0^1$ ,  $E_+$  loses its stability and an attracting periodic solution appears. Increasing  $\tau$  to  $\tau = 8$ , kinks appear on the periodic solution. Increasing  $\tau = 13.7 > \tau_0^2$ ,  $E_+$  regains its stability and remains stable until  $\tau = 19.56$ . After that  $E_+$  does not exist since its second component  $y_+(\tau)$  becomes negative, and  $E_1$  is globally asymptotically stable.

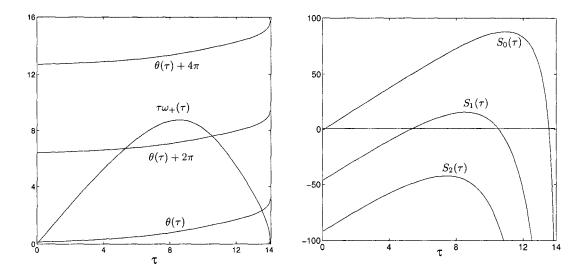


Figure 2.14: Four delay values for Hopf bifurcation.

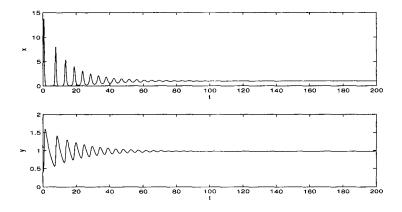


Figure 2.15: Equilibrium  $E_+(\tau)$  is stable when  $\tau = 0.05$ .

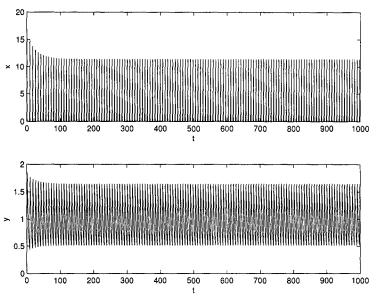


Figure 2.16: A solution converging to the stable periodic solution when  $\tau = 0.14$ .

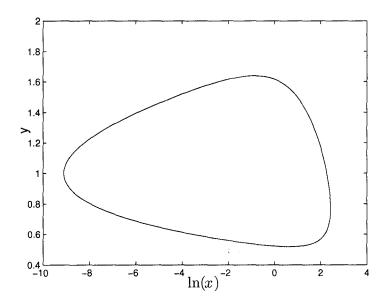


Figure 2.17: The periodic orbit shown in Figure 2.16 in phase space when  $\tau = 0.14$ . The vertical axis is y and the horizontal is  $\ln(x)$ .

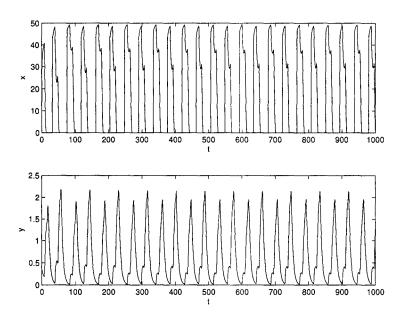


Figure 2.18: Time series of an attracting solution with kinks when  $\tau = 8$ .

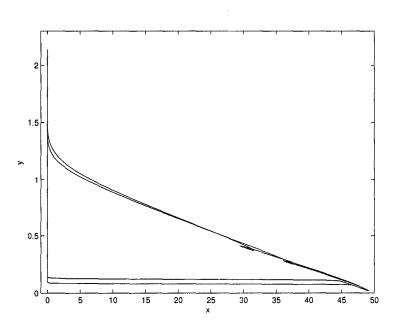


Figure 2.19: The periodic orbit shown in Figure 2.18 in phase space when  $\tau = 8$ . The shape of periodic solution is different from the one when  $\tau = 0.14$ .

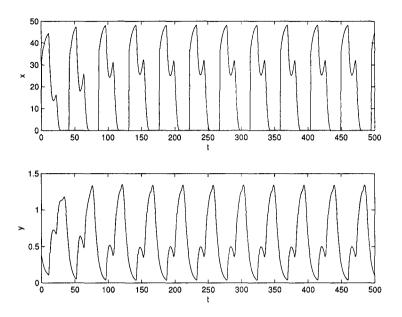


Figure 2.20: Time series of an attracting solution when  $\tau = 10.08$ .

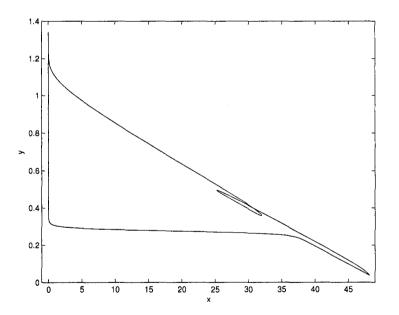


Figure 2.21: The periodic orbit shown in Figure 2.20 for  $\tau = 10.08$  has a kink. It is quite close to the vertical axis on the left, but remains positive.

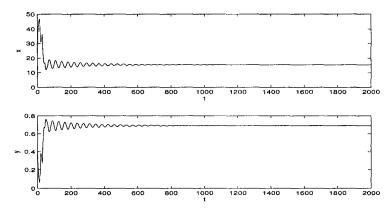


Figure 2.22: Equilibrium  $E_{+}(\tau)$  is stable again when  $\tau = 13.7$ . It regains stability by the secondary Hopf bifurcation at  $\tau_0^2$ .

### 2.5 Discussion

Gourley and Kuang [21] studied a stage structured predator-prey model with constant maturation time delay. Although the interpretation of the time delay was different, they considered the same model studied here. They considered the possibility of stability switches, in this case and concluded that there is a range of the parameter modeling the time delay for which there are periodic solutions. We improve their results by giving more complete analytical results.

As pointed out by Gourley and Kuang [21], one cannot in practice compute the stability switches analytically. Therefore, they apply the approach developed in Beretta and Kuang [5]. Their main result states that if  $\omega(\tau)$  is a positive real root of (2.3.13) and  $S_k(\hat{\tau}) = 0$  for some nonnegative integer k, then the characteristic equation (2.3.9) has a pair of pure imaginary roots at  $\tau = \hat{\tau}$ . Hence the stability switch of the interior equilibrium is determined by the zeros of function  $S_k(\tau)$ . But the remaining question is whether there exists a positive root  $\omega(\tau)$ . Also note that the definition of  $S_k(\tau)$  involves the function  $\theta(\tau)$ , which is only implicitly defined as a solution of (2.3.20), and whether or not such a function  $\theta(\tau)$  exists is not determined. Although we cannot study stability switches completely analytically, more complete analytical results than those given in [21] are possible. From the analysis in this chapter, we proved that one positive root  $\omega_{+}(\tau)$  of (2.3.13) is possible. In Theorem 2.7, we provided the explicit definition of  $\theta(\tau)$  and hence determine precisely when such a solution of (2.3.20) exists. The proof required introducing the function  $\Gamma(\omega, \tau)$  and using the Implicit Function Theorem. Theorem 2.9 gives conditions for when (2.3.12) has solutions, or equivalently, when the characteristic equation (2.3.9) has pure imaginary eigenvalues. It states that Hopf bifurcation is possible for the model considered and for what parameter range we can expect the periodic solutions.

In [13], Cooke, Elderkin, and Huang considered a model similar to the one in Gourley and Kuang [21], and obtained results concerning Hopf bifurcation of a scaled version. However the scaling they used eliminated the bifurcation parameter  $\tau$ . Therefore made the analysis much easier. However this is not without sacrifice. To interpret their results with respect to the unscaled model became delicate. They must take care of the delay parameter again.

In Chapter 3, we simplify the approach studied here in order to make it more easily applied to the other models. In Chapter 4, we generalize that method so that it can be applied to general second order transcendental equations.

# Chapter 3

# A Predator-Prey Model in the Chemostat with Time Delay

# 3.1 Model Considered

Consider a chemostat involving a predator-prey interaction. Assuming it takes  $\tau$  units of time for the predator to convert prey to viable biomass once the prey is captured. The model is given by

$$\begin{cases} \dot{s}(t) = (s^{0} - s(t))D_{0} - \frac{x(t)f(s(t))}{\eta}, \\ \dot{x}(t) = x(t)\left(-D + f(s(t))\right) - \frac{y(t)g(x(t))}{\xi}, \quad t > 0, \\ \dot{y}(t) = -\Delta y(t) + e^{-\Delta\tau}y(t - \tau)g(x(t - \tau)). \end{cases}$$
(3.1.1)

For  $t \in [-\tau, 0]$ ,

$$s(0) = s_0 \in \operatorname{int}\mathbb{R}_+, \quad \text{and} \quad (x(t), y(t)) = (\phi, \psi) \in \mathbb{C}([-\tau, 0], \operatorname{int}\mathbb{R}^2_+), \quad (3.1.2)$$

where  $s^0$ ,  $D_0$ ,  $\eta$ ,  $\xi$ ,  $D \ge D_0$ , and  $\Delta \ge D_0$  are positive constants and  $\tau$  is a nonnegative constant. In this model, s(t) denotes the concentration of substrate in the growth chamber at time t, x(t) the biomass density of the prey population, and y(t) the biomass density of predator population.  $s^0$  is the concentration of nutrient in the feed bottle and  $D_0$  denotes the input rate from the feed bottle and output rate from the growth chamber. Parameters  $\eta$  and  $\xi$  denote the growth yield constants. D and  $\Delta$  denote the sum of the washout rate  $D_0$  and the natural death rate of prey and predators, respectively. Hence  $D \ge D_0$  and  $\Delta \ge D_0$ . The functional responses are given by f(s) and g(x). It is assumed that the process of conversion from prey to predator is not instantaneous, but rather takes  $\tau$  units of time. Hence,  $e^{-\Delta\tau}y(t-\tau)$ represents the concentration of the predator population in the growth chamber at time t that were available at time  $t - \tau$  to capture prey and were able to avoid death and washout during the  $\tau$  units of time required to process the captured prey.

#### 3.2 Scaling of the Model and Existence of Solutions

Suppose that functions f(s) and g(s) are of Holling type I form i.e.  $f(s) = \alpha s$ ( $\alpha > 0$ ) and g(x) = kx (k > 0). System (3.1.1) reduces to

$$\begin{cases} \dot{s}(t) = (s^{0} - s(t))D_{0} - \frac{\alpha x(t)s(t)}{\eta}, \\ \dot{x}(t) = x(t)\left(-D + \alpha s(t)\right) - \frac{kx(t)y(t)}{\xi}, \quad t > 0, \\ \dot{y}(t) = -\Delta y(t) + ke^{-\Delta\tau}y(t - \tau)x(t - \tau). \end{cases}$$
(3.2.3)

Introducing the following change of variables

$$\begin{split} \breve{t} &= D_0 t, \qquad \breve{s}(\breve{t}) = \frac{s(t)}{s^0}, \qquad \breve{x}(\breve{t}) = \frac{x(t)}{s^0\eta}, \qquad \breve{y}(\breve{t}) = \frac{y(t)}{\xi s^0\eta}, \\ \breve{\tau} &= D_0 \tau, \qquad \breve{D} = \frac{D}{D_0}, \qquad \breve{\Delta} = \frac{\Delta}{D_0}, \qquad \breve{k} = \frac{k s^0 \eta}{D_0}, \qquad \breve{\alpha} = \frac{\alpha s^0}{D_0}, \end{split}$$

and using (3.2.3) gives

$$\begin{aligned} \frac{\mathrm{d}\breve{s}(\breve{t})}{\mathrm{d}\breve{t}} &= \frac{1}{s^0} \frac{\mathrm{d}s(t)}{\mathrm{d}t} \frac{\mathrm{d}t}{\mathrm{d}\breve{t}} = \frac{1}{s^0 D_0} \frac{\mathrm{d}s(t)}{\mathrm{d}t} \\ &= \frac{1}{s^0 D_0} \left( (s^0 - s(t)) D_0 - \frac{\alpha x(t) s(t)}{\eta} \right) \\ &= 1 - \frac{s(t)}{s^0} - \frac{\alpha s^0}{D_0} \frac{x(t)}{s^0 \eta} \frac{s(t)}{s^0} \\ &= 1 - \breve{s}(\breve{t}) - \breve{\alpha}\breve{x}(\breve{t})\breve{s}(\breve{t}), \end{aligned}$$

$$\begin{aligned} \frac{\mathrm{d}\breve{x}(\breve{t})}{\mathrm{d}\breve{t}} &= \frac{1}{s^0\eta} \frac{\mathrm{d}x(t)}{\mathrm{d}t} \frac{\mathrm{d}t}{\mathrm{d}\breve{t}} = \frac{1}{s^0\eta D_0} \frac{\mathrm{d}x(t)}{\mathrm{d}t} \\ &= \frac{1}{s^0\eta D_0} \bigg( x(t) \left( -D + \alpha s(t) \right) - \frac{kx(t)y(t)}{\xi} \bigg) \\ &= \frac{x(t)}{s^0\eta} \big( -\frac{D}{D_0} + \frac{\alpha s^0}{D_0} \frac{s(t)}{s^0} \big) - \frac{ks^0\eta}{D_0} \frac{x(t)}{s^0\eta} \frac{y(t)}{s^0\eta\xi} \\ &= \breve{x}(\breve{t}) \big( -\breve{D} + \breve{\alpha}\breve{s}(\breve{t}) \big) - \breve{k}\breve{x}(\breve{t})\breve{y}(\breve{t}), \end{aligned}$$

and

$$\begin{split} \frac{\mathrm{d}\breve{y}(\breve{t})}{\mathrm{d}\breve{t}} &= \frac{1}{s^0 \eta \xi} \frac{\mathrm{d}y(t)}{\mathrm{d}t} \frac{\mathrm{d}t}{\mathrm{d}\breve{t}} = \frac{1}{s^0 \eta \xi D_0} \frac{\mathrm{d}y(t)}{\mathrm{d}t} \\ &= \frac{1}{s^0 \eta \xi D_0} \left( -\Delta y(t) + k e^{-\Delta \tau} y(t-\tau) x(t-\tau) \right) \\ &= \frac{-\Delta y(t)}{s^0 \eta \xi D_0} + \frac{k e^{-\Delta \tau}}{s^0 \eta \xi D_0} y(t-\tau) x(t-\tau) \\ &= \frac{-\Delta}{D_0} \frac{y(t)}{s^0 \eta \xi} + \frac{k s^0 \eta}{D_0} e^{-\frac{\Delta}{D_0} D_0 \tau} \frac{y(t-\tau)}{s^0 \eta \xi} \frac{x(t-\tau)}{s^0 \eta} \\ &= -\breve{\Delta}\breve{y}(\breve{t}) + \breve{k} e^{-\breve{\Delta}\breve{\tau}}\breve{y}(\breve{t}-\breve{\tau})\breve{x}(\breve{t}-\breve{\tau}). \end{split}$$

With this change of variables, omitting the for convenience system (3.2.3) becomes

$$\dot{s}(t) = 1 - s(t) - \alpha x(t)s(t),$$
  

$$\dot{x}(t) = x(t) (-D + \alpha s(t)) - ky(t)x(t),$$
  

$$\dot{y}(t) = -\Delta y(t) + ke^{-\Delta \tau}y(t - \tau)x(t - \tau),$$
  
(3.2.4)

where  $\Delta \ge 1$  and  $D \ge 1$ , with initial data given by (3.1.2). For biological significance, a point is assumed to be a critical point of (3.2.4) only if all its components are nonnegative.

Let  $\tau = 0$ . Model (3.2.4) reduces to a special case of the model considered in [55]. If  $D > \alpha$ , the model has only one equilibrium point (1, 0, 0) which is globally asymptotically stable. If  $D < \alpha$  and  $1 - \frac{D}{\alpha} - \frac{\Delta D}{k} < 0$ , the model has a second equilibrium point  $(\frac{D}{\alpha}, \frac{\alpha-D}{\alpha D}, 0)$  which is globally asymptotically stable. When  $1 - \frac{D}{\alpha} - \frac{\Delta D}{k} > 0$ , the model has a third equilibrium point  $(\frac{k}{k+\alpha\Delta}, \frac{\Delta}{k}, \frac{\alpha}{k+\alpha D} - \frac{D}{k})$  which is the global attractor. This implies that model (3.1.1) with Holling type I response functions has no periodic solutions when there is no time delay. If g(x) is of Holling type II form, Butler and Wolkowicz [8] proved that a Hopf bifurcation is possible resulting in a periodic solution for a certain range of parameter values. It is for this reason that in this thesis we restrict our attention to the simplest case for both response functions, i.e. Holling type I, to see whether delay can be responsible for periodic solutions in (3.1.1).

**Theorem 3.1.** Assume  $(s_0, \phi(\theta), \psi(\theta)) \in int \mathbb{R}_+ \times \mathbb{C}([-\tau, 0], int \mathbb{R}^2_+)$ . Then there exists a unique solution (s(t), x(t), y(t)) of (3.2.4) passing through  $(s_0, \phi(\theta), \psi(\theta))$  with s(t) > 0, x(t) > 0 and y(t) > 0 for  $t \in [0, \infty)$ . The solution is bounded. In particular, given any  $\epsilon_0$ ,  $x(t) < 1 + \epsilon_0$  for all sufficiently large t.

**Proof.** Since the right hand side of (3.2.4) is continuous, by Theorem B.1 in Appendix **B**, the existence of solutions can be obtained for any  $t \ge 0$ . Next we prove s(t) > 0 for all t > 0. By the method of contradiction, we suppose there exists a first  $t^*$  such that  $s(t^*) = 0$  and s(t) > 0 for  $t \in [0, t^*)$ . Then  $\dot{s}(t^*) \le 0$ . But from the first equation of (3.2.4)

$$\dot{s}(t^{\star}) = 1 - s(t^{\star}) - \alpha x(t^{\star})s(t^{\star}) = 1 > 0,$$

a contradiction.

To prove x(t) > 0, divide both side of the second equation of (3.2.4) and integrate from 0 to t, to obtain

$$x(t) = \phi(0) \exp\left(\int_0^t \left(-D + \alpha s(t) - ky(t)\right) \mathrm{d}t\right) > 0.$$

To show that y(t) is positive on  $[0, \infty)$ , we use the method of contradiction. Suppose that there exists  $t^* > 0$  such that

$$y(t^{\star}) = 0$$
, and  $y(t) > 0$  for  $t \in [0, t^{\star})$ . Then  $\dot{y}(t^{\star}) \leq 0$ .

From the third equation of (3.2.4), we have

$$\begin{split} \dot{y}(t^{\star}) &= -\Delta y(t^{\star}) + k e^{-\Delta \tau} y(t^{\star} - \tau) x(t^{\star} - \tau) \\ &= k e^{-\Delta \tau} y(t^{\star} - \tau) x(t^{\star} - \tau) > 0, \end{split}$$

a contradiction.

To prove the boundedness, define

$$\omega(t) = s(t) + x(t) + e^{\Delta \tau} y(t+\tau) - 1, \quad \text{for} \quad t \ge 0.$$

It follows that

$$\begin{split} \dot{\omega}(t) &= 1 - s(t) - Dx(t) - \Delta e^{\Delta \tau} y(t+\tau) \\ &\leqslant 1 - s(t) - x(t) - e^{\Delta \tau} y(t+\tau) \\ &\leqslant -\omega(t), \end{split}$$

where the first inequality holds since  $D \ge 1$ ,  $\Delta \ge 1$ , x(t) > 0 and  $y(t + \tau) > 0$ . It follows that

$$s(t) + x(t) + e^{\Delta \tau} y(t+\tau) \leq 1 + \left(s_0 + x(0) + e^{\Delta \tau} y(\tau) - 1\right) e^{-t} \to 1 \quad \text{as} \quad t \to \infty.$$

Therefore the solution (s(t), x(t), y(t)) is bounded, and  $x(t) < 1 + \epsilon_0$  for sufficiently large t and any small positive  $\epsilon_0$ .

Now we are ready to prove the uniqueness of the solution. For any  $t \in [0, \tau]$ , (3.2.4) with initial data  $(s_0, \phi(\theta), \psi(\theta))$  is a system of nonautonomous ordinary differential equations:

$$\dot{s}(t) = 1 - s(t) - \alpha x(t) s(t) = F(s, x), 
\dot{x}(t) = x(t) (-D + \alpha s(t)) - ky(t) x(t) = G_1(s, x, y), 
\dot{y}(t) = -\Delta y(t) + k e^{-\Delta \tau} \psi(t - \tau) \phi(t - \tau) = G_2(\phi, \psi, y), 
s(0) = s_0, x(0) = \phi(0), y(0) = \psi(0).$$
(3.2.5)

Noting that a solution (s(t), x(t), y(t)) of (3.2.4) with initial data  $(s_0, \phi(\theta), \psi(\theta))$ exists and is bounded, let M > 0 such that |s(t)| < M, |x(t)| < M, and |y(t)| < M. For any  $(t, s, x, y) \in [0, \tau] \times [0, M] \times [0, M] \times [0, M]$ , F(s, x),  $G_1(s, x, y)$ , and  $G_2(\phi, \psi, y)$ are continuous and their partial derivatives with respect to s, x, and y are continuous and bounded on  $[0, \tau] \times [0, M] \times [0, M] \times [0, M]$ . By Corollary 4.3 in [41], solution (s(t), x(t), y(t)) of (3.2.5) for  $t \in [0, \tau]$  is unique. Hence the solution (s(t), x(t), y(t))of (3.2.4) is unique for  $t \in [0, \tau]$ . For  $t \in [\tau, 2\tau]$ , consider the renewed initial data  $(s_0, \phi(t - \tau), \psi(t - \tau)) = (s(\tau), x(t - \tau), y(t - \tau))$ . System (3.2.4) with the renewed initial data becomes a system of ordinary differential equations (3.2.5) with initial values  $(s(\tau), x(\tau), y(\tau))$ . Similarly, by Corollary 4.3 in [41], the solution (s(t), x(t), y(t)) of (3.2.5) is unique on  $t \in [\tau, 2\tau]$ . Hence solution (s(t), x(t), y(t)) of (3.2.4) is unique on  $t \in [\tau, 2\tau]$ . Step by step, it can be proved that solution (s(t), x(t), y(t)) of (3.2.4) is unique on  $[n\tau, (n+1)\tau]$  for any integer  $n \ge 0$ .

### 3.3 Equilibria and Stability

Model (3.2.4) has three equilibria  $E_1 = (1, 0, 0), \quad E_2 = \left(\frac{D}{\alpha}, \frac{\alpha - D}{\alpha D}, 0\right)$ , and

$$E_{+} = (s_{+}(\tau), x_{+}(\tau), y_{+}(\tau)) = \left(\frac{1}{1 + \frac{\alpha\Delta}{k}e^{\Delta\tau}}, \frac{\Delta}{k}e^{\Delta\tau}, \frac{\alpha}{k + \alpha\Delta e^{\Delta\tau}} - \frac{D}{k}\right).$$
(3.3.6)

We call  $E_2$  the single species equilibrium and  $E_+$  the coexistence equilibrium. For the sake of biological significance,  $E_+$  exists (distinct from  $E_2$ ) if and only if its third coordinate  $y_+(\tau) = \frac{\alpha s_+(\tau) - D}{k} > 0$ , i.e.  $s_+(\tau) > \frac{D}{\alpha}$ , or equivalently,  $\tau$  lies between 0 and  $\tau_c$ , where

$$\tau_c = \frac{1}{\Delta} \ln \left( \frac{k}{\Delta} \left( \frac{1}{D} - \frac{1}{\alpha} \right) \right).$$
(3.3.7)

Note that if  $\frac{k}{\Delta} \left(\frac{1}{D} - \frac{1}{\alpha}\right) \leq 1$ , the equilibrium  $E_+$  does not exist no matter the value of  $\tau \ (\geq 0)$ . In fact if  $\frac{k}{\Delta} \left(\frac{1}{D} - \frac{1}{\alpha}\right) = 1$ , then  $E_+ = E_2$ .

The linearization of (3.2.4) about an equilibrium (s, x, y) is

$$\begin{bmatrix} \dot{z}_{1}(t) \\ \dot{z}_{2}(t) \\ \dot{z}_{3}(t) \end{bmatrix} = \begin{bmatrix} -1 - \alpha x & -\alpha s & 0 \\ \alpha x & -D + \alpha s - ky & -kx \\ 0 & 0 & -\Delta \end{bmatrix} \begin{bmatrix} z_{1}(t) \\ z_{2}(t) \\ z_{3}(t) \end{bmatrix} + \begin{bmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & ke^{\Delta \tau} y & ke^{\Delta \tau} x \end{bmatrix} \begin{bmatrix} z_{1}(t - \tau) \\ z_{2}(t - \tau) \\ z_{3}(t - \tau) \end{bmatrix}.$$
(3.3.8)

The associated characteristic equation is given by

$$\det \begin{bmatrix} -1 - \alpha x - \lambda & -\alpha s & 0 \\ \alpha x & -D + \alpha s - ky - \lambda & -kx \\ 0 & ke^{-\Delta \tau - \lambda \tau}y & -\Delta + ke^{-\Delta \tau - \lambda \tau}x - \lambda \end{bmatrix} = 0. \quad (3.3.9)$$

Direct calculation of the left hand side of (3.3.9) gives

$$\begin{split} (-\Delta + ke^{-(\Delta+\lambda)\tau}x - \lambda) \left\{ (-1 - \alpha x - \lambda)(-D + \alpha s - ky - \lambda) + \alpha^2 sx \right\} \\ + kxke^{-(\Delta+\lambda)\tau}y(-1 - \alpha x - \lambda) \\ = (-\Delta - \lambda) \left\{ (1 + \alpha x + \lambda)(D - \alpha s + ky + \lambda) + \alpha^2 sx \right\} + e^{-(\Delta+\lambda)\tau}kx \\ \left\{ ky(-1 - \alpha x - \lambda) + (1 + \alpha x + \lambda)(D - \alpha s + ky + \lambda) + \alpha^2 sx \right\} \\ = (-\Delta - \lambda) \left\{ (1 + \alpha x + \lambda)(D - \alpha s + ky + \lambda) + \alpha^2 sx \right\} \\ + e^{-(\Delta+\lambda)\tau}kx \left\{ (1 + \alpha x + \lambda)(D - \alpha s + \lambda) + \alpha^2 sx \right\} \\ = (-\Delta - \lambda) \left\{ (\lambda + 1)(\lambda + D + ky) + \alpha x(\lambda + D + ky) - \alpha s(\lambda + 1) \right\} \\ + e^{-(\Delta+\lambda)\tau}kx \left\{ (\lambda + 1)(\lambda + D) + \alpha x(\lambda + D) - \alpha s(\lambda + 1) \right\}. \end{split}$$

For convenience, define

$$P(\lambda) := (-\Delta - \lambda) \left\{ (\lambda + 1)(\lambda + D + ky) + \alpha x(\lambda + D + ky) - \alpha s(\lambda + 1) \right\}$$
$$+ e^{-(\Delta + \lambda)\tau} kx \left\{ (\lambda + 1)(\lambda + D) + \alpha x(\lambda + D) - \alpha s(\lambda + 1) \right\}.$$

**Theorem 3.2.** Equilibrium  $E_1$  is stable if  $\alpha < D$  and unstable if  $\alpha > D$ .

**Proof.** Evaluating the characteristic equation at  $E_1$  gives

$$P(\lambda)|_{E_1} = -(\Delta + \lambda)(\lambda + 1)(\lambda + D - \alpha) = 0.$$

The eigenvalues -1 and  $-\Delta$  are both negative. The third eigenvalue is  $-D + \alpha$ . Therefore the equilibrium  $E_1$  is stable if  $\alpha < D$  and unstable if  $\alpha > D$ .  $\Box$ 

**Remark** If  $\alpha < D$ , then there is only one equilibrium,  $E_1$ . If  $\alpha > D$ , equilibrium  $E_2$  also exists.

**Lemma 3.3.** Assume  $\alpha > D$ . The characteristic equation at  $E_2$  has two negative eigenvalues, and the remaining eigenvalues are solutions of

$$(\lambda + \Delta)e^{(\lambda + \Delta)\tau} = k\left(\frac{1}{D} - \frac{1}{\alpha}\right).$$
(3.3.10)

In addition, the characteristic equation at  $E_2$  has zero as an eigenvalue if and only if  $\tau = \tau_c$ .

**Proof.** Assume  $\alpha > D$ . Equilibrium  $E_2$  exists. Consider the characteristic equation at  $E_2$ . Since  $\frac{\alpha - D}{\alpha D} = \frac{1 - s}{\alpha s}$  at  $E_2$ ,

$$P(\lambda)|_{E_2} = \{(\lambda+1)(\lambda+D) + \alpha x(\lambda+D) - \alpha s(\lambda+1)\}$$

$$(-\lambda - \Delta + e^{-(\Delta+\lambda)\tau}kx)$$

$$= \{(\lambda+1)(\lambda+D) + \frac{1-s}{s}(\lambda+D) - D(\lambda+1)\}$$

$$\left(-\lambda - \Delta + e^{-(\Delta+\lambda)\tau}k\frac{\alpha-D}{\alpha D}\right)$$

$$= \{\lambda(\lambda+1) - (\lambda+D) + \frac{\lambda+D}{s}\}\left(-\lambda - \Delta + k\frac{\alpha-D}{\alpha D}e^{-(\Delta+\lambda)\tau}\right)$$

$$= -(\lambda^2 + \frac{\alpha}{D}\lambda + \alpha - D)\left(\lambda + \Delta - k\frac{\alpha-D}{\alpha D}e^{-(\Delta+\lambda)\tau}\right)$$

$$= -e^{(\Delta+\lambda)\tau}(\lambda - \lambda_1)(\lambda - \lambda_2)\left((\lambda+\Delta)e^{(\Delta+\lambda)\tau} - k\left(\frac{1}{D} - \frac{1}{\alpha}\right)\right) = 0,$$

where  $\lambda_1 + \lambda_2 = -\frac{\alpha}{D}$  and  $\lambda_1 \lambda_2 = \alpha - D > 0$ . Therefore,  $\lambda_1$  and  $\lambda_2$  have negative real parts. The rest of the eigenvalues are roots of (3.3.10).

Assuming that  $\lambda = 0$  is a root of (3.3.10), we have

$$\Delta e^{\Delta \tau} = k \left( \frac{1}{D} - \frac{1}{\alpha} \right).$$

Solving for  $\tau$  gives

$$\tau = \frac{1}{\Delta} \ln \left( \frac{k}{\Delta} \left( \frac{1}{D} - \frac{1}{\alpha} \right) \right) = \tau_c.$$

**Theorem 3.4.** Assume that  $D \ge 1$ ,  $\Delta \ge 1$ , k > 0,  $\alpha > 0$ , and  $\frac{k}{\Delta} \left(\frac{1}{D} - \frac{1}{\alpha}\right) \ge 1$  so that  $\tau_c \ge 0$ . Equilibrium  $E_2$  is locally asymptotically stable if  $\tau > \tau_c$  and unstable if  $\tau < \tau_c$ . If D = 1, then equilibrium  $E_2$  is globally asymptotically stable for  $\tau > \frac{1}{\Delta} \ln \left(\frac{k}{\Delta}\right)$ .

**Proof.** Assume that  $\tau > \tau_c$ . Assumptions k > 0,  $\Delta \ge 1$ , and  $\frac{k}{\Delta} \left(\frac{1}{D} - \frac{1}{\alpha}\right) \ge 1$ imply  $\frac{1}{D} > \frac{1}{\alpha}$ , or equivalently  $\alpha > D$ . By Lemma 3.3, to prove equilibrium  $E_2$  is locally asymptotically stable, one only needs to show that (3.3.10) admits no root with nonnegative real part.

Consider the real roots of (3.3.10) first. Note that  $\frac{1}{D} > \frac{1}{\alpha}$ . (3.3.10) has no solution for  $\lambda \leq -\Delta$ , otherwise the left hand side would be less than zero, but the right hand side would be greater than zero. Assume  $\lambda > -\Delta$ . The left hand side of (3.3.10) is a monotone increasing function in both  $\lambda$  and  $\tau$ , and takes value 0 at  $\lambda = -\Delta$  and goes to positive infinity as  $\lambda \to +\infty$  or  $\tau \to +\infty$ . By Lemma 3.3, when  $\tau = \tau_c$ , then  $\lambda = 0$  is a solution of (3.3.10). Thus for  $\tau > \tau_c$ , any real root  $\lambda$  of (3.3.10) must satisfy  $-\Delta < \lambda < 0$ .

For any  $\tau = \tilde{\tau} < \tau_c$ , we have  $(\lambda + \Delta)e^{(\lambda + \Delta)\tau}|_{\tau = \tilde{\tau}, \lambda = 0} < k\left(\frac{1}{D} - \frac{1}{\alpha}\right)$  and

 $\lim_{\lambda\to+\infty} (\lambda + \Delta) e^{(\lambda + \Delta)\tilde{\tau}} = +\infty$ . Therefore there exists at least one  $\lambda = \tilde{\lambda} > 0$  such that  $(\tilde{\tau}, \tilde{\lambda})$  is a solution of (3.3.10). Equilibrium  $E_2$  is unstable if  $\tau < \tau_c$ .

In what follows, we prove that if  $\tau > \tau_c$  all complex eigenvalues of (3.3.10) have negative real parts. Suppose that  $\lambda + \Delta = \gamma + i\beta$  ( $\beta > 0$ ) is a solution of (3.3.10). Using the Euler formula, we have

$$\gamma\cos(\beta\tau) - \beta\sin(\beta\tau) + i(\gamma\sin(\beta\tau) + \beta\cos(\beta\tau)) = k\left(\frac{1}{D} - \frac{1}{\alpha}\right)e^{-\gamma\tau}.$$

Equating the real part and imaginary part of the equation, we have

$$\gamma \cos(\beta \tau) - \beta \sin(\beta \tau) = k \left(\frac{1}{D} - \frac{1}{\alpha}\right) e^{-\gamma \tau}$$
$$\gamma \sin(\beta \tau) + \beta \cos(\beta \tau) = 0.$$

Squaring both equations, adding, and taking the square root on both sides gives

$$\sqrt{\gamma^2 + \beta^2} \ e^{\gamma\tau} = k \left(\frac{1}{D} - \frac{1}{\alpha}\right). \tag{3.3.11}$$

The left hand side of (3.3.11) is monotonically increasing in  $\gamma$ ,  $\beta$ , and  $\tau$  provided that  $\gamma > 0$ . Since (3.3.11) has solution  $\gamma = \Delta$ ,  $\beta = 0$  at  $\tau = \tau_c$ , any roots of (3.3.11) must satisfy  $\gamma < \Delta$  since  $\tau > \tau_c$ . Hence  $\operatorname{Re}\{\lambda\} = \gamma - \Delta < 0$ . Therefore (3.3.10) has no complex eigenvalue with nonnegative real part and so  $E_2$  is locally asymptotically stable for  $\tau > \tau_c$ .

Assume that D = 1. Now we prove  $E_2$  is globally asymptotically stable when  $\tau > \frac{1}{\Delta} \ln \left(\frac{k}{\Delta}\right)$ , or equivalently  $ke^{-\Delta\tau} < \Delta$ . In this case, choose  $\epsilon_0 > 0$  small enough such that  $ke^{-\Delta\tau}(1+\epsilon_0) < \Delta$ . By Theorem 3.1, for such  $\epsilon_0$ , there exists a T > 0 so that  $0 < x(t) < 1 + \epsilon_0$  for t > T. Hence, for  $t > T + \tau$ ,  $ke^{-\Delta\tau}x(t-\tau) < \Delta$ . In Lemma A.1, choose  $\rho(t) = \tau$ ,  $a(t) = \Delta$ ,  $b(t) = ke^{-\Delta\tau}x(t-\tau)$ , and  $\alpha = \Delta/2$ . The third equation of (3.2.4) is in the form of (A.0.1). Also equation (A.0.2) is satisfied,

 $(\alpha + k)\epsilon > 0$ . For such  $\epsilon$ , there exists a sufficiently large t so that  $s(t) > 1 - \epsilon$  and  $0 < y(t) < \epsilon$ . Recalling that x(t) > 0, by (3.2.4)

$$\dot{x}(t) > x(t)(-D + \alpha(1 - \epsilon) - k\epsilon) = x(t)(\alpha - D - \alpha\epsilon - k\epsilon) > 0,$$

for all sufficiently large t. Therefore it is impossible for x(t) to approach 0 from above. A contradiction. Therefore, we must have  $(\bar{s}, \bar{x}) = (\frac{1}{\alpha}, \frac{\alpha-1}{\alpha})$ .

Now suppose that the limits do not exist. In particular if x(t) does not converge, then let  $\bar{x} = \limsup_{t\to\infty} x(t)$  and  $\underline{x} = \liminf_{t\to\infty} x(t)$ . By Lemma (A.6), there exists  $\{t_m\} \uparrow \infty$  and  $\{s_m\} \uparrow \infty$  such that

$$\lim_{m \to \infty} x(t_m) = \bar{x} \quad \text{and} \quad \lim_{m \to \infty} \dot{x}(t_m) = 0,$$

and

$$\lim_{m \to \infty} x(s_m) = \underline{x} \quad \text{and} \quad \lim_{m \to \infty} \dot{x}(s_m) = 0.$$

From (3.2.4),

$$x(t_m)(-D + \alpha s(t_m) + ky(t_m)) = 0.$$

Noting that  $x(t_m) > 0$ , we have  $s(t_m) = \frac{1-ky(t_m)}{\alpha}$ . Since  $\lim_{t\to\infty} y(t) = 0$ ,  $\lim_{t\to\infty} s(t_m) = \frac{1}{\alpha}$ .  $\frac{1}{\alpha}$ . By (3.3.12),  $\lim_{t\to\infty} x(t_m) = \lim_{t\to\infty} (x(t_m) + s(t_m)) - s(t_m) = 1 - \frac{1}{\alpha} = \frac{\alpha-1}{\alpha}$ . Therefore  $\bar{x} = \frac{\alpha-1}{\alpha}$ . Similarly we can show that  $\underline{x} = \frac{\alpha-1}{\alpha}$ . This implies that  $\lim_{t\to\infty} x(t) = \frac{\alpha-1}{\alpha}$ , a contradiction.

Since s(t) + x(t) converges and x(t) converges, then s(t) must also converge. Hence  $\lim_{t\to\infty} s(t) = \frac{1}{\alpha}$  and  $\lim_{t\to\infty} x(t) = \frac{\alpha-1}{\alpha}$ . It follows that  $E_2$  is globally asymptotically stable.

## **3.4** Hopf Bifurcations at $E_+$ assuming $D = \Delta = 1$

Now consider the stability of  $E_+$ . The characteristic equation at  $E_+$  is

$$\begin{split} P(\lambda)|_{E_{+}} = &(-\Delta - \lambda) \left( (1 + \alpha x_{+}(\tau) + \lambda) (D - \alpha s_{+}(\tau) + k y_{+}(\tau) + \lambda) + \alpha^{2} s_{+}(\tau) x_{+}(\tau) \right) \\ &+ e^{-(\Delta + \lambda)\tau} k x_{+}(\tau) \left( (\lambda + 1) (\lambda + D) + \alpha x_{+}(\tau) (\lambda + D) - \alpha s_{+}(\tau) (\lambda + 1) \right) \\ = &(-\Delta - \lambda) \left( (1 + \alpha x_{+}(\tau) + \lambda) \lambda + \alpha^{2} s_{+}(\tau) x_{+}(\tau) \right) \\ &+ e^{-(\Delta + \lambda)\tau} k x_{+}(\tau) \left( (\lambda + 1) (\lambda + D) + \alpha x_{+}(\tau) (\lambda + D) - \alpha s_{+}(\tau) (\lambda + 1) \right) \\ = &(-\Delta - \lambda) \left( \left( \frac{1}{s_{+}(\tau)} + \lambda \right) \lambda + \alpha (1 - s_{+}(\tau)) \right) \\ &+ e^{-\lambda \tau} \Delta \left( (\lambda + 1) (\lambda + D) + \frac{1 - s_{+}(\tau)}{s_{+}(\tau)} (\lambda + D) - \alpha s_{+}(\tau) (\lambda + 1) \right) \\ = &(-\Delta - \lambda) \left( \lambda^{2} + \frac{\lambda}{s_{+}(\tau)} + \alpha (1 - s_{+}(\tau)) \right) \\ &+ \Delta e^{-\lambda \tau} \left( \left( \lambda + \frac{1}{s_{+}(\tau)} \right) (\lambda + D) - \alpha s_{+}(\tau) (\lambda + 1) \right) = 0. \end{split}$$

By assumption  $\Delta = D = 1$ ,

$$P(\lambda)|_{E_{+}} = -(\lambda+1)\left(\lambda^{2} + \frac{\lambda}{s_{+}(\tau)} + \alpha(1-s_{+}(\tau)) + e^{-\lambda\tau}\left(-\lambda + \alpha s_{+}(\tau) - \frac{1}{s_{+}(\tau)}\right)\right)$$
$$= -(\lambda+1)\left(\lambda^{2} + p(\tau)\lambda + \beta(\tau) + e^{-\lambda\tau}(q\lambda + c(\tau))\right) = 0,$$
(3.4.13)

where

$$p(\tau) = \frac{1}{s_{+}(\tau)}, \quad \beta(\tau) = \alpha(1 - s_{+}(\tau)), \quad q = -1, \quad c(\tau) = \alpha s_{+}(\tau) - \frac{1}{s_{+}(\tau)}. \quad (3.4.14)$$

The characteristic equation at  $E_+$  has one eigenvalue -1 and the others are given by solutions of the equation

$$\lambda^2 + p(\tau)\lambda + \beta(\tau) + e^{-\lambda\tau}(q\lambda + c(\tau)) = 0.$$
(3.4.15)

**Lemma 3.5.** Assuming k > 0,  $\alpha > 0$ , and  $k\left(1 - \frac{1}{\alpha}\right) \ge 1$  so that  $\tau_c = \ln\left(k\left(1 - \frac{1}{\alpha}\right)\right) \ge 0$ , then  $E_+$  has no zero eigenvalue for  $\tau \in (0, \tau_c)$ .

**Proof.** Assume that  $\tau \in (0, \tau_c)$ . By the method of contradiction, suppose there exists a zero root of (3.4.15). Therefore

$$\beta(\tau) + c(\tau) = \alpha - \frac{1}{s_+(\tau)} = 0.$$

But for any  $\tau < \tau_c$ ,

$$\alpha - \frac{1}{s_+(\tau)} = \alpha - 1 - \frac{\alpha}{k}e^{\tau} > \alpha - 1 - \alpha\left(1 - \frac{1}{\alpha}\right) = 0.$$

A contradiction.

**Lemma 3.6.** Assume k > 0,  $\alpha > 0$ ,  $k(1 - \frac{1}{\alpha}) > 1$ . Equilibrium  $E_+$  is asymptotically stable when  $\tau = 0$ .

**Proof.** For  $\tau = 0$ , (3.4.15) reduces to

$$\lambda^{2} + p(0)\lambda + \beta(0) + (q\lambda + c(0)) = \lambda^{2} + \left(\frac{1}{s_{+}(0)} - 1\right)\lambda + \alpha - \frac{1}{s_{+}(0)}$$

Both coefficients are positive, since

$$\frac{1}{s_{+}(0)} - 1 = \frac{\alpha}{k} > 0$$

and

$$\alpha - \frac{1}{s_+(0)} = \alpha - 1 - \frac{\alpha}{k} = \alpha \left(1 - \frac{1}{\alpha} - \frac{1}{k}\right) > 0,$$

since  $k(1-\frac{1}{\alpha}) > 1$  implies  $1-\frac{1}{\alpha} > \frac{1}{k}$ . Therefore, all the roots of the characteristic equation have negative real parts.

**Lemma 3.7.** As  $\tau$  is increased from 0, a root of (3.4.15) with positive real part can only appear if a root with negative real parts crosses the imaginary axis.

**Proof.** The proof is similar to the proof of Lemma 2.5 and the details are omitted.  $\hfill \Box$ 

For  $\tau \neq 0$ , assuming  $\lambda = i\omega \ (\omega > 0)$  is a root of  $P(\lambda)|_{E_+} = 0$ ,

$$-\omega^2 + ip(\tau)\omega + \beta(\tau) + e^{-i\omega\tau}(iq\omega + c(\tau)) = 0.$$
(3.4.16)

As in Chapter 2, substituting  $e^{i\theta} = \cos \theta + i \sin \theta$  into (3.4.16) gives

$$-\omega^2 + \beta(\tau) + q\omega\sin(\omega\tau) + c(\tau)\cos(\omega\tau) + i\left(p(\tau)\omega + q\omega\cos(\omega\tau) - c(\tau)\sin(\omega\tau)\right) = 0.$$

Separating the real and imaginary parts, we obtain

$$c(\tau)\cos(\omega\tau) + q\omega\sin(\omega\tau) = \omega^2 - \beta(\tau),$$
  
$$c(\tau)\sin(\omega\tau) - q\omega\cos(\omega\tau) = p(\tau)\omega.$$

Solving for  $\cos(\omega \tau)$  and  $\sin(\omega \tau)$  gives

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$$\begin{cases} \sin(\omega\tau) = \frac{c(\tau)(p(\tau)\omega) + q\omega(\omega^2 - \beta(\tau))}{c(\tau)^2 + q^2\omega^2}, \\ \cos(\omega\tau) = \frac{c(\tau)(\omega^2 - \beta(\tau)) + q\omega(-p(\tau)\omega)}{c(\tau)^2 + q^2\omega^2}. \end{cases}$$
(3.4.17)

Noting  $\sin^2(\omega \tau) + \cos^2(\omega \tau) = 1$ , squaring both sides of equations (3.4.17), adding, and rearranging gives

$$\omega^4 + (p(\tau)^2 - q^2 - 2\beta(\tau))\omega^2 + \beta(\tau)^2 - c(\tau)^2 = 0.$$
 (3.4.18)

Solving for  $\omega$ ,

$$\omega_{1}(\tau) = \frac{1}{\sqrt{2}} \left( q^{2} - p^{2}(\tau) + 2\beta(\tau) + \sqrt{(q^{2} - p^{2}(\tau) + 2\beta(\tau))^{2} - 4(\beta^{2}(\tau) - c^{2}(\tau))} \right)^{\frac{1}{2}}$$

$$= \frac{1}{s_{+}(\tau)\sqrt{2}} \left( (1 - s_{+}(\tau))(2\alpha s_{+}^{2}(\tau) - s_{+}(\tau) - 1) + \sqrt{(s_{+}^{2}(\tau) - 1)^{2} + 4\alpha s_{+}^{2}(\tau)(s_{+}^{2}(\tau) - 1)(1 - s_{+}(\tau)) + 4s_{+}^{2}(\tau)(\alpha s_{+}^{2}(\tau) - 1)^{2}} \right)^{\frac{1}{2}}$$

$$(3.4.19)$$

and

$$\omega_{2}(\tau) = \frac{1}{\sqrt{2}} \left( q^{2} - p^{2}(\tau) + 2\beta(\tau) - \sqrt{(q^{2} - p^{2}(\tau) + 2\beta(\tau))^{2} - 4(\beta^{2}(\tau) - c^{2}(\tau))} \right)^{\frac{1}{2}}$$
  
$$= \frac{1}{s_{+}(\tau)\sqrt{2}} \left( (1 - s_{+}(\tau))(2\alpha s_{+}^{2}(\tau) - s_{+}(\tau) - 1) - \sqrt{(s_{+}^{2}(\tau) - 1)^{2} + 4\alpha s_{+}^{2}(\tau)(s_{+}^{2}(\tau) - 1)(1 - s_{+}(\tau)) + 4s_{+}^{2}(\tau)(\alpha s_{+}^{2}(\tau) - 1)^{2}} \right)^{\frac{1}{2}}$$
  
$$= \sqrt{(s_{+}^{2}(\tau) - 1)^{2} + 4\alpha s_{+}^{2}(\tau)(s_{+}^{2}(\tau) - 1)(1 - s_{+}(\tau)) + 4s_{+}^{2}(\tau)(\alpha s_{+}^{2}(\tau) - 1)^{2}} \right)^{\frac{1}{2}}$$
(3.4.20)

Define conditions  $(H_1)$  and  $(H_2)$  as follows

$$(H_1) \begin{cases} q^2 - p^2(\tau) + 2\beta(\tau) > 0, & \beta^2(\tau) - c^2(\tau) > 0, \\ (q^2 - p^2(\tau) + 2\beta(\tau))^2 - 4 \left(\beta^2(\tau) - c^2(\tau)\right) \ge 0. \\ (H_2) & \beta^2(\tau) - c^2(\tau) < 0, \text{ or } \beta^2(\tau) - c^2(\tau) = 0 \& q^2 - p^2(\tau) + 2\beta(\tau) > 0. \end{cases}$$

**Lemma 3.8.** If  $(H_1)$  holds for all  $\tau$  in some interval I, then (3.4.18) has two positive roots  $\omega_1(\tau) \ge \omega_2(\tau)$  for all  $\tau \in I$  with  $\omega_1(\tau) > \omega_2(\tau)$  when all the inequalities in  $(H_1)$  are strict. If  $(H_2)$  holds for all  $\tau$  in some interval I, then (3.4.18) has only one positive root,  $\omega_1(\tau)$  for all  $\tau \in I$ . If no interval exists where either  $(H_1)$  or  $(H_2)$ holds, then there are no positive real roots of (3.4.18).

Define the interval

$$J = \left[ \ln\left(\frac{k}{\alpha} \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)\right), \quad \ln\left(\frac{k(\sqrt[4]{\alpha} - 1)}{\alpha}\right) \right].$$

When the end points of J are real and  $J \neq \emptyset$ , define

$$I_1 = [0, \tau_c) \bigcap J.$$
 (3.4.21)

We prove that  $(H_1)$  holds for any  $\tau \in I_1$ . From  $D = \Delta = 1$ ,

$$\tau_c = \frac{1}{\Delta} \ln\left(\frac{k}{\Delta}\left(\frac{1}{D} - \frac{1}{\alpha}\right)\right) = \ln\left(\frac{k\left(\alpha - 1\right)}{\alpha}\right).$$

If  $\alpha > 1$ , then  $\alpha > \sqrt[4]{\alpha}$ . It follows that

$$\tau_c > \ln\left(\frac{k(\sqrt[4]{\alpha}-1)}{\alpha}\right).$$

Therefore

$$I_{1} = \left[ \max\left\{ 0, \ln\left(\frac{k}{\alpha} \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)\right) \right\}, \quad \ln\left(\frac{k(\sqrt[4]{\alpha} - 1)}{\alpha}\right) \right].$$
(3.4.22)

**Theorem 3.9.** Assume  $\alpha > \frac{7+3\sqrt{5}}{2}$  and  $k > \frac{\alpha}{\sqrt[4]{\alpha-1}}$ . Then  $I_1$  is not empty, and for any  $\tau \in I_1$ , but  $\tau \neq \ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4}+\sqrt{\frac{1}{16}+\frac{1}{2\alpha}}}-1\right)\right)$ , condition  $(H_1)$  holds and  $\omega_1(\tau) > \omega_2(\tau) > 0$ . If  $\tau = \ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4}+\sqrt{\frac{1}{16}+\frac{1}{2\alpha}}}-1\right)\right) \in I_1$ , then  $\omega_1(\tau) > \omega_2(\tau) = 0$ .

**Proof.** For any  $\alpha > \frac{7+3\sqrt{5}}{2}$ , we have  $1 - \frac{1}{\sqrt[4]{\alpha}} > 0$  and therefore

$$\frac{1}{\sqrt[4]{\alpha}} + \frac{1}{2} - \frac{\sqrt{5}}{2} < \frac{1}{\sqrt[4]{\frac{7+3\sqrt{5}}{2}}} + \frac{1}{2} - \frac{\sqrt{5}}{2} = 0.$$

Hence

$$\left(\frac{1}{\sqrt[4]{\alpha}} - \frac{1}{4}\right)^2 - \left(\sqrt{\frac{1}{16} + \frac{1}{2\alpha}}\right)^2 = \frac{1}{\sqrt{\alpha}} - \frac{1}{2\sqrt[4]{\alpha}} - \frac{1}{2\alpha}$$

$$= \frac{-1}{2\sqrt[4]{\alpha}} \left(\left(\frac{1}{\sqrt[4]{\alpha}}\right)^3 + 1 - \frac{2}{\sqrt[4]{\alpha}}\right)$$

$$= \frac{1}{2\sqrt[4]{\alpha}} \left(1 - \frac{1}{\sqrt[4]{\alpha}}\right) \left(\left(\frac{1}{\sqrt[4]{\alpha}}\right)^2 + \frac{1}{\sqrt[4]{\alpha}} - 1\right)$$

$$= \frac{1}{2\sqrt[4]{\alpha}} \left(1 - \frac{1}{\sqrt[4]{\alpha}}\right) \left(\left(\frac{1}{\sqrt[4]{\alpha}} + \frac{1}{2}\right)^2 - \frac{5}{4}\right)$$

$$= \frac{1}{2\sqrt[4]{\alpha}} \left(1 - \frac{1}{\sqrt[4]{\alpha}}\right) \left(\frac{1}{\sqrt[4]{\alpha}} + \frac{1}{2} - \frac{\sqrt{5}}{2}\right) \left(\frac{1}{\sqrt[4]{\alpha}} + \frac{1}{2} + \frac{\sqrt{5}}{2}\right) < 0.$$

$$= \frac{1}{2\sqrt[4]{\alpha}} \left(1 - \frac{1}{\sqrt[4]{\alpha}}\right) \left(\frac{1}{\sqrt[4]{\alpha}} + \frac{1}{2} - \frac{\sqrt{5}}{2}\right) \left(\frac{1}{\sqrt[4]{\alpha}} + \frac{1}{2} + \frac{\sqrt{5}}{2}\right) < 0.$$

Therefore  $\frac{1}{\sqrt[4]{\alpha}} - \frac{1}{4} < \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}$ . Since  $\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} < \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{7+3\sqrt{5}}} < 1$ . It follows that

$$\frac{1}{\sqrt[4]{\alpha}} < \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} < 1.$$
(3.4.23)

Hence

$$\ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4}+\sqrt{\frac{1}{16}+\frac{1}{2\alpha}}}-1\right)\right) < \ln\left(\frac{k(\sqrt[4]{\alpha}-1)}{\alpha}\right).$$

From  $k > \frac{\alpha}{(\sqrt[4]{\alpha}-1)}$ , we have  $\ln\left(\frac{k(\sqrt[4]{\alpha}-1)}{\alpha}\right) > 0$ . Therefore

$$\max\left\{0, \ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)\right)\right\} < \ln\left(\frac{k(\sqrt[4]{\alpha} - 1)}{\alpha}\right)$$

and so  $I_1$  is not empty. Noting  $s_+(\tau) = \frac{1}{1+\frac{\alpha\Delta}{k}e^{\Delta\tau}}$  and  $\Delta = 1$ , for any  $\tau \in I_1$ , but  $\tau \neq \ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4}+\sqrt{\frac{1}{16}+\frac{1}{2\alpha}}}-1\right)\right)$ , we have  $s_+(\tau) \in \left[\frac{1}{\sqrt[4]{\alpha}}, \frac{1}{4}+\sqrt{\frac{1}{16}+\frac{1}{2\alpha}}\right)$ .

In what follows, we intend to show for any such  $\tau$ , condition  $(H_1)$  holds. From

(3.4.14),

$$q^{2} - p^{2}(\tau) + 2\beta(\tau) = (-1)^{2} - \frac{1}{s_{+}^{2}(\tau)} + 2\alpha(1 - s_{+}(\tau))$$
  
$$= \frac{(1 - s_{+}(\tau))2\alpha}{s_{+}^{2}(\tau)} \left(s_{+}(\tau)^{2} - \frac{s_{+}(\tau)}{2\alpha} - \frac{1}{2\alpha}\right)$$
  
$$= \frac{(1 - s_{+}(\tau))2\alpha}{s_{+}^{2}(\tau)} \left(\left(s_{+}(\tau) - \frac{1}{4\alpha}\right)^{2} - \frac{1}{16\alpha^{2}} - \frac{1}{2\alpha}\right).$$

Since  $s_{+}(\tau) < 1$ , to show that the first inequality in  $(H_{1})$  holds, it suffices to show that factor on the right hand side of above the expression is positive. Since  $\alpha > \frac{7+3\sqrt{5}}{2}$ ,  $\frac{1}{\sqrt{\alpha}} - \frac{1}{4\alpha} = \frac{1}{\sqrt{\alpha}} \left(1 - \frac{1}{4\sqrt{\alpha}}\right) > 0$  and  $\left(\sqrt{\frac{1}{16\alpha^{2}} + \frac{1}{2\alpha}}\right)^{2} - \left(\frac{1}{\sqrt{\alpha}} - \frac{1}{4\alpha}\right)^{2} = \frac{1}{16\alpha^{2}} + \frac{1}{2\alpha} - \frac{1}{\alpha} + \frac{1}{2\alpha\sqrt{\alpha}} - \frac{1}{16\alpha^{2}}$  $= \frac{1}{2\alpha} \left(\frac{1}{\sqrt{\alpha}} - 1\right) < 0.$ 

Since  $\frac{1}{\sqrt{\alpha}} < \frac{1}{\sqrt[4]{\alpha}}$  for  $\alpha > \frac{7+3\sqrt{5}}{2}$ ,

$$\frac{1}{4\alpha} + \sqrt{\frac{1}{16\alpha^2} + \frac{1}{2\alpha}} < \frac{1}{\sqrt{\alpha}} < \frac{1}{\sqrt{\alpha}}.$$

For any  $s_+(\tau) > \frac{1}{\sqrt[4]{\alpha}}$ ,

$$s_{+}(\tau) - \frac{1}{4\alpha} \ge \frac{1}{\sqrt[4]{\alpha}} - \frac{1}{4\alpha} > \sqrt{\frac{1}{16\alpha^{2}} + \frac{1}{2\alpha}}.$$

Hence

$$\left(s_+(\tau) - \frac{1}{4\alpha}\right)^2 \ge \frac{1}{16\alpha^2} + \frac{1}{2\alpha}.$$

Next consider the second inequality in  $(H_1)$ . For  $\alpha > \frac{7+3\sqrt{5}}{2}$ , since  $\frac{1}{\sqrt[4]{\alpha}} > \frac{1}{\alpha}$ ,  $s_+(\tau) \ge \frac{1}{\sqrt[4]{\alpha}} > \frac{1}{\alpha}$ . Therefore  $\alpha s_+(\tau) > 1$ . For  $s_+(\tau) \in \left[\frac{1}{\sqrt[4]{\alpha}}, \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}\right)$ .

$$\begin{split} \beta^{2}(\tau) - c^{2}(\tau) &= (\beta(\tau) - c(\tau))(\beta(\tau) + c(\tau)) \\ &= \left(\alpha - 2\alpha s_{+}(\tau) + \frac{1}{s_{+}(\tau)}\right) \left(\alpha - \frac{1}{s_{+}(\tau)}\right) \\ &= -\frac{2\alpha}{s_{+}^{2}(\tau)} \left(s_{+}^{2}(\tau) - \frac{s_{+}(\tau)}{2} - \frac{1}{2\alpha}\right) (\alpha s_{+}(\tau) - 1) \\ &= -\frac{2\alpha}{s_{+}^{2}(\tau)} \left(\left(s_{+}(\tau) - \frac{1}{4}\right)^{2} - \frac{1}{16} - \frac{1}{2\alpha}\right) (\alpha s_{+}(\tau) - 1) > 0. \end{split}$$

Finally,

$$\begin{split} \left(q^2 - p^2(\tau) + 2\beta(\tau)\right)^2 &- 4\left(\beta^2(\tau) - c^2(\tau)\right) = \left(q^2 - p^2(\tau)\right)\left(q^2 - p^2(\tau) + 4\beta(\tau)\right) + 4c^2(\tau) \\ &= \left(1 - \frac{1}{s_+^2(\tau)}\right)\left(1 - \frac{1}{s_+^2(\tau)} + 4\alpha(1 - s_+(\tau))\right) + 4\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2 \\ &= \left(1 - \frac{1}{s_+^2(\tau)}\right)^2 + 4\alpha\left(1 - \frac{1}{s_+^2(\tau)}\right)(1 - s_+(\tau)) + 4s_+(\tau)^2\alpha^2 - 8\alpha + \frac{4}{s_+^2(\tau)} \\ &= 4s_+(\tau)^2\alpha^2 + 4\alpha\left(\left(1 - \frac{1}{s_+^2(\tau)}\right)(1 - s_+(\tau))\right) - 8\alpha + \left(1 - \frac{1}{s_+^2(\tau)}\right)^2 + \frac{4}{s_+^2(\tau)} \\ &= 4s_+(\tau)^2\alpha^2 + 4\alpha\left(\left(1 - \frac{1}{s_+^2(\tau)}\right)(1 - s_+(\tau)) - 2\right) + \left(1 + \frac{1}{s_+^2(\tau)}\right)^2 \\ &= (\alpha - \alpha_1)(\alpha - \alpha_2), \end{split}$$

where

$$\alpha_{1} = \frac{2 - \left(1 - \frac{1}{s_{+}^{2}(\tau)}\right) \left(1 - s_{+}(\tau)\right) + \sqrt{\left(\frac{1}{s_{+}^{2}(\tau)} + 2s_{+}(\tau) + 1\right) \left(\frac{1}{s_{+}(\tau)} - 1\right)^{2}}}{2s_{+}^{2}(\tau)},$$
$$\alpha_{2} = \frac{2 - \left(1 - \frac{1}{s_{+}^{2}(\tau)}\right) \left(1 - s_{+}(\tau)\right) - \sqrt{\left(\frac{1}{s_{+}^{2}(\tau)} + 2s_{+}(\tau) + 1\right) \left(\frac{1}{s_{+}(\tau)} - 1\right)^{2}}}{2s_{+}^{2}(\tau)}.$$

Since  $s_+(\tau) < 1$ ,

$$2 - \left(1 - \frac{1}{s_+^2(\tau)}\right) \left(1 - s_+(\tau)\right) = s_+(\tau) + 1 + \frac{1 - s_+(\tau)}{s_+^2(\tau)} > 0,$$

and

$$\begin{split} &\left(2 - \left(1 - \frac{1}{s_{+}^{2}(\tau)}\right)(1 - s_{+}(\tau))\right)^{2} \\ &> \left(2 - \left(1 - \frac{1}{s_{+}^{2}(\tau)}\right)(1 - s_{+}(\tau))\right)^{2} - s_{+}^{2}(\tau)\left(1 + \frac{1}{s_{+}^{2}(\tau)}\right)^{2} \\ &= \left(\frac{1}{s_{+}^{2}(\tau)} + 2s_{+}(\tau) + 1\right)\left(\frac{1}{s_{+}(\tau)} - 1\right)^{2} \\ &> 0. \end{split}$$

It follows that  $0 < \alpha_2 < \alpha_1$ . Again noting that  $s_+(\tau) < 1$ ,

$$\begin{split} \alpha_1 &< \frac{2 - \left(1 - \frac{1}{s_+^2(\tau)}\right) \left(1 - s_+(\tau)\right) + \sqrt{\left(\frac{1}{s_+^2(\tau)} + \frac{2}{s_+(\tau)} + 1\right) \left(\frac{1}{s_+(\tau)} - 1\right)^2}}{2s_+^2(\tau)} \\ &= \frac{2 - \left(1 - \frac{1}{s_+^2(\tau)}\right) \left(1 - s_+(\tau)\right) + \left(\frac{1}{s_+(\tau)} + 1\right) \left(\frac{1}{s_+(\tau)} - 1\right)}{2s_+^2(\tau)} \\ &= \frac{2 - \left(1 - s_+(\tau) - \frac{1}{s_+^2(\tau)} + \frac{1}{s_+(\tau)}\right) + \frac{1}{s_+^2(\tau)} - 1}{2s_+^2(\tau)} \\ &= \frac{s_+(\tau) + \frac{2}{s_+^2(\tau)} - \frac{1}{s_+(\tau)}}{2s_+^2(\tau)} = \frac{1}{2} \left(\frac{2}{s_+^4(\tau)} - \left(\frac{1}{s_+^3(\tau)} - \frac{1}{s_+(\tau)}\right)\right) \\ &< \frac{1}{2} \frac{2}{s_+^4(\tau)} = \frac{1}{s_+^4(\tau)}. \end{split}$$

Hence, for any  $s_+(\tau) > \frac{1}{\sqrt[4]{\alpha}}$ , we have  $\alpha > \frac{1}{s_+^4(\tau)} > \alpha_1 > \alpha_2$ . This leads to

$$(q^{2} - p^{2}(\tau) + 2\beta(\tau))^{2} - 4(\beta^{2}(\tau) - c^{2}(\tau)) = (\alpha - \alpha_{1})(\alpha - \alpha_{2}) > 0.$$

Hence  $(H_1)$  holds for any  $\tau \in I_1$ . By Lemma 3.8, both  $\omega_1(\tau) > 0$  and  $\omega_2(\tau) > 0$ .

If  $\tau = \ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4}+\sqrt{\frac{1}{16}+\frac{1}{2\alpha}}}-1\right)\right) \in I_1$ , we have  $s_+(\tau) = \frac{1}{4} + \sqrt{\frac{1}{16}+\frac{1}{2\alpha}}$ . Noting (3.4.23), we obtain

$$\begin{aligned} q^2 - p^2(\tau) + 2\beta(\tau) &> 0, \qquad \beta^2(\tau) - c^2(\tau) = 0, \\ \left(q^2 - p^2(\tau) + 2\beta(\tau)\right)^2 - 4\left(\beta^2(\tau) - c^2(\tau)\right) &> 0. \end{aligned}$$

By (3.4.19) and (3.4.20), we know  $\omega_1(\tau) > 0$  and  $\omega_2(\tau) = 0$ .

Now we define interval  $I_2$  and prove that  $(H_2)$  holds on  $I_2$ .

$$I_2 := [0, \tau_c) \bigcap \left( -\infty, \ln \left( \frac{k}{\alpha} \left( \frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1 \right) \right) \right].$$

In the following theorem, we consider the case that parameters are chosen so that

$$I_2 = \left[0, \ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)\right)\right].$$
 (3.4.24)

**Theorem 3.10.** Assume  $\alpha > 1$  and  $k > \alpha \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)^{-1}$ . Interval  $I_2$  given by (3.4.24) is not empty. For any  $\tau \in I_2$ ,  $(H_2)$  holds and hence  $\omega_1(\tau) > 0$ .

**Proof.** Assume  $\alpha > 1$ . Letting

$$G(\alpha) = \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} - \frac{1}{\alpha},$$

then

$$\frac{\mathrm{d}G(\alpha)}{\mathrm{d}\alpha} = -\frac{1}{4\alpha^2 \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} + \frac{1}{\alpha^2} = \frac{1}{\alpha^2} \left(\frac{-1}{\sqrt{1 + \frac{8}{\alpha}}} + 1\right) > 0$$

 $G(\alpha)$  is an increasing function of  $\alpha$  and G(1) = 0.  $G(\alpha) > G(1)$  implies that  $\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} - \frac{1}{\alpha} > 0$ . Therefore

$$1 > \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} > \frac{1}{\alpha}.$$
(3.4.25)

This gives

$$\alpha - 1 > \frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1 > 0.$$

By assumption  $k > \alpha \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)^{-1}$ , we obtain $\frac{k(\alpha - 1)}{\alpha} > \frac{k}{\alpha} \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right) > 1.$ 

Noting that  $D = \Delta = 1$  and  $\tau_c$  is defined in (3.3.7),

$$\tau_c = \ln\left(\frac{k\left(\alpha - 1\right)}{\alpha}\right) > \ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)\right) > 0.$$

Therefore  $I_2$  is given by (3.4.24) is not empty. For any  $\tau \in I_2$ , noting  $s_+(\tau) = \frac{1}{1+\frac{\alpha\Delta}{k}e^{\Delta\tau}}$ and  $\Delta = 1$ , we have  $s_+(\tau) \in [\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}, \frac{1}{1+\alpha/k}) \subset [\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}, 1).$ 

In what follows, we intend to show for any  $\tau \in I_2$ , or equivalently  $s_+(\tau) \in \left[\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}, 1\right)$ ,  $(H_2)$  holds. For any  $s_+(\tau) \in \left[\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}, 1\right)$ , by (3.4.25), it follows that  $s_+(\tau) > \frac{1}{\alpha}$  and so  $\alpha s_+(\tau) > 1$ . Hence

$$\beta^{2}(\tau) - c^{2}(\tau) = -\frac{2\alpha}{s_{+}^{2}(\tau)} \left( \left( s_{+}(\tau) - \frac{1}{4} \right)^{2} - \frac{1}{16} - \frac{1}{2\alpha} \right) (\alpha s_{+}(\tau) - 1) \leqslant 0.$$

For any  $s_{+}(\tau) \in \left[\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}, 1\right)$ , we have  $s_{+}(\tau) > \frac{1}{4\alpha} + \sqrt{\frac{1}{16\alpha^{2}} + \frac{1}{2\alpha}}$ , since  $\frac{1}{4} > \frac{1}{4\alpha}$ and  $\frac{1}{16} > \frac{1}{16\alpha^{2}}$  imply that

$$\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} > \frac{1}{4\alpha} + \sqrt{\frac{1}{16\alpha^2} + \frac{1}{2\alpha}}.$$

Therefore

$$q^{2} - p^{2}(\tau) + 2\beta(\tau) = \frac{(1 - s_{+}(\tau))2\alpha}{s_{+}^{2}(\tau)} \left( \left(s_{+}(\tau) - \frac{1}{4\alpha}\right)^{2} - \frac{1}{16\alpha^{2}} - \frac{1}{2\alpha} \right) > 0.$$

Condition ( $H_2$ ) holds. By Lemma 3.8,  $\omega_1(\tau) > 0$ .

Next, to determine whether (3.4.13) has a pair of pure imaginary eigenvalues, we consider

$$\begin{split} c(\tau)^2 + q^2 \omega^2 &= \left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2 + (-1)^2 \omega^2 = \left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2 + \omega^2, \\ c(\tau)(p(\tau)\omega) + q\omega(\omega^2 - \beta(\tau)) = \omega(c(\tau)p(\tau) + q(\omega^2 - \beta(\tau))) \\ &= \omega \left(\alpha - \frac{1}{s_+^2(\tau)} - \omega^2 + \alpha(1 - s_+(\tau))\right), \end{split}$$

and

$$c(\tau)(\omega^2 - \beta(\tau)) + q\omega(-p(\tau)\omega)$$
  
=  $\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right) \left(\omega^2 - \alpha(1 - s_+(\tau))\right) + (-1)\omega\left(\frac{-\omega}{s_+(\tau)}\right)$   
=  $\alpha \left(s_+(\tau)\omega^2 - (1 - s_+(\tau))\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)\right).$ 

We obtain

$$\begin{cases} \sin(\omega\tau) = -\omega \frac{\omega^2 - \left(\alpha - \frac{1}{s_+^2(\tau)}\right) - \alpha(1 - s_+(\tau))}{\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2 + \omega^2}, \\ \cos(\omega\tau) = \alpha s_+(\tau) \frac{\omega^2 - (1 - s_+(\tau))\left(\alpha - \frac{1}{s_+^2(\tau)}\right)}{\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2 + \omega^2}. \end{cases}$$
(3.4.26)

If there exists  $(\tau, \omega)$  satisfying (3.4.26), then (3.4.13) has a pair of pure imaginary roots  $\pm i\omega$ . A necessary condition for (3.4.26) to have solutions is  $\alpha s_+^2(\tau) \neq 1$ . Otherwise  $\alpha s_+^2(\tau) = 1$ , and the second equation of (3.4.26) becomes  $\cos(\omega \tau) = \alpha s_+(\tau)$ . However for any  $\tau \in (0, \tau_c)$ , we have  $\alpha s_+(\tau) > 1$ , since

$$\alpha s_{+}(\tau) = \frac{\alpha}{1 + \frac{\alpha e^{\tau}}{k}} > \frac{\alpha}{1 + \frac{\alpha}{k}k\left(1 - \frac{1}{\alpha}\right)} = \frac{\alpha}{1 + \alpha(1 - \frac{1}{\alpha})} = \frac{\alpha}{\alpha} = 1.$$

Hence the second equation of (3.4.26) has no solution. Assume  $\alpha s^2_+(\tau) \neq 1$  for  $\omega \ge 0$ and  $\tau \in [0, \tau_c]$  and denote the right hand sides of (3.4.26) by

$$h_{1}(\omega,\tau) = \frac{c(\tau)(p(\tau)\omega) + q\omega(\omega^{2} - \beta(\tau))}{c^{2}(\tau) + q^{2}\omega^{2}}$$
  
$$= -\omega \frac{\omega^{2} - \left(\alpha - \frac{1}{s_{+}^{2}(\tau)}\right) - \alpha(1 - s_{+}(\tau))}{\left(\alpha s_{+}(\tau) - \frac{1}{s_{+}(\tau)}\right)^{2} + \omega^{2}},$$
  
$$h_{2}(\omega,\tau) = \frac{c(\tau)(\omega^{2} - \beta(\tau)) + q\omega(-p(\tau)\omega)}{c^{2}(\tau) + q^{2}\omega^{2}}$$
  
$$= \alpha s_{+}(\tau) \frac{\omega^{2} - (1 - s_{+}(\tau))\left(\alpha - \frac{1}{s_{+}^{2}(\tau)}\right)}{\left(\alpha s_{+}(\tau) - \frac{1}{s_{+}(\tau)}\right)^{2} + \omega^{2}}.$$

Define functions

$$\theta_1(\tau) = \arccos(h_2(\omega_1(\tau), \tau)) \quad \text{if} \quad h_2(\omega_1(\tau), \tau) \in [-1, 1], \quad (3.4.27)$$

and

$$\theta_2(\tau) = \arccos(h_2(\omega_2(\tau), \tau)) \quad \text{if} \quad h_2(\omega_2(\tau), \tau) \in [-1, 1].$$
(3.4.28)

**Lemma 3.11.** Assume  $\alpha > \frac{7+3\sqrt{5}}{2}$  and  $k > \frac{\alpha}{\sqrt[4]{\alpha}-1}$ . For any  $\tau \in I_1$  given by (3.4.21), there exists  $\epsilon_j > 0$  and  $\theta_j(\tau)$  with  $\epsilon_j \leq \theta_j(\tau) \leq \pi$  (j=1,2) such that

$$\begin{cases} \sin(\theta_j(\tau) + 2n\pi) = h_1(\omega_j(\tau), \tau), \\ \cos(\theta_j(\tau) + 2n\pi) = h_2(\omega_j(\tau), \tau). \end{cases} \quad n = 0, 1, 2, \dots \qquad (3.4.29)$$

**Proof.** For any  $\tau \in I_1$ , by Theorem 3.9,  $\omega_1(\tau) > 0$  and  $\omega_2(\tau) \ge 0$ . We know  $h_1(0,\tau) = 0$  and  $\lim_{\omega \to +\infty} h_1(\omega,\tau) = -\infty$ . There are two roots of  $h_1(z,\tau) = 0$ ,  $z_1 = 0$  and

$$z_2(\tau) = \sqrt{\alpha - \frac{1}{s_+^2(\tau)} + \alpha(1 - s_+(\tau))}.$$

Hence  $h_1(\omega, \tau) > 0$  for  $0 < \omega < z_2(\tau)$ . For any  $\tau \in I_1$ , as shown in Theorem 3.9,  $s_+(\tau) \in \left[\frac{1}{\sqrt[4]{\alpha}}, \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}\right]$ . This implies  $s_+(\tau) \ge \frac{1}{\sqrt[4]{\alpha}} > \frac{1}{\sqrt{\alpha}} > \frac{1}{\alpha}$ . Therefore  $\alpha s_+^2(\tau) > 1$  and  $\alpha s_+(\tau) > 1$ . The function  $h_2(\omega, \tau)$  is monotonically increasing for  $\omega \ge 0$  since

$$\begin{aligned} \frac{\partial h_2(\omega,\tau)}{\partial \omega} &= \alpha s_+(\tau) \frac{2\omega \left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right) - 2\omega \left( \omega^2 - (1 - s_+(\tau)) \left( \alpha - \frac{1}{s_+^2(\tau)} \right) \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha s_+(\tau) \omega \frac{\left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + (1 - s_+(\tau)) \left( \alpha - \frac{1}{s_+^2(\tau)} \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha s_+(\tau) \omega \frac{\left( \alpha - \frac{1}{s_+^2(\tau)} \right) \left( s_+^2(\tau) \left( \alpha - \frac{1}{s_+^2(\tau)} \right) + 1 - s_+(\tau) \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha s_+(\tau) \omega \frac{\left( \alpha - \frac{1}{s_+^2(\tau)} \right) s_+(\tau) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= 2\alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= \alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= \alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \left( \alpha s_+(\tau) - \frac{1}{s_+(\tau)} \right)^2 + \omega^2 \right)^2} \\ &= \alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)} \\ &= \alpha \omega \frac{\left( \alpha s_+^2(\tau) - 1 \right) \left( \alpha s_+(\tau) - 1 \right)}{\left( \alpha s_+^2(\tau)$$

Since  $s_+(\tau) < 1$ ,

$$h_2(0,\tau) = -\alpha s_+(\tau) \frac{\left(1 - s_+(\tau)\right) \left(\alpha - \frac{1}{s_+^2(\tau)}\right)}{\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2} = -\frac{\alpha s_+(\tau)(1 - s_+(\tau))}{\alpha s_+^2(\tau) - 1} < 0.$$

Also  $\lim_{\omega \to \infty} h_2(\omega, \tau) = \alpha s_+(\tau) > 1$ . Therefore there exists a unique  $\omega = l_{max}(\tau) = \sqrt{\alpha - \frac{1}{s_+^2(\tau)}} > 0$  such that  $h_2(l_{max}(\tau), \tau) = 1$ . Solving  $h_2(l_{max}, \tau) = 1$  for  $l_{max}$  and

noting that  $\alpha - \frac{1}{s_+^2(\tau)} \neq 0$ , it is easy to see that  $l_{max}(\tau) = \sqrt{\alpha - \frac{1}{s_+^2(\tau)}}$ :

$$\begin{split} l_{max}^{2}(\alpha s_{+}(\tau)-1) &= \alpha s_{+}(\tau)(1-s_{+}(\tau))\left(\alpha - \frac{1}{s_{+}^{2}(\tau)}\right) + \left(\alpha s_{+}(\tau) - \frac{1}{s_{+}(\tau)}\right)^{2} \\ &= \alpha s_{+}(\tau)\left(\alpha - \frac{1}{s_{+}^{2}(\tau)} - \alpha s_{+}(\tau) + \frac{1}{s_{+}(\tau)}\right) + \alpha^{2}s_{+}^{2}(\tau) - 2\alpha + \frac{1}{s_{+}^{2}(\tau)} \\ &= \alpha^{2}s_{+}(\tau) - \frac{\alpha}{s_{+}(\tau)} - \alpha^{2}s_{+}^{2}(\tau) + \alpha + \alpha^{2}s_{+}^{2}(\tau) - 2\alpha + \frac{1}{s_{+}^{2}(\tau)} \\ &= \alpha^{2}s_{+}(\tau) - \frac{\alpha}{s_{+}(\tau)} - \alpha + \frac{1}{s_{+}^{2}(\tau)} \\ &= \left(\alpha - \frac{1}{s_{+}^{2}(\tau)}\right)(\alpha s_{+}(\tau) - 1). \end{split}$$

Then  $h_2(\omega, \tau) \leq 1$  for any  $\omega \in [0, l_{max}(\tau)]$ . Since  $s_+(\tau) < 1$ ,  $l_{max}(\tau) < z_2(\tau)$ . Therefore  $h_1(\omega, \tau) > 0$  for any  $\omega \in [0, l_{max}(\tau)]$ . Since  $\omega_1(\tau)$  is a positive root of  $h_1^2(\omega, \tau) + h_2^2(\omega, \tau) = 1$ , we have  $h_2(\omega_1(\tau), \tau) \leq 1$ , which implies that  $0 < \omega_1(\tau) \leq l_{max}(\tau) < z_2(\tau)$ . Therefore  $h_1(\omega_1(\tau), \tau) > 0$ , and so  $h_1(\omega_1(\tau), \tau) = \sqrt{1 - h_2(\omega_1(\tau), \tau)}$ . In fact

$$\omega_1(\tau) < l_{max}(\tau), \tag{3.4.30}$$

since

$$h_2^2(l_{max}(\tau), \tau) + h_1^2(l_{max}(\tau), \tau) = 1 + h_1^2(l_{max}(\tau), \tau) > 1.$$

Thus  $\theta_1(\tau)$  is defined and  $0 \leq \theta_1(\tau) \leq \pi$ . Since  $\cos(\theta_1(\tau) + 2n\pi) = h_2(\omega_1(\tau), \tau)$ ,

$$\sin(\theta_1(\tau) + 2n\pi) = \sqrt{1 - \cos^2(\theta_1(\tau) + 2n\pi)}$$
$$= \sqrt{1 - h_2^2(\omega_1(\tau), \tau)}$$
$$= h_1(\omega_1(\tau), \tau).$$

Hence  $\theta_1(\tau)$  satisfies (3.4.29). From (3.4.30),  $h_2(\omega_1(\tau), \tau) < h_2(l_{max}(\tau), \tau) = 1$  and so  $\theta_1(\tau) > 0$ . Since  $\theta_1(\tau)$  is continuous on the interval  $I_1$  and  $I_1$  is closed, there exists  $\epsilon_1 > 0$  such that  $\theta_1(\tau) \ge \epsilon_1$ . Similarly we can prove the existence of  $\theta_2(\tau)$ .  $\Box$  **Lemma 3.12.** Assume  $\alpha > 1$  and  $k > \alpha \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)^{-1}$ . For any  $\tau \in I_2$  given by (3.4.24), there exists  $\epsilon > 0$  and  $\theta_1(\tau)$  such that  $\epsilon \leq \theta_1(\tau) < \pi$  and  $\theta_1(\tau)$  satisfies (3.4.29) for j = 1.

**Proof.** For any  $\tau \in I_2$ , by Theorem 3.10, only  $\omega_1(\tau) > 0$ .

As in Lemma 3.11, we have  $h_1(\omega, \tau) > 0$  for  $0 < \omega < z_2(\tau)$ . For any  $\tau \in I_2$ , as shown in Theorem 3.10,  $s_+(\tau) \in [\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}, 1)$ . Letting

$$G(\alpha) = \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} - \frac{1}{\sqrt{\alpha}}, \qquad \alpha > 1,$$

we have

$$\frac{\mathrm{d}G(\alpha)}{\mathrm{d}\alpha} = -\frac{1}{4\alpha^2\sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} + \frac{1}{2\alpha\sqrt{\alpha}} = \frac{1}{2\alpha}\left(\frac{-1}{\sqrt{\frac{\alpha^2}{4} + 2\alpha}} + \frac{1}{\sqrt{\alpha}}\right) > 0.$$

 $G(\alpha)$  is an increasing function and G(1) = 0. Since  $G(\alpha) > G(1)$ , it follows that  $\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} > \frac{1}{\sqrt{\alpha}}$ . Therefore, for any  $s_+(\tau) > \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}$ , we obtain  $s_+(\tau) > \frac{1}{\sqrt{\alpha}}$ , or equivalently  $\alpha > \frac{1}{s_+^2(\tau)}$ . Since

$$\frac{\partial h_2(\omega,\tau)}{\partial \omega} = 2\alpha s_+(\tau)\omega \frac{\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2 + (1 - s_+(\tau))\left(\alpha - \frac{1}{s_+^2(\tau)}\right)}{\left(\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2 + \omega^2\right)^2} \ge 0,$$

 $h_2(\omega,\tau)$  is monotonically increasing for any  $\omega \ge 0$ . For any  $s_+(\tau) > \frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}$ ,

$$\left(s_{+}(\tau) - \frac{1}{4}\right)^{2} - \frac{1}{16} - \frac{1}{2\alpha} = s_{+}^{2}(\tau) - \frac{s_{+}(\tau)}{2} - \frac{1}{2\alpha} = \frac{1}{2\alpha} \left(2\alpha s_{+}^{2}(\tau) - \alpha s_{+}(\tau) - 1\right)$$
$$= \frac{1}{2\alpha} \left(\alpha s_{+}^{2}(\tau) - 1 - \left(\alpha s_{+}(\tau) - \alpha s_{+}^{2}(\tau)\right)\right)$$
$$= \frac{\alpha s_{+}^{2}(\tau) - 1}{2\alpha} \left(1 - \frac{\alpha s_{+}(\tau)(1 - s_{+}(\tau))}{\alpha s_{+}^{2}(\tau) - 1}\right) > 0,$$

which implies that  $\frac{\alpha s_+(\tau)(1-s_+(\tau))}{\alpha s_+^2(\tau)-1} < 1$ . Hence

$$0 > h_2(0,\tau) = -\alpha s_+(\tau) \frac{(1-s_+(\tau))\left(\alpha - \frac{1}{s_+^2(\tau)}\right)}{\left(\alpha s_+(\tau) - \frac{1}{s_+(\tau)}\right)^2} = -\frac{\alpha s_+(\tau)(1-s_+(\tau))}{\alpha s_+^2(\tau) - 1} > -1.$$

For  $\tau \in [0, \tau_c)$ ,  $\lim_{\omega \to \infty} h_2(\omega, \tau) = \alpha s_+(\tau) > 1$ , since

$$\alpha s_{+}(\tau) = \frac{\alpha}{1 + \frac{\alpha e^{\tau}}{k}} > \frac{\alpha}{1 + \frac{\alpha}{k}k\left(1 - \frac{1}{\alpha}\right)} = \frac{\alpha}{1 + \alpha(1 - \frac{1}{\alpha})} = \frac{\alpha}{\alpha} = 1$$

As in the proof of Lemma 3.11, there exists a unique  $l_{max}(\tau) = \sqrt{\alpha - \frac{1}{s_{+}^{2}(\tau)}} > 0$ such that  $h_{2}(l_{max}(\tau), \tau) = 1$ . Then  $l_{max}(\tau) < z_{2}(\tau)$ . Therefore  $h_{1}(\omega, \tau) > 0$  for any  $\omega \in [0, l_{max}(\tau)]$ . The rest of the proof is similar to the proof of Lemma 3.11. Furthermore  $\theta_{1}(\tau) < \pi$ , since  $h_{2}(\omega_{1}(\tau), \tau) > -1$  for any  $\omega_{1}(\tau) \in [0, l_{max}(\tau))$ .

**Theorem 3.13.** Consider system (3.2.4) with  $D = \Delta = 1$ .

1) Suppose  $\alpha > \frac{\tau+3\sqrt{5}}{2}$ ,  $k > \frac{\alpha}{\sqrt[4]{\alpha-1}}$ , and  $\tau \in I_1$  given by (3.4.22). For  $\tau \in I_1$ and j = 1, 2,  $\omega_j(\tau)$  is nonnegative and there exists  $\epsilon_j > 0$  and  $\theta_j(\tau)$  such that  $\epsilon_j \leq \theta_j(\tau) \leq \pi$  and  $\theta_j(\tau)$  satisfies (3.4.29). If there exists  $n \geq 0$  such that  $\theta_j(\tau) + 2n\pi$  intersects  $\tau \omega_j(\tau)$  at some  $\tau_n^j \in I_1$ , then equation (3.4.15) has a pair of pure imaginary eigenvalues  $\lambda = \pm i\omega_j(\tau_n^j)$ . System (3.2.4) undergoes a Hopf bifurcation at  $\tau_n^j$  provided  $\frac{d\operatorname{Re}(\lambda(\tau))}{d\tau}\Big|_{\tau=\tau_n^j} \neq 0$ .

2) Suppose 
$$\alpha > 1$$
,  $k > \alpha \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)^{-1}$ , and  $\tau \in I_2$  given by (3.4.24).  
For  $\tau \in I_2$ , only  $\omega_1(\tau)$  is positive and there exists  $\epsilon > 0$  and  $\theta_1(\tau)$  such that  $\epsilon \leqslant \theta_1(\tau) < \pi$  and  $\theta_1(\tau)$  satisfies (3.4.29) for  $j = 1$ . If there exists  $n \ge 0$  such that  $\theta_1(\tau) + 2n\pi$  intersects  $\tau \omega_1(\tau)$  at some  $\tau_n^1 \in I_2$ , then equation (3.4.15) has a pair of pure imaginary eigenvalues  $\lambda = \pm i\omega_1(\tau_n^1)$ . System (3.2.4) undergoes a Hopf bifurcation at  $\tau_n^1$  provided  $\frac{\mathrm{dRe}(\lambda(\tau))}{\mathrm{d}\tau}\Big|_{\tau=\tau_n^1} \neq 0$ .

**Proof.** Assume  $D = \Delta = 1$  in system (3.2.4).

**Case 1)** Suppose  $\tau \in I_1$ . By Theorem 3.9,  $\omega_j(\tau) \ge 0$  for j = 1, 2. By Lemma 3.11, there exists  $\epsilon_j > 0$  and  $\theta_j(\tau)$  such that  $\epsilon_j \le \theta_j(\tau) \le \pi$  and  $\theta_j(\tau)$  satisfies (3.4.29). Assume there exists a positive integer  $\tau_n^j \in I_1$  such that  $\theta_j(\tau_n^j) + 2n\pi = \tau_n^j \omega_j(\tau_n^j)$  for some integer  $n \ge 0$ . Then system (3.4.26) has one solution  $(\tau_n^j, \omega_j(\tau_n^j))$ . Equation (3.4.15) has a pair of pure imaginary eigenvalues  $\lambda = \pm i \omega_j(\tau_n^j)$ .

In what follows, we show that the conditions required for a Hopf Bifurcation (see Theorem A.2 in **Appendix A**) are satisfied by the linearization (3.3.8) of (3.2.4) at  $E_+$ . In (A.0.3), choosing  $\tau$  as the bifurcation parameter and letting

$$D(\tau, z_t) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} z_1(t) \\ z_2(t) \\ z_3(t) \end{bmatrix}$$

and

$$L(\tau, z_t) = \begin{bmatrix} -1 - \alpha x_+ & -\alpha s_+ & 0\\ \alpha x_+ & -D + \alpha s_+ - k y_+ & -k x_+\\ 0 & 0 & -\Delta \end{bmatrix} \begin{bmatrix} z_1(t)\\ z_2(t)\\ z_3(t) \end{bmatrix} + \begin{bmatrix} 0 & 0 & 0\\ 0 & 0 & 0\\ 0 & k e^{\Delta \tau} y_+ & k e^{\Delta \tau} x_+ \end{bmatrix} \begin{bmatrix} z_1(t - \tau)\\ z_2(t - \tau)\\ z_3(t - \tau) \end{bmatrix},$$

the linearization (3.3.8) of (3.2.4) at  $E_+$  is of the form (A.0.3). Taking *a* to be any positive real number and  $b = \frac{1}{2}$ , hypothesis (S<sub>1</sub>) in the Hopf Bifurcation Theorem

holds since

$$\left| \det\left(\sum_{k=0}^{\infty} A_k(\alpha) e^{-\lambda r_k(\alpha)}\right) \right| = \left| \det\left[ \begin{array}{ccc} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{array} \right] \right| = 1 \ge \frac{1}{2}$$

and

$$\left|\det\left(\sum_{k=0}^{\infty}A_{k}(\alpha)e^{-\lambda r_{k}(\alpha)}+\int_{-1}^{0}A(\alpha,\ \theta)e^{\lambda\theta}\mathrm{d}\theta\right)\right|=\left|\det\left[\begin{array}{ccc}1&0&0\\0&1&0\\0&0&1\end{array}\right]\right|=1\geqslant\frac{1}{2}$$

for all  $\tau \in \mathbb{R}$  and  $|\text{Re}\lambda| < a$ .

The characteristic equation (3.4.15) of (3.3.8) at  $E_+$  has a pair of pure imaginary eigenvalues  $\lambda = \pm \omega_1(\tau_n^j)$  and no other root of (3.4.15) is an integral multiple of  $\pm \omega_1(\tau_n^j)$ . Hence the hypothesis ( $S_2$ ) in the Hopf Bifurcation Theorem holds. Therefore, (3.2.4) undergoes a Hopf bifurcation at  $E_+$  when  $\tau = \tau_n^j$  provided  $\frac{\mathrm{d}\mathrm{Re}(\lambda(\tau))}{\mathrm{d}\tau}\Big|_{\tau=\tau_n^j} \neq 0.$ 

Case 2) Suppose  $\tau \in I_2$ . By Theorem 3.9, only  $\omega_1(\tau) > 0$ . By Lemma 3.12, there exists  $\epsilon > 0$  and  $\theta_1(\tau)$  such that  $\epsilon \leq \theta_1(\tau) < \pi$  and  $\theta_1(\tau)$  satisfies (3.4.29). Assume there exists  $\tau_n^1 \in I_2$  such that  $\theta_1(\tau_n^1) + 2n\pi = \tau_n^1 \omega_1(\tau_n^1)$  for some integer  $n \ge 0$ . Then system (3.4.26) has one solution  $(\tau_n^1, \omega_1(\tau_n^1))$ . Equation (3.4.15) has a pair of pure imaginary eigenvalues  $\lambda = \pm i\omega_1(\tau_n^1)$ . The rest of the proof is similar to Case 1) when j = 1.

**Corollary 3.14.** Consider system (3.2.4) with  $D = \Delta = 1$ .

1) Suppose  $\alpha > \frac{7+3\sqrt{5}}{2}$ ,  $k > \frac{\alpha}{\sqrt[4]{\alpha-1}}$ , and  $\tau \in I_1$  given by (3.4.22). For  $\tau \in I_1$ ,  $\omega_j(\tau)$  is nonnegative and there exists  $\epsilon_j > 0$  and  $\theta_j(\tau)$  such that  $\epsilon_j \leq \theta_j(\tau) \leq \pi$  and

 $\theta_j(\tau) \text{ satisfies } (3.4.29) \text{ for } j = 1, 2. \text{ If there exists a positive integer } n_j \ge 0 \text{ such }$ that  $\min_{\tau \in I_1} \tau \omega_j(\tau) \le 2n_j \pi$  and  $\max_{\tau \in I_1} \tau \omega_j(\tau) > (2n_j + 1)\pi$ , then  $\theta_j(\tau) + 2n_j \pi$ intersects  $\tau \omega_j(\tau)$  at least once at some  $\tau_{n_j}^j \in I_1$ . System (3.2.4) undergoes a
Hopf bifurcation at  $\tau_{n_j}^j$  provided  $\frac{\mathrm{dRe}(\lambda(\tau))}{\mathrm{d}\tau}\Big|_{\tau=\tau_{n_j}^j} \ne 0.$ 

2) Suppose  $\alpha > 1$ ,  $k > \alpha \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)^{-1}$ , and  $\tau \in I_2$  defined in (3.4.24). For  $\tau \in I_2$ , only  $\omega_1(\tau)$  is positive. There exists  $\epsilon > 0$  and  $\theta_1(\tau)$  such that  $\epsilon \leqslant \theta_1(\tau) < \pi$  and  $\theta_1(\tau)$  satisfies (3.4.29) for j = 1. If there exists a positive integer  $N \ge 0$  such that  $\max_{\tau \in I_2} \tau \omega_1(\tau) > (2N+1)\pi$ , then for any  $0 \leqslant n \leqslant N$ ,  $\theta_1(\tau) + 2n\pi$  intersects  $\tau \omega_1(\tau)$  at least once at some  $\tau_n^1 \in I_2$ . System (3.2.4) undergoes a Hopf bifurcation at  $\tau_n^1$  provided  $\frac{\mathrm{dRe}(\lambda(\tau))}{\mathrm{d}\tau}\Big|_{\tau=\tau_n^1} \neq 0$ .

**Proof.** Assume  $D = \Delta = 1$  in system (3.2.4).

Case 1) Suppose  $\tau \in I_1$ . By Theorem 3.9,  $\omega_j(\tau) \ge 0$  for j = 1, 2. By Lemma 3.11, there exists  $\epsilon_j > 0$  and  $\theta_j(\tau)$  such that  $\epsilon_j \le \theta_j(\tau) \le \pi$  and  $\theta_j(\tau)$ satisfies equations (3.4.29). Assume that there exists a positive integer  $n_j \ge 0$  such that  $\min_{\tau \in I_1} \tau \omega_j(\tau) \le 2n_j \pi$  and  $\max_{\tau \in I_1} \tau \omega_j(\tau) > (2n_j + 1)\pi$ . For such  $n_j$ ,

$$\min_{\tau \in I_1} \tau \omega_j(\tau) < \epsilon_j + 2n_j \pi \leqslant \theta_j(\tau) + 2n_j \pi \leqslant (2n_j + 1)\pi < \max_{\tau \in I_1} \tau \omega_j(\tau).$$

By the Mean Value Theorem, there exists  $\tau_{n_j}^j \in I_1$  such that  $\theta_j(\tau_{n_j}^j) + 2n_j\pi = \tau_{n_j}^j \omega_j(\tau_{n_j}^j)$ . By Theorem 3.13. Case 1), the conclusion follows.

**Case 2)** Suppose  $\tau \in I_2$ . By Theorem 3.9, only  $\omega_1(\tau) > 0$ . By Lemma 3.12, there exists  $\epsilon > 0$  and  $\theta_1(\tau)$  such that  $\epsilon \leq \theta_1(\tau) < \pi$  and  $\theta_1(\tau)$  satisfies equations (3.4.29). Assume that there exists a positive integer  $N \ge 0$  such that  $\max_{\tau \in I_2} \tau \omega_1(\tau) > (2N+1)\pi$ . By (3.4.24),  $0 \in I_2$ . Therefore  $\min_{\tau \in I_2} \tau \omega_1(\tau) = 0$ . For

 $0 \leq n \leq N$ ,

$$\min_{\tau \in I_2} \tau \omega_1(\tau) < \epsilon + 2n\pi \leqslant \theta_i(\tau) + 2n\pi \leqslant (2n+1)\pi < \max_{\tau \in I_2} \tau \omega_1(\tau)$$

By the Mean Value Theorem, there exists  $\tau_n^1 \in I_2$  such that  $\theta_1(\tau_n^1) + 2n\pi = \tau_n^1 \omega_1(\tau_n^1)$ . By Theorem 3.13. Case 2), the conclusion follows.

Corollary 3.15. Consider system (3.2.4) with  $D = \Delta = 1$ . Assume  $\alpha > \frac{7+3\sqrt{5}}{2}$  and  $k > \frac{\alpha}{\sqrt[4]{\alpha-1}}$ . If  $\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} > \frac{k}{\alpha+k}$ , then  $I_1 = \begin{bmatrix} 0, & \ln\left(\frac{k}{\alpha}(\sqrt[4]{\alpha} - 1)\right) \end{bmatrix}$ , where  $I_1$  was defined in (3.4.22). For any  $\tau \in I_1$ ,  $\omega_j(\tau)$  is nonnegative and there exists  $\epsilon_j > 0$  and  $\theta_j(\tau)$  such that  $\epsilon_j \leq \theta_j(\tau) \leq \pi$  and  $\theta_j(\tau)$  satisfies (3.4.29) for j = 1, 2. If there exists a positive integer  $N_j \geq 0$  (j = 1, 2) such that  $\max_{\tau \in I_1} \tau \omega_j(\tau) > (2N_j + 1)\pi$ , then for any  $0 \leq n \leq N_j$ ,  $\theta_j(\tau) + 2n\pi$  intersects  $\tau \omega_j(\tau)$  at least once at some  $\tau_n^j \in I_1$ . System (3.2.4) undergoes a Hopf bifurcation at  $\tau_n^j$  provided  $\frac{\operatorname{dRe}(\lambda(\tau))}{\operatorname{d\tau}}|_{\tau=\tau_n^j} \neq 0$ .

**Proof.** Assume  $\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}} > \frac{k}{\alpha+k}$ . Then  $\ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)\right) < 0$ . By (3.4.22),

$$I_{1} = \left[ \max\left\{ 0, \ln\left(\frac{k}{\alpha} \left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)\right) \right\}, \ln\left(\frac{k(\sqrt[4]{\alpha} - 1)}{\alpha}\right) \right]$$
$$= \left[ 0, \ln\left(\frac{k}{\alpha}(\sqrt[4]{\alpha} - 1)\right) \right].$$

For any  $\tau \in I_1$ , by Theorem 3.9,  $\omega_j(\tau) \ge 0$  for j = 1, 2. By Lemma 3.11, there exists  $\epsilon_j > 0$  and  $\theta_j(\tau)$  such that  $\epsilon_j \le \theta_j(\tau) \le \pi$  and  $\theta_j(\tau)$  satisfies equations (3.4.29). Noting  $0 \in I_1$ ,  $\min_{\tau \in I_1} \tau \omega_j(\tau) = 0$ . Assume there exists a positive integer  $N_j \ge 0$  (j = 1, 2) such that  $\max_{\tau \in I_1} \tau \omega_j(\tau) > (2N_j + 1)\pi$ . For any  $0 \le n \le N_j$ ,  $\min_{\tau \in I_1} \tau \omega_j(\tau) = 0 \le 2n\pi$  and  $\max_{\tau \in I_1} \tau \omega_j(\tau) > (2N_j + 1)\pi \ge (2n + 1)\pi$ . By Corollary 3.14, the conclusion follows.

### 3.5 Numerical Results

This section includes bifurcation diagrams involving the interior equilibrium  $E_+$  and numerical simulations of periodic solutions of the predator-prey model in the chemostat.

#### 3.5.1 Variation of Eigenvalues and a Bifurcation Diagram

To study the stability switches of  $E_+$ , DDEBIFTOOL (see [17], [51]) was chosen to illustrate how the real part of the eigenvalues of (3.4.13) change as parameters  $\alpha$  and  $\tau$  vary.

First fix parameters  $D = \Delta = 1$ , k = 24, and  $\tau = 0.5$ . Taking  $\alpha$  as the bifurcation parameter and varying it from 0 to 10, the real part of the eigenvalues with largest real part of (3.4.13) was plotted in Figure 3.1. At  $\alpha \approx 1.15$  and  $\alpha \approx 1.5$ , there is either a zero eigenvalue or a pair of pure imaginary roots. For  $\alpha \in (1.15, 1.5)$ , all eigenvalues have negative real parts. For example, taking  $\alpha = 1.3$ , Figure 3.2 (TOP) shows that the eigenvalues of (3.4.13) with largest real part (the ones in the circle) have negative real parts. Note that due to the scaling, the eigenvalues in the circle seems to be indistinguishable from zero. But in fact, they are a pair of complex eigenvalues with real parts slightly less than zero. DDEBIFTOOL can keep track of the occurrence of a pair of pure imaginary eigenvalues as  $\alpha$  varies in the neighborhood of  $\alpha = 1.5$ . Figure 3.2 (BOTTOM) clearly shows that there is a pair of pure imaginary eigenvalues. Hence Hopf bifurcation is possible. Note that by continuation, the pair of eigenvalues with largest real parts in Figure 3.2 (TOP) for  $\alpha = 1.3$  become the pair of pure imaginary eigenvalues in Figure 3.2 (BOTTOM) for

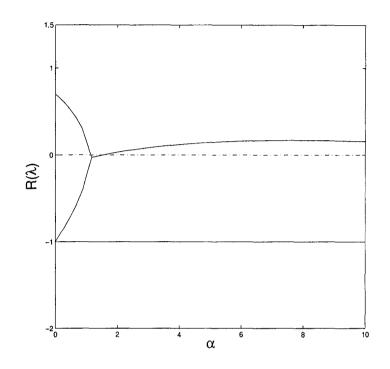


Figure 3.1: Variation of the largest real part of eigenvalues as the bifurcation parameter  $\alpha$  is varied. At  $\alpha \approx 1.15$  and 1.5, the largest real part crosses zero and it seems that there is a zero eigenvalue for  $\alpha \approx 1.15$  and a pair of pure imaginary eigenvalues for  $\alpha \approx 1.5$ . The largest real part becomes positive as  $\alpha$  increases through 1.5. But as  $\alpha$  increases further, for  $\alpha \approx 17$ , the largest real part crosses zero again and remains negative thereafter. There is a second Hopf bifurcation at  $\alpha \approx 17$ . This is consistent with what is observed in Figure 3.3 when  $\tau = 0.5$  and  $\alpha$  varies from 0 to 30. Parameters  $D = \Delta = 1$ , k = 24, and  $\tau = 0.5$ .

 $\alpha \approx 1.5.$ 

Finally fix all parameters as before and vary  $\tau$  and  $\alpha$ . In Figure 3.3, we plot the Hopf bifurcation diagram in  $\alpha$  and  $\tau$  parameter space. The curve at the left upper corner is  $\tau = \tau_c$ . For any pair  $(\alpha, \tau)$  below that curve, a coexistence

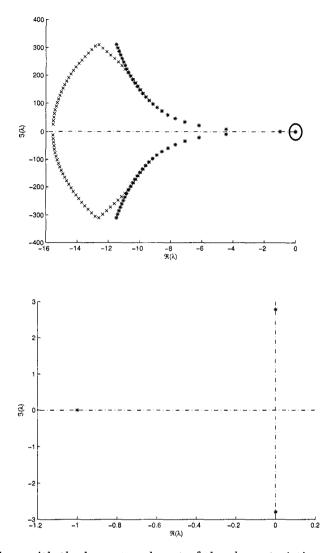


Figure 3.2: Eigenvalues with the largest real part of the characteristic equation (3.4.13) at  $E_+$ . Parameters are the same as in Figure 3.1 except  $\alpha = 1.3$  for the TOP and  $\alpha \approx 1.5$  for the BOTTOM graph. Due to the scaling, the eigenvalues in the circle (see the TOP) seem indistinguishable from zero. In fact, they are a pair of complex eigenvalues with real parts slightly less than zero. As  $\alpha$  varies from 1.3 to 1.5, the pair of complex eigenvalues with largest real part becomes a pair of pure imaginary roots in the figure (BOTTOM). The eigenvalue with the second largest real part remains equal to -1. This is consistent with our analytical results that showed (3.4.13) has a constant eigenvalue -1 when  $D = \Delta = 1$ .

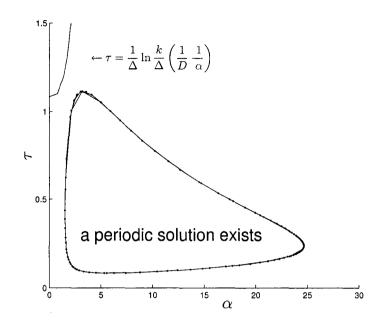


Figure 3.3: The bifurcation diagram of  $E_+$  in  $\tau$  and  $\alpha$  parameter space. Parameters are the same as in Figure 3.1 except  $\tau$  and  $\alpha$  are allowed to vary. For any pair  $(\alpha, \tau)$  on the closed curve, there is a Hopf bifurcation. Inside the closed curve, there is a periodic solution surrounding  $E_+$ . For any  $(\alpha, \tau)$  outside the closed curve and below  $\tau = \tau_c$ , the coexistence equilibrium  $E_+$  is stable.

equilibrium  $E_+$  exists (i.e. all components are positive). For any pair  $(\alpha, \tau)$  on the closed curve, there is a Hopf bifurcation. Inside the closed curve, there is a periodic solution surrounding  $E_+$ . For any  $(\alpha, \tau)$  outside the closed curve and below  $\tau = \tau_c$ , the coexistence equilibrium  $E_+$  is stable.

#### 3.5.2 Simulations Demonstrating Hopf Bifurcations

In this section, we illustrate Theorem 3.13 for system (3.2.4). Take  $D = \Delta = 1$  and let  $\tau$  vary. We choose parameters  $\alpha = 100$  and k = 100 for case 1), and  $\alpha = 2$  and

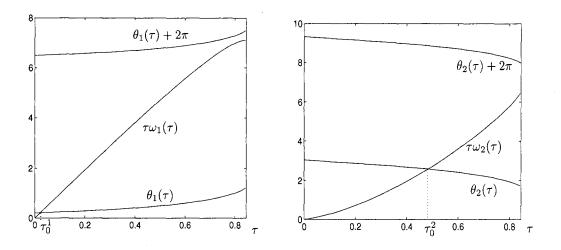


Figure 3.4: Critical value of delay  $\tau$  at which a Hopf Bifurcations occur.

k = 20 for case 2).

Case 1). Note that  $I_1$  is given by (3.4.22). Since  $\ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4}+\sqrt{\frac{1}{16}+\frac{1}{2\alpha}}}-1\right)\right) = -0.03$ ,

$$\max\left\{0, \ln\left(\frac{k}{\alpha}\left(\frac{1}{\frac{1}{4} + \sqrt{\frac{1}{16} + \frac{1}{2\alpha}}} - 1\right)\right)\right\} = 0.$$

Also  $\ln\left(\frac{k(\sqrt[4]{\alpha}-1)}{\alpha}\right) \approx 0.77$ . Therefore  $I_1 \approx [0, 0.77]$ . By Theorem 3.13,  $\omega_j(\tau)$  is positive and  $\theta_j(\tau)$  satisfies (3.4.29) for any  $\tau \in I_1$  and j = 1, 2.

Figure 3.4 shows that  $\theta_j(\tau)$  intersects  $\tau \omega_j(\tau)$  at some  $\tau_0^j$  with  $\tau_0^1 \approx 0.022$  and  $\tau_0^2 \approx 0.48$ . We see that  $\theta_j(\tau) + 2n\pi$  has no intersection with  $\tau \omega_j(\tau)$  for  $n \ge 2$  and j = 1, 2. By Theorem 3.13, (3.4.15) has two pairs of pure imaginary eigenvalues with distinct frequency  $\lambda = \pm i \omega_j(\tau_0^j)$ . Next we need to check if  $\operatorname{Re} \frac{d\lambda(\tau)}{d\tau}\Big|_{\tau=\tau_0^j} \neq 0$ .

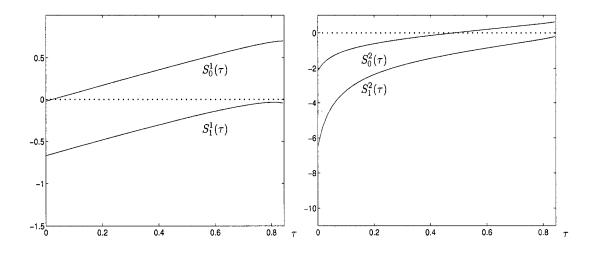


Figure 3.5: When the slope of  $S_n^j(\tau)$  is nonzero at  $\tau$  when  $S_n^j(\tau) = 0$  (j = 1, 2), the transversality condition holds and there is a Hopf bifurcations.

As in Kuang [5], we can define

$$S_n^j(\tau) = \tau - \frac{\theta_j(\tau) + 2n\pi}{\omega_j(\tau)}, \quad \text{for} \quad j = 1, 2, \quad n = 0, 1, 2..$$

Any zero  $\tau_n^j$  of  $S_n^j(\tau)$  is an intersection of  $\theta_j(\tau) + 2n\pi$  and  $\tau \omega_j(\tau)$ , and versa vice. By (4.10) in Beretta and Kuang [5] and noting that  $(q^2 - p^2(\tau) + 2\alpha^2(\tau))^2 - 4(\alpha^2(\tau) - c^2(\tau)) > 0$ , we have the relation

$$\operatorname{sign}\left\{\operatorname{Re}\frac{\mathrm{d}\lambda(\tau)}{\mathrm{d}\tau}\Big|_{\tau=\tau_{n}^{j}}\right\}$$

$$= \pm \operatorname{sign}\left\{\left(q^{2}-p^{2}(\tau)+2\alpha^{2}(\tau)\right)^{2}-4\left(\alpha^{2}(\tau)-c^{2}(\tau)\right)\right\}\operatorname{sign}\left\{\frac{\mathrm{d}S_{n}^{j}(\tau)}{\mathrm{d}\tau}\Big|_{\tau=\tau_{n}^{j}}\right\}$$

$$= \pm \operatorname{sign}\left\{\frac{\mathrm{d}S_{n}^{j}(\tau)}{\mathrm{d}\tau}\Big|_{\tau=\tau_{n}^{j}}\right\},$$
(3.5.31)

where we take + for j = 1 and - for j = 2.

From Figure 3.5 (LEFT), it is observed that  $S_n^1$  has only one zero  $\tau_0^1 \approx 0.022$ 

at n = 0 with sign  $\left\{ \frac{dS_0^1(\tau)}{d\tau} \Big|_{\tau=\tau_0^1} \right\} > 0$ . Hence, sign  $\left\{ \operatorname{Re} \frac{d\lambda(\tau)}{d\tau} \Big|_{\tau=\tau_0^1} \right\} > 0$ . By Theorem 3.13, system (3.2.4) undergoes a Hopf bifurcation at  $\tau_0^1$ . Similarly from Figure 3.5 (RIGHT),  $S_n^2$  has only one zero  $\tau_0^2 \approx 0.48$  for n = 0 and (3.2.4) undergoes a Hopf bifurcation at  $\tau_0^2$ .

Next we used MATLAB to simulate solutions of model (3.2.4) for several values of  $\tau$ . For each fixed delay  $\tau$ , we chose initial data  $s(t) = s_{+}(\tau) - 0.01$ ,  $x(t) = x_{+}(\tau) + 0.01$ , and  $y(t) = y_{+}(\tau) + 0.001$  for  $t \in [-\tau, 0]$ . From Figures 3.6, we can see the equilibrium  $E_{+}$  is stable if  $\tau = 0.02 < \tau_{0}^{1}$ . As delay  $\tau$  increases past  $\tau_{0}^{1} \approx 0.022$ , where Hopf bifurcation occurs, a pair of complex eigenvalues of (3.4.15) enter the right half plane. The equilibrium  $E_{+}$  loses its stability and a periodic solution bifurcates from  $E_{+}$  (see Figures 3.7 and 3.8). As we increase the delay further to  $\tau = 0.4 < \tau_{0}^{2}$ , the periodic solution still exists and remains stable (see Figure 3.9 and 3.10). However, as the delay  $\tau$  increases further, past  $\tau_{0}^{2}$ , the stable periodic solution disappears and  $E_{+}$  regains stability (see Figures 3.11). We also obtain the bifurcation diagram as  $\tau$  varies (see Figure 3.12). For any  $\tau \in (\tau_{0}^{1}, \tau_{0}^{2})$ , there exists a stable periodic solution.

Case 2). Take k = 20 and  $\alpha = 2$ . For such parameters,  $I_2 \approx [0, 0.85]$ . By Theorem 3.13,  $\omega_1(\tau)$  is positive and  $\theta_1(\tau)$  satisfies (3.4.29) for j = 1 and  $\tau \in I_2$ . Figure 3.13 shows that  $\theta_1(\tau)$  intersects  $\tau \omega_1(\tau)$  twice. To distinguish them, denote as  $\tau_{0,1}^1 \approx 0.22$  and  $\tau_{0,2}^1 \approx 0.65$ . But  $\theta_1(\tau) + 2\pi$  has no intersection with  $\tau \omega_1(\tau)$ .

From Figure 3.14,

$$\operatorname{sign}\left\{\frac{\mathrm{d}S_{0}^{1}(\tau)}{\mathrm{d}\tau}\Big|_{\tau=\tau_{0,1}^{1}}\right\} > 0, \qquad \operatorname{sign}\left\{\frac{\mathrm{d}S_{1}^{1}(\tau)}{\mathrm{d}\tau}\Big|_{\tau=\tau_{0,2}^{1}}\right\} < 0.$$

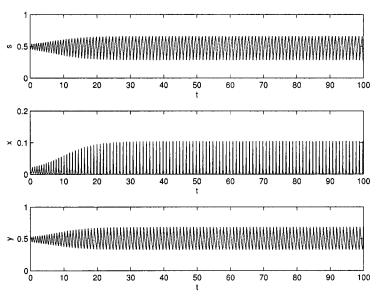


Figure 3.7: Time series of a periodic solution, for  $\tau = 0.03$ .

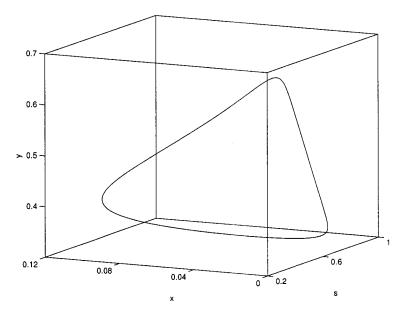


Figure 3.8: The trajectory in phase space of the periodic solution in Figure 3.7 for  $\tau = 0.03$ 

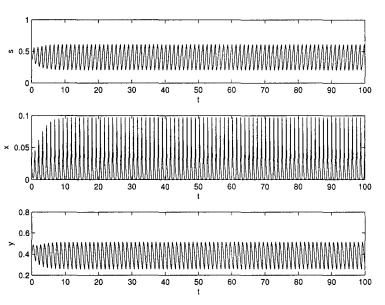


Figure 3.9: Time series of a periodic solution for  $\tau = 0.4$ .

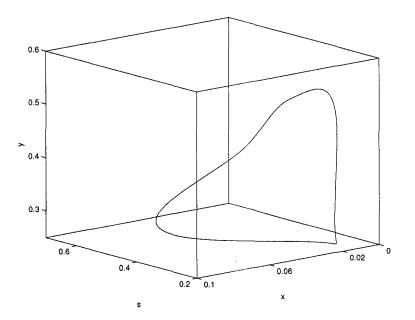


Figure 3.10: The trajectory in phase space of the periodic solution shown in Figure 3.9.

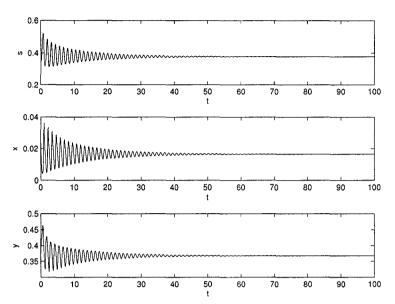


Figure 3.11: The periodic solution disappears at the secondary Hopf bifurcation at  $\tau_0^2 \approx$  0.48 and  $E_+$  regains stability. In this figure  $\tau = 0.5 > \tau_0^2$ .

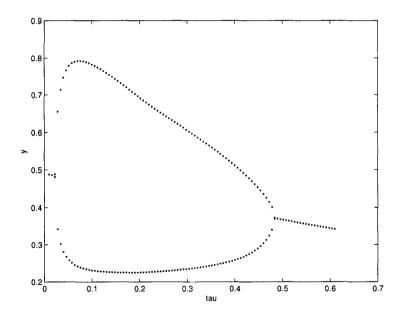


Figure 3.12: Bifurcation diagram as the delay varies.

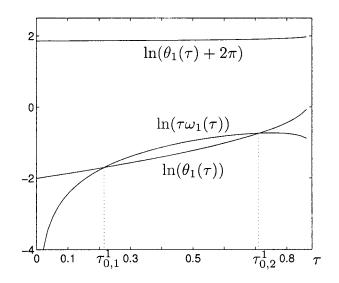


Figure 3.13: Intersections indicate critical values of the delay at which Hopf bifurcations occur.

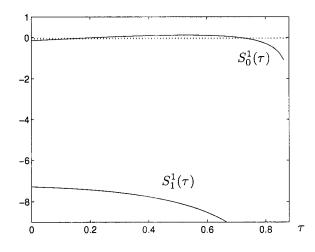


Figure 3.14: Verification of the transversality condition required for Hopf bifurcation.

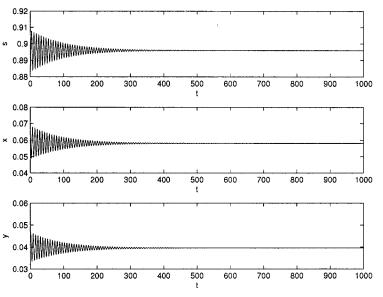


Figure 3.15: Equilibrium  $E_+(\tau)$  is stable when  $\tau = 0.15 < \tau_{0,1}^1$ .

# 3.6 Comparison between the Predator-Prey Model and the Predator-Prey Model in the Chemostat

We studied the classical predator-prey model in Chapter 2 and the corresponding predator-prey model in the chemostat in Chapter 3. Based on our analysis, the dynamics of the two models appear to have some similarities and some difference.

For both models, we linearized the system and evaluated the characteristic equation at the interior equilibrium. The amplitude of any possible pure imaginary root is a solution of a quadratic equation in  $\omega^2$  (see (2.3.13) for the classical Gause type predator-prey model and (3.4.18) for the predator-prey model in the chemostat). For the classical Gause type predator-prey model, (2.3.13) has at most one positive root,  $\omega_{+}(\tau)$  defined in (2.3.15). However for the predator-prey model in the

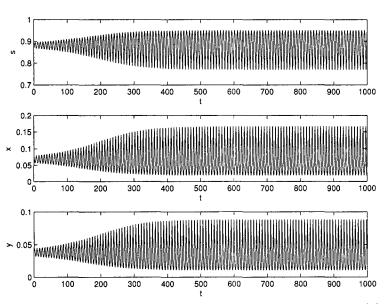


Figure 3.16: Time series of a solution with constant initial data s(0) = 0.87, x(t) = 0.077, and y(t) = 0.048 for  $t \in [-0.3, 0]$ , that approaches a stable periodic solution as time increases. In this figure,  $\tau = 0.3$ .

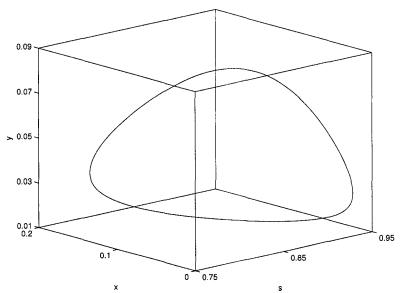


Figure 3.17: The attracting periodic solution shown in Figure 3.16 in the phase space for  $\tau = 0.3 > \tau_{0,1}^1$ .

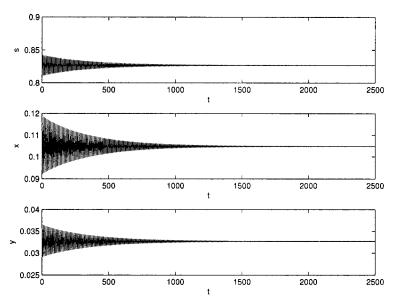


Figure 3.18: Periodic solution disappears and  $E_{+}(\tau)$  regains stability for  $\tau > \tau_0^2$ . In this figure,  $\tau = 0.74$ .

chemostat, (3.4.18) can have two positive roots  $\omega_1(\tau)$  and  $\omega_2(\tau)$  defined in (3.4.19) and (3.4.20), respectively. Theorem 2.9 in Chapter 2 gives conditions for Hopf bifurcations related to  $\omega_+(\tau)$ . Theorem 3.13. Case 2) in this chapter gives conditions for Hopf bifurcations related to  $\omega_1(\tau)$ . But Theorem 3.13. Case 1) is a result about Hopf bifurcations that involves both  $\omega_1(\tau)$  and  $\omega_2(\tau)$ . This does not occur in the Gause type predator-prey model.

However the effect of delays on the dynamics of the Gause type predator-prey model and predator-prey model in the chemostat do have some similarities. The interior equilibrium in both models is stable at delay equal to 0 and loses stability as delay increases. It regains stability by a secondary Hopf bifurcation at a larger delay value and remains stable until the critical value of the delay is reached and eventually the interior equilibrium disappears.

In Chapter 2, Figure 2.12 shows that the Gause type predator-prey model has other interesting bifurcations besides the Hopf bifurcation. We did not see evidence for these other bifurcations in the predator-prey model in the chemostat for the parameters used (see Figure 3.12). In an attempt to find these interesting dynamics, we rescaled the predator-prey model in the chemostat and chose parameters so that without predators, the dynamics of the prey were almost identical in both models. Introducing predators with delay in exactly the same way in both models, we expected that the dynamics of the two models would be the same, in the sense that they would have the same sequence of bifurcation as the delay  $\tau$  was increased.

Figure 2.12 was obtained by using model (2.1.1) with parameter m = 1, r = 10, Y = 0.2, s = 0.2, and k = 30. For initial data, we used x(t) = 1.6 and y(t) = 0.4 for  $t \in [-\tau, 0]$ . By the change of variable (2.2.2), we have

$$\breve{s} = 0.02, \ \breve{Y} = 0.6, \ \breve{x}(\breve{t} - \breve{\tau}) = 0.053, \ \breve{y}(\breve{t} - \breve{\tau}) = 0.04.$$

Noting that (2.2.3) is the scaled model omitting  $\ddot{}$ , we have

$$\begin{cases} \dot{x}(t) = x(t)(1 - x(t)) - y(t)x(t), \\ \dot{y}(t) = -0.02y(t) + 0.6e^{-s\tau}y(t - \tau)x(t - \tau), \\ x(\theta) = 0.053, \quad y(\theta) = 0.04 \quad \text{for} \quad \theta \in [-\tau, 0] \end{cases}$$

To make the dynamics of the predator-prey model in the chemostat comparable with the Gause type predator prey model as described above, we introduced the following change of variables

$$\hat{t} = D_0 t, \qquad \hat{s}(\hat{t}) = \frac{s(t)}{s^0}, \qquad \hat{x}(\hat{t}) = \frac{\alpha x(t)}{D_0 \eta}, \qquad \hat{y}(\hat{t}) = \frac{ky(t)}{D_0 \xi},$$

$$\hat{\tau} = D_0 \tau, \qquad \hat{D} = \frac{D}{D_0}, \qquad \hat{\Delta} = \frac{\Delta}{D_0}, \qquad \hat{k} = \frac{k\eta}{\alpha}, \qquad \hat{\alpha} = \frac{\alpha s^0}{D_0}.$$

In (3.6.32), choose D = 1,  $\Delta = 0.02$ , k = 0.6 and  $\alpha = 2$ . Taking s(0) = 0.5and the same initial data for x and y gives

$$\dot{s}(t) = 1 - s(t) - x(t)s(t),$$

$$\dot{x}(t) = x(t)(-1 + 2s(t)) - y(t)x(t),$$

$$\dot{y}(t) = -0.02y(t) + 0.6e^{-\Delta\tau}y(t - \tau)x(t - \tau),$$

$$s(0) = 0.5, \quad x(\theta) = 0.053, \quad y(\theta) = 0.04 \quad \text{for} \quad \theta \in [-\tau, 0].$$
(3.6.33)

We chose D and  $\alpha$  so that without predation the prey in the chemostat grows similarly as the prey in the predator-prey model.

The maximum delay which guarantees the coexistence equilibrium of system (3.6.33) exists is  $\tau \approx 170.05$ . We used MATLAB to produce the bifurcation diagram as  $\tau$  was increased from 0 to 170.05 (see Figure 3.19). The bifurcation diagram clearly shows the effect of varying the delay on the predator-prey model in the chemostat gives a less complicated sequence of bifurcations than for the Gause type predator-prey model. Other interesting bifurcations in between the two Hopf bifurcations do not occur for the predator-prey model in the chemostat as they do for the classical Gause type predator-prey model.

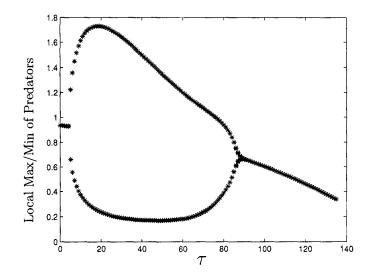


Figure 3.19: Bifurcation diagram as the delay varies.

#### Chapter 4

# Pure Imaginary Roots of General $2^{nd}$ Order Transcendental Equations

In this chapter we generalize the method in Chapter 3. For a delay differential equation, its stability is related to the distribution of eigenvalues of its characteristic equation. A system of delay differential equations can result in a characteristic equation of the special form

$$P(\lambda) = \lambda^2 + p(\tau)\lambda + (q(\tau)\lambda + c(\tau))e^{-\lambda\tau} + \alpha(\tau) = 0.$$
(4.0.1)

For example, Cooke, Elderkin, and Huang [12], Kuang and So [37], Gourley and Kuang [21] considered models for which the analysis required study a characteristic equation of this form. If  $q(\tau) = c(\tau) = 0$ , then (4.0.1) is a quadratic equation in  $\lambda$ , and the roots are easily determined. If  $q(\tau)$  or  $c(\tau)$  is nonzero, (4.0.1) is a transcendental equation and it is much hard to find its roots analytically. We assume that both  $c(\tau)$  and  $q(\tau)$  are not equal to zero simultaneously and investigate when (4.0.1) has pure imaginary roots. This is of importance, since the existence of a pair of pure imaginary roots is a necessary condition for Hopf bifurcations.

As before, to determine whether (4.0.1) has pure imaginary roots, assume that  $\lambda = i\omega$  ( $\omega > 0$ ) is a root of (4.0.1). Then

$$P(i\omega) = -\omega^2 + ip(\tau)\omega + (iq(\tau)\omega + c(\tau))e^{-i\omega\tau} + \alpha(\tau) = 0.$$

Using Euler's identity  $e^{i\theta} = \cos \theta + i \sin \theta$ ,

$$-\omega^2 + \alpha(\tau) + q(\tau)\omega\sin(\omega\tau) + c(\tau)\cos(\omega\tau) + i\left(p(\tau)\omega + q(\tau)\omega\cos(\omega\tau) - c(\tau)\sin(\omega\tau)\right) = 0.$$

Separating the real and imaginary parts,

$$c(\tau)\cos(\omega\tau) + q(\tau)\omega\sin(\omega\tau) = \omega^2 - \alpha(\tau),$$
  

$$c(\tau)\sin(\omega\tau) - q(\tau)\omega\cos(\omega\tau) = p(\tau)\omega.$$
(4.0.2)

Solving for  $\cos(\omega \tau)$  and  $\sin(\omega \tau)$ , we obtain

$$\begin{cases} \sin(\omega\tau) = \frac{c(\tau)(p(\tau)\omega) + q(\tau)\omega(\omega^2 - \alpha(\tau))}{c^2(\tau) + q^2(\tau)\omega^2}, \\ \cos(\omega\tau) = \frac{c(\tau)(\omega^2 - \alpha(\tau)) + q(\tau)\omega(-p(\tau)\omega)}{c^2(\tau) + q^2(\tau)\omega^2}. \end{cases}$$
(4.0.3)

Note that if one can find  $(\tau, \omega)$  satisfying (4.0.3), then (4.0.1) will have a pair of pure imaginary roots  $\pm i\omega$  at  $\tau$ . Our goal in the remaining part of this chapter is to find solutions of (4.0.3).

Recalling that  $\sin^2(\omega \tau) + \cos^2(\omega \tau) = 1$ , squaring both sides of the equations in (4.0.3), and adding them, and rearranging gives

$$\omega^4 + (p^2(\tau) - q^2(\tau) - 2\alpha(\tau))\omega^2 + \alpha^2(\tau) - c^2(\tau) = 0.$$
(4.0.4)

Solving for potential positive roots of (4.0.4), we obtain,

$$\omega_1(\tau) = \sqrt{\frac{1}{2} \left( q^2(\tau) - p^2(\tau) + 2\alpha(\tau) + \sqrt{(q^2(\tau) - p^2(\tau) + 2\alpha(\tau))^2 - 4(\alpha^2(\tau) - c^2(\tau))} \right)}$$
(4.0.5)

and

$$\omega_2(\tau) = \sqrt{\frac{1}{2} \left( q^2(\tau) - p^2(\tau) + 2\alpha(\tau) - \sqrt{(q^2(\tau) - p^2(\tau) + 2\alpha(\tau))^2 - 4(\alpha^2(\tau) - c^2(\tau))} \right)}$$
(4.0.6)

Beretta and Kuang obtained (4.0.4) in [5], They were also interested in whether (4.0.1) has pure imaginary roots. In their method, they assume that  $\theta$  is a solution of (4.0.3) with  $\theta$  in the position of  $\omega\tau$  at the left hand side of (4.0.3). However (4.0.3) may or may not have solutions. Here, we show how to determine whether or not such a solution  $\theta$  exists based on conditions in terms of  $p(\tau)$ ,  $q(\tau)$ ,  $c(\tau)$ , and  $\alpha(\tau)$  and when it does, we give out explicit expression for  $\theta$ .

**Remark.** Note that a solution of (4.0.3) must satisfy (4.0.4), but the converse need not be true, since (4.0.4) is obtained by squaring and adding the equations in (4.0.3).

Define conditions  $(H_1)$  and  $(H_2)$  as follows:

$$(H_1) \begin{cases} q^2(\tau) - p^2(\tau) + 2\alpha(\tau) > 0, \\ \alpha^2(\tau) - c^2(\tau) > 0, \\ (q^2(\tau) - p^2(\tau) + 2\alpha(\tau))^2 - 4(\alpha^2(\tau) - c^2(\tau)) \ge 0. \end{cases}$$
  
$$(H_2) \quad \alpha^2(\tau) - c^2(\tau) < 0, \quad \text{or} \quad \alpha^2(\tau) - c^2(\tau) = 0 \quad \& \quad q^2(\tau) - p^2(\tau) + 2\alpha(\tau) > 0. \end{cases}$$

**Lemma 4.1.** If  $(H_1)$  holds for all  $\tau$  in some interval I, then (4.0.4) has two positive roots  $\omega_1(\tau) \ge \omega_2(\tau)$  for all  $\tau \in I$  with  $\omega_1(\tau) > \omega_2(\tau)$  when all the inequalities in  $(H_1)$  are strict. If  $(H_2)$  holds for all  $\tau$  in some interval I, then (4.0.4) has only one positive root,  $\omega_1(\tau)$  for all  $\tau \in I$ . If no interval exists where either  $(H_1)$  or  $(H_2)$ holds, then there are no positive real roots of (4.0.4). **Corollary 4.2.** A necessary condition for Hopf bifurcations is that there exists some interval I such that for all  $\tau \in I$ ,  $(q^2(\tau) - p^2(\tau) + 2\alpha(\tau))^2 - 4(\alpha^2(\tau) - c^2(\tau)) \ge 0$ , and if  $\alpha^2(\tau) - c^2(\tau) \le 0$ , then  $q^2(\tau) - p^2(\tau) + 2\alpha(\tau) > 0$ .

To simplify notation, denote the right hand sides of (4.0.3) as follows

$$h_1(\omega,\tau) = \frac{c(\tau)(p(\tau)\omega) + q(\tau)\omega(\omega^2 - \alpha(\tau))}{c^2(\tau) + q^2(\tau)\omega^2}, \qquad \omega \ge 0, \tag{4.0.7}$$

$$h_2(\omega,\tau) = \frac{c(\tau)(\omega^2 - \alpha(\tau)) + q(\tau)\omega(-p(\tau)\omega)}{c^2(\tau) + q^2(\tau)\omega^2}, \qquad \omega \ge 0.$$
(4.0.8)

In most cases, it is a challenge to seek solutions of (4.0.3) directly. Instead, in what follows, we consider the associated systems of the form

$$\begin{cases} \sin(\theta(\tau) + 2k\pi) = h_1(\omega_i(\tau), \tau), \\ \cos(\theta(\tau) + 2k\pi) = h_2(\omega_i(\tau), \tau), \end{cases} \quad i = 1, 2, \quad k = 0, 1, 2, \dots \quad (4.0.9)$$

where  $\omega_i(\tau)$  given by (4.0.5) for i = 1 or (4.0.6) for i = 2.

**Theorem 4.3.** If  $\theta(\tau)$  satisfies (4.0.9) and  $\theta(\tau) + 2k\pi$  (k nonnegative integer) intersects  $\tau \omega_i(\tau)$  at some  $\bar{\tau}_i$ , then  $(\bar{\tau}_i, \omega_i(\bar{\tau}_i))$  will be a solution of (4.0.3), and hence, (4.0.1) has a pair of pure imaginary roots  $\pm i\omega_i(\bar{\tau}_i)$ .

Now we start to investigate when (4.0.9) has a solution  $\theta(\tau)$ . To avoid zero denominators in (5.0.7) and (5.0.8), we consider the two cases  $c(\tau) \neq 0$ , and  $c(\tau) = 0$  but  $q(\tau) \neq 0$  separately.

#### 4.1 The case $c(\tau) \neq 0$ .

For a fixed  $\tau$ , assume that  $\omega_i(\tau)$  is positive (i = 1, 2). By (4.0.7) and (4.0.8) noting that  $\omega_i(\tau)$  is a root of (4.0.4), we obtain  $h_1^2(\omega_i(\tau), \tau) + h_2^2(\omega_i(\tau), \tau) = 1$ . Define functions

$$\theta_i(\tau) = \arccos(h_2(\omega_i(\tau), \tau)), \quad i = 1, 2.$$
(4.1.10)

It follows that  $\theta_i(\tau) \in [0, \pi]$ . If  $h_1(\omega_i(\tau), \tau) \ge 0$ , then  $\sin(\theta_i(\tau) + 2k\pi) = h_1(\omega_i(\tau), \tau)$ . Hence  $\theta_i(\tau)$  satisfies (4.0.9). If  $h_1(\omega_i(\tau), \tau) < 0$ , then

$$\cos(2\pi - \theta_i(\tau) + 2k\pi) = \cos(\theta_i(\tau)) = h_2(\omega_i(\tau), \tau)$$

and

$$\sin(2\pi - \theta_i(\tau) + 2k\pi) = -\sqrt{1 - \cos^2(2\pi - \theta_i(\tau) + 2k\pi)} = h_1(\omega_i(\tau), \tau).$$

Therefore  $2\pi - \theta_i(\tau)$  satisfies (4.0.9).

**Theorem 4.4.** Assume that  $\omega_i(\tau)$  is positive (i = 1, 2). Consider the following conditions:

$$\begin{array}{lll} (i) & q(\tau) > 0 & and & \alpha(\tau)q(\tau) - c(\tau)p(\tau) < 0. \\ (ii) & q(\tau) < 0, & \alpha(\tau)q(\tau) - c(\tau)p(\tau) < 0, & and & \omega_i^2(\tau) < \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}. \\ (iii) & q(\tau) > 0, & \alpha(\tau)q(\tau) - c(\tau)p(\tau) > 0, & and & \omega_i^2(\tau) > \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}. \\ (iv.a) & q(\tau) = 0 & and & \frac{p(\tau)}{c(\tau)} \ge 0. \\ (iv.b) & q(\tau) = 0 & and & \frac{p(\tau)}{c(\tau)} < 0. \end{array}$$

If one of (i),(ii),(iii), or (iv.a) holds, then  $\theta_i(\tau) \in [0,\pi]$  and satisfies (4.0.9). If (iv.b) holds, then  $2\pi - \theta_i(\tau) \in [\pi, 2\pi]$  and satisfies (4.0.9).

**Proof.** For any fixed  $\tau$ , assume  $\omega_i(\tau)$  is positive. From (4.0.7) and (4.0.8)

$$\begin{split} & h_1^2(\omega,\tau) + h_2^2(\omega,\tau) \\ &= \frac{c^2(\tau)p^2(\tau)\omega^2 + q^2(\tau)\omega^2(\omega^2 - \alpha(\tau))^2 + 2c(\tau)p(\tau)\omega q(\tau)\omega(\omega^2 - \alpha(\tau))}{(c^2(\tau) + q^2(\tau)\omega^2)^2} \\ &+ \frac{c^2(\tau)(\omega^2 - \alpha(\tau))^2 + q^2(\tau)\omega^2p^2(\tau)\omega^2 - 2c(\tau)p(\tau)\omega q(\tau)\omega(\omega^2 - \alpha(\tau))}{(c^2(\tau) + q^2(\tau)\omega^2)^2} \\ &= \frac{(c^2(\tau) + q^2(\tau)\omega^2)(p^2(\tau)\omega^2 + (\omega^2 - \alpha(\tau))^2)}{(c^2(\tau) + q^2(\tau)\omega^2)^2} \\ &= \frac{p^2(\tau)\omega^2 + (\omega^2 - \alpha(\tau))^2}{c^2(\tau) + q^2(\tau)\omega^2}. \end{split}$$

A rearrangement of (4.0.4), noting that  $\omega_i(\tau)$  is a root gives

$$h_1^2(\omega_i(\tau),\tau) + h_2^2(\omega_i(\tau),\tau) = 1.$$
(4.1.11)

(i) By (4.0.7),  $h_1(0, \tau) = 0$  and  $\lim_{\omega \to +\infty} h_1(\omega, \tau) = +\infty$ . From a straightforward calculation using the assumption that  $q(\tau) > 0$  and  $\alpha(\tau)q(\tau) - c(\tau)p(\tau) < 0$ , it follows that  $\omega = 0$  is the only root of  $h_1(\omega, \tau) = 0$ . Hence,  $h_1(\omega, \tau) > 0$  for any  $\omega > 0$ . For  $\omega_i(\tau) > 0$ , we obtain  $h_1(\omega_i(\tau), \tau) > 0$ . Therefore,  $\theta_i(\tau)$  satisfies (4.0.9).

(ii) By (4.0.7),  $h_1(0,\tau) = 0$  and  $\lim_{\omega \to +\infty} h_1(\omega,\tau) = -\infty$ . By assumption

$$\frac{\partial h_1(\omega,\tau)}{\partial \omega}\Big|_{\omega=0} = -\frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{c^2(\tau)} > 0.$$

Solving  $h_1(z(\tau), \tau) = 0$  for  $z(\tau)$ , we obtain the unique positive root

$$z(\tau) = \sqrt{\frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}}.$$
(4.1.12)

Therefore  $h_1(\omega, \tau) > 0$  for  $\omega \in (0, z(\tau))$  and  $h_1(\omega, \tau) < 0$  for  $\omega \in (z(\tau), +\infty)$  (see Figure 4.1(a)).

From assumption  $\omega_i^2(\tau) < \frac{\alpha(\tau)q(\tau)-c(\tau)p(\tau)}{q(\tau)}$  and (4.1.12), we have  $\omega_i(\tau) < z(\tau)$ . It follows that  $h_1(\omega_i(\tau), \tau) > 0$ . Therefore,  $\theta_i(\tau)$  satisfies (4.0.9).

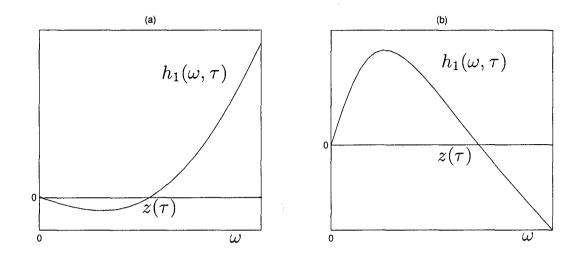


Figure 4.1: A schematic diagram of  $h_1(\omega, \tau)$  for fixed  $\tau$ . (a) Case *(ii)* holds. (b) Case *(iii)* holds.

(*iii*) By (4.0.7),  $h_1(0, \tau) = 0$  and  $\lim_{\omega \to +\infty} h_1(\omega, \tau) = +\infty$ . By assumption

$$\frac{\partial h_1(\omega,\tau)}{\partial \omega}\Big|_{\omega=0} = -\frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{c^2(\tau)} < 0.$$

As in (*ii*),  $z(\tau) = \sqrt{\frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}}$  is the unique positive root of  $h_1(z(\tau), \tau) = 0$ . Therefore  $h_1(\omega, \tau) < 0$  for any  $\omega \in (0, z(\tau) \text{ and } h_1(\omega, \tau) > 0$  for  $\omega \in (z(\tau), +\infty)$ (see Figure 4.1(b)). From assumption  $\omega_i^2(\tau) > \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}$  and (4.1.12), we have  $\omega_i(\tau) > z(\tau)$ . This implies that  $h_1(\omega_i(\tau), \tau) > 0$ . Therefore  $\theta_i(\tau)$  satisfies (4.0.9).

(*iv.a*) Since  $q(\tau) = 0$ , functions  $h_1(\omega, \tau)$  and  $h_2(\omega, \tau)$  reduce to the following simpler form:

$$h_1(\omega,\tau) = \frac{p(\tau)\omega}{c(\tau)}, \qquad h_2(\omega,\tau) = \frac{\omega^2 - \alpha(\tau)}{c(\tau)}.$$

From  $\frac{p(\tau)}{c(\tau)} \ge 0$ , we have  $h_1(\omega, \tau) \ge 0$  for any  $\omega \ge 0$ . For  $\omega_i(\tau) > 0$ , we obtain  $h_1(\omega_1(\tau), \tau) \ge 0$ . Therefore  $\theta_i(\tau)$  satisfies (4.0.9).

(iv.b) Since  $q(\tau) = 0$ , functions  $h_1(\omega, \tau)$  and  $h_2(\omega, \tau)$  have the following

simpler form

$$h_1(\omega, \tau) = \frac{p(\tau)\omega}{c(\tau)}, \qquad h_2(\omega, \tau) = \frac{\omega^2 - \alpha(\tau)}{c(\tau)}.$$

From  $\frac{p(\tau)}{c(\tau)} < 0$ , we have  $h_1(\omega, \tau) < 0$  for any  $\omega \ge 0$ . For  $\omega_i(\tau) > 0$ , we obtain  $h_1(\omega_i(\tau), \tau) < 0$ . It follows that  $2\pi - \theta_i(\tau)$  satisfies (4.0.9). Noting that  $0 \le \theta_i(\tau) \le \pi$ , we obtain  $2\pi - \theta_i(\tau) \in [\pi, 2\pi]$ .

In Theorem 4.4 all of the conditions in (*ii*) and (*iii*) are easy to verify except whether  $\omega_i^2(\tau) < \frac{\alpha(\tau)q(\tau)-c(\tau)p(\tau)}{q(\tau)}$  (or >). For this reason we introduce conditions  $(A_2), (A_3), (A_5)$  and  $(A_6)$ , that may appear more complicated, but are more easily verified. Conditions  $(A_1)$  and  $(A_7)$  are both sufficient conditions ensuring (4.0.9) has no solutions. If  $A_4$  holds the following results does not apply. Instead one can try to apply theorem 4.4 directly.

$$\begin{aligned} (A_1) & -\frac{\alpha(\tau)}{c(\tau)} > 1, \quad \frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)} > 1. \\ (A_2) & -\frac{\alpha(\tau)}{c(\tau)} > 1, \quad \frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)} < 1, \text{ and } \frac{c(\tau)\alpha(\tau) + c^2(\tau)}{c(\tau) - p(\tau)q(\tau) - q^2(\tau)} > \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}. \\ (A_3) & -\frac{\alpha(\tau)}{c(\tau)} < 1, \quad \frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)} > 1, \text{ and } \frac{c(\tau)\alpha(\tau) + c^2(\tau)}{c(\tau) - p(\tau)q(\tau) - q^2(\tau)} < \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}. \\ (A_4) & -1 < -\frac{\alpha(\tau)}{c(\tau)} < 1, \quad -1 < \frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)} < 1. \\ (A_5) & -\frac{\alpha(\tau)}{c(\tau)} > -1, \quad \frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)} < -1, \text{ and } \frac{c(\tau)\alpha(\tau) - c^2(\tau)}{c(\tau) - p(\tau)q(\tau) + q^2(\tau)} < \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}. \\ (A_6) & -\frac{\alpha(\tau)}{c(\tau)} < -1, \quad \frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)} > -1, \text{ and } \frac{c(\tau)\alpha(\tau) - c^2(\tau)}{c(\tau) - p(\tau)q(\tau) + q^2(\tau)} > \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}. \\ (A_7) & -\frac{\alpha(\tau)}{c(\tau)} < -1, \quad \frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)} < -1, \end{aligned}$$

When a positive root  $l(\tau)$ ,  $L(\tau)$  satisfies  $h_2(l(\tau), \tau) = 1$  or  $h_2(L(\tau), \tau) = -1$  respectively, it is unique and given by

$$l(\tau) = \sqrt{\frac{c(\tau)\alpha(\tau) + c^2(\tau)}{c(\tau) - p(\tau)q(\tau) - q^2(\tau)}} \text{ and } L(\tau) = \sqrt{\frac{c(\tau)\alpha(\tau) - c^2(\tau)}{c(\tau) - p(\tau)q(\tau) + q^2(\tau)}}.$$
 (4.1.13)

**Theorem 4.5.** Assume that  $\omega_i(\tau) > 0$ . If either  $(A_3)$  or  $(A_5)$  holds, then  $\omega_i^2(\tau) < \frac{\alpha(\tau)q(\tau)-c(\tau)p(\tau)}{q(\tau)}$ . If either  $(A_2)$  or  $(A_6)$  holds, then  $\omega_i^2(\tau) > \frac{\alpha(\tau)q(\tau)-c(\tau)p(\tau)}{q(\tau)}$ .

**Proof.** For any fixed  $\tau$ . From (4.0.8),

$$h_2(0,\tau) = -\frac{\alpha(\tau)}{c(\tau)}$$
 and  $\lim_{\omega \to \infty} h_2(\omega,\tau) = \frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)}.$  (4.1.14)

First assume  $(A_3)$  holds. From (4.1.14),  $h_2(0, \tau) < 1$  and  $\lim_{\omega \to \infty} h_2(\omega, \tau) > 1$ . There exists a unique  $l(\tau) > 0$  (see (4.1.13)) such that  $h_2(l(\tau), \tau) = 1$ . Therefore  $h_2(\omega, \tau) \leq 1$  for any  $\omega \in [0, l(\tau)]$  and  $h_2(\omega, \tau) > 1$  for  $\omega > l(\tau)$  (see Figure 4.2(b)). The last inequality of assumption that  $(A_3)$  implies that  $l(\tau) < z(\tau)$  (see (4.1.12)). By (4.1.11), we have  $-1 \leq h_2(\omega_i(\tau), \tau) \leq 1$ , which implies that  $\omega_i(\tau) \leq l(\tau)$ . Therefore

$$\omega_i^2(\tau) \leqslant l^2(\tau) < z^2(\tau) = \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}.$$

Suppose (A<sub>5</sub>) holds. By (4.1.14),  $h_2(0,\tau) > -1$  and  $\lim_{\omega \to \infty} h_2(\omega,\tau) < -1$ .

There exists a unique  $L(\tau) > 0$  (see (4.1.13)) such that  $h_2(L(\tau), \tau) = -1$ . Hence  $h_2(\omega, \tau) \ge -1$  for any  $\omega \in [0, L(\tau)]$  and  $h_2(\omega, \tau) < -1$  for  $\omega > L(\tau)$  (see Figure 4.2(c)). By the last inequality of  $(A_5)$ ,  $L(\tau) < z(\tau)$ . By (4.1.11), we have  $-1 \le h_2(\omega_i(\tau), \tau) \le 1$ , which implies that  $\omega_i(\tau) \le L(\tau)$ . Therefore

$$\omega_i^2(\tau) \leqslant L(\tau) < z^2(\tau) = \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}.$$

Assume  $(A_2)$  holds. By (4.1.14),  $h_2(0,\tau) > 1$  and  $\lim_{\omega\to\infty} h_2(\omega,\tau) < 1$ . There exists a unique  $l(\tau) > 0$  such that  $h_2(l(\tau),\tau) = 1$ . Hence  $h_2(\omega,\tau) \leq 1$  for any  $\omega \in (l(\tau), +\infty)$  and  $h_2(\omega,\tau) > 1$  for  $\omega \in (0, l(\tau))$  (see Figure 4.2(a)). By the last inequality of  $(A_2)$ ,  $l(\tau) > z(\tau)$ . By (4.1.11), we have  $-1 \leq h_2(\omega_i(\tau),\tau) \leq 1$ , which implies that  $\omega_i(\tau) \geq l(\tau)$ . Therefore

$$\omega_i^2(\tau) \geqslant l^2(\tau) > z^2(\tau) = \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}$$

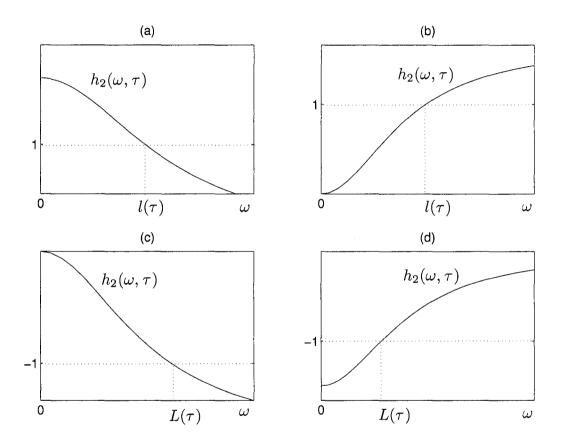


Figure 4.2: A schematic diagram of  $h_2(\omega, \tau)$  for fixed  $\tau$ . (a) The case  $(A_2)$  holds.(b) The case  $(A_3)$  holds.(c) The case  $(A_5)$  holds.(d) The case  $(A_6)$  holds.

Suppose  $(A_6)$  holds. From (4.1.14),  $h_2(0,\tau) < -1$  and  $\lim_{\omega \to \infty} h_2(\omega,\tau) > -1$ . There exists a unique  $L(\tau) > 0$  such that  $h_2(L(\tau),\tau) = -1$ . Hence  $h_2(\omega,\tau) \ge -1$ for any  $\omega \in (L(\tau), +\infty)$  and  $h_2(\omega,\tau) < -1$  for  $\omega \in (0, L(\tau))$  (see Figure 4.2(d)). By the last inequality of  $(A_6)$ ,  $l(\tau) > z(\tau)$ . By (4.1.11), we have  $-1 \le h_2(\omega_i(\tau),\tau) \le 1$ , which implies that  $\omega_i(\tau) \ge l(\tau)$ . Therefore

$$\omega_i^2(\tau) \geqslant l^2(\tau) > z^2(\tau) = \frac{\alpha(\tau)q(\tau) - c(\tau)p(\tau)}{q(\tau)}.$$

Note that if the last inequality in assumptions  $(A_2)$ ,  $(A_3)$ ,  $(A_5)$ , or  $(A_6)$  is violated, our method breaks down because the relative relationship between  $\omega_i^2(\tau)$  and  $\frac{\alpha(\tau)q(\tau)-c(\tau)p(\tau)}{q(\tau)}$  is uncertain.

**Theorem 4.6.** If either  $(A_1)$  or  $(A_7)$  holds, then system (4.0.9) has no solutions.

**Proof.** For any fixed  $\tau$ . Assume  $(A_1)$  holds. Multiplying  $c^2(\tau)$  on both sides of  $-\frac{\alpha(\tau)}{c(\tau)} > 1$  gives  $c(\tau)\alpha(\tau) + c^2(\tau) < 0$ . From the second inequality of  $(A_1)$ , we have  $c(\tau) - p(\tau)q(\tau) - q^2(\tau) > 0$ . Hence  $l(\tau) < 0$  (see (4.1.13) for the definition of  $l(\tau)$ ). Then  $h_2(\omega, \tau) = 1$  has no positive root. Hence,  $h_2(\omega, \tau) > 1$  for any  $\omega > 0$ . Therefore the equation for  $\cos(\theta + 2\pi)$  in (4.0.9) has no solutions.

Assume  $(A_7)$  holds. Multiplying  $c^2(\tau)$  on both sides of  $-\frac{\alpha(\tau)}{c(\tau)} < -1$  gives  $c(\tau)\alpha(\tau) - c^2(\tau) > 0$ . From  $\frac{c(\tau) - p(\tau)q(\tau)}{q^2(\tau)} < -1$ , we have  $c(\tau) - p(\tau)q(\tau) + q^2(\tau) > 0$ . Hence  $L(\tau) < 0$  (see (4.1.13) for the definition of  $L(\tau)$ ). We have  $h_2(\omega, \tau) < -1$  for any  $\omega > 0$ . Again, the equation for  $\cos(\theta + 2\pi)$  in (4.0.9) has no solutions. The conclusion follows.

**Theorem 4.7.** Assume that  $\omega_i(\tau) > 0$  and  $\theta_i(\tau)$  is a solution of (4.0.9) for  $\tau \in I_i$ , where  $I_i$  is a closed interval including 0. Let  $M_i = \max_{\tau \in I_i} \tau \omega_i(\tau)$ . If  $(2n+1)\pi < 0$   $M_i < 2(n+1)\pi$ , then  $\theta_i(\tau) + 2k\pi$  and  $\tau \omega_i(\tau)$  have at least one intersection, where  $1 \leq k \leq n$ , and n = 1, 2, ...

**Proof.** By (4.1.10),  $\theta_i(\tau) \in [0, \pi]$ . Therefore  $\theta_i(\tau) + 2k\pi \in [2k\pi, (2k+1)\pi]$ . Since  $0 \in I_i$ , we obtain  $\min_{\tau \in I_i} \tau \omega_i(\tau) = 0 < \theta_i(\tau) + 2k\pi$ . If  $(2n+1)\pi < M_i < 2(n+1)\pi$ , noting  $1 \leq k \leq n$ , we have  $(2k+1)\pi < M_i$ . This implies that  $\max_{\tau \in I_i} \tau \omega_i(\tau) > \theta_i(\tau) + 2k\pi$ . By the Mean Value Theorem, the conclusion follows.  $\Box$ 

Later in section 4.3, we provide an application where we apply theorem 4.7 and define interval  $I_i$  explicitly guaranteeing that  $\theta_i(\tau) + 2k\pi$  and  $\tau\omega_i(\tau)$  have at least one intersection in the interval.

#### 4.2 The case $c(\tau) = 0$ and $q(\tau) \neq 0$ .

When  $c(\tau) = 0$ , in Theorem 4.4, the proof for the case (*ii*) or (*iii*) fails, since the proof involves the derivative of  $h_1(\omega, \tau)$  at  $\omega = 0$  and the derivative has  $c(\tau)$  as a denominator. Also cases (*iv.a*) and (*iv.b*) do not work since again a denominator is equal to  $c(\tau)$ . Similarly conditions  $(A_1) - (A_7)$  are no longer defined. In this section we consider  $c(\tau) = 0$ . Note that this case is simpler and some of the proofs in the proceeding section still work, even if  $c(\tau) = 0$ .

If  $c(\tau) = 0$ , (4.0.3) reduces to the simpler form

$$\begin{cases} \sin(\omega\tau) = \frac{\omega^2 - \alpha(\tau)}{q(\tau)\omega}, \\ \cos(\omega\tau) = \frac{-p(\tau)}{q(\tau)}. \end{cases}$$
(4.2.15)

This results in  $h_1(\omega, \tau)$  and  $h_2(\omega, \tau)$  are simpler

$$h_1(\omega,\tau) = \frac{\omega^2 - \alpha(\tau)}{q(\tau)\omega}, \qquad h_2(\tau) = \frac{-p(\tau)}{q(\tau)} \qquad \text{for} \qquad \omega > 0.$$
(4.2.16)

Note that  $h_2(\omega, \tau)$  does not depend explicitly on  $\omega$  and can be considered as a function of  $\tau$  alone,  $h_2(\tau)$ . Since  $\omega$  is a factor in the denominator of  $h_1(\omega, \tau)$ , in this section, we consider  $h_1(\omega, \tau)$  and  $h_2(\tau)$  for  $\omega > 0$ . Define

$$\theta(\tau) = \arccos(h_2(\tau)) \text{ for } h_2(\tau) \in [-1, 1],$$
 (4.2.17)

and consider the associated system

$$\begin{cases} \sin(\theta + 2\pi) = \frac{\omega^2 - \alpha(\tau)}{q(\tau)\omega}, \\ \cos(\theta + 2\pi) = \frac{-p(\tau)}{q(\tau)}. \end{cases}$$
(4.2.18)

**Theorem 4.8.** Consider system (4.2.18)

(i) 
$$\alpha(\tau) = 0$$
,  $q^{2}(\tau) - p^{2}(\tau) > 0$ , and  $q(\tau) > 0$ .  
(ii)  $\alpha(\tau) < 0$ ,  $q^{2}(\tau) - p^{2}(\tau) + 4\alpha(\tau) > 0$ , and  $q(\tau) > 0$ .  
(iii)  $\alpha(\tau) > 0$ ,  $q^{2}(\tau) - p^{2}(\tau) > 0$ ,  $q(\tau) > 0$ , and  $\omega_{i}(\tau) > \sqrt{\alpha(\tau)}$ .  
(iv)  $\alpha(\tau) > 0$ ,  $q^{2}(\tau) - p^{2}(\tau) > 0$ ,  $q(\tau) < 0$ , and  $\omega_{i}(\tau) < \sqrt{\alpha(\tau)}$ .

If (i) holds, then (H<sub>2</sub>) holds and  $\theta(\tau) \in (0, \pi]$  satisfies (4.2.18) with  $\omega = \omega_1(\tau)$ . If one of (ii), (iii), or (iv) holds, then (H<sub>1</sub>) holds and  $\theta(\tau) \in (0, \pi]$  satisfies (4.2.18) with  $\omega = \omega_i(\tau) > 0$  (i = 1, 2).

**Proof.** For any fixed  $\tau$ .

(*i*) From  $c(\tau) = 0$ ,  $\alpha(\tau) = 0$  and  $q^2(\tau) - p^2(\tau) > 0$ , it follows that  $(H_2)$  holds. By Lemma 4.1,  $\omega_1(\tau)$  is positive, but  $\omega_2(\tau)$  is not positive. By (4.1.11), we have  $-1 \leq h_2(\omega_1(\tau), \tau) \leq 1$ . Then  $\theta(\tau)$  is defined and  $0 \leq \theta(\tau) \leq \pi$ . >From  $\omega_1(\tau) > 0$ and  $q(\tau) > 0$ , we obtain  $h_1(\omega_1(\tau), \tau) = \frac{\omega_1(\tau)}{q(\tau)} > 0$ . Again by (4.1.11),

$$h_1(\omega_1(\tau), \tau) = \sqrt{1 - h_2^2(\omega_1(\tau), \tau)}.$$

Since  $\cos(\theta(\tau) + 2k\pi) = h_2(\tau)$ ,  $\sin(\theta(\tau) + 2k\pi) = h_1(\omega_1(\tau), \tau)$ , which implies that  $\theta(\tau)$  satisfies (4.2.18).

(*ii*) By  $c(\tau) = 0$ ,  $\alpha(\tau) < 0$ , and  $q^2(\tau) - p^2(\tau) + 4\alpha(\tau) > 0$ , it follows that  $(H_1)$  holds. By Lemma 4.1, both roots  $\omega_i(\tau)$  are positive (i = 1, 2). As in (*i*),  $\theta(\tau)$  is defined and  $0 \leq \theta(\tau) \leq \pi$ . Since  $\alpha(\tau) < 0$  and  $q(\tau) > 0$ , function  $h_1(\omega_1(\tau), \tau) = \frac{\omega_1^2(\tau) - \alpha(\tau)}{q(\tau)\omega_1(\tau)} > 0$ . The rest of the proof is similar to (*i*).

(*iii*) From  $c(\tau) = 0$ ,  $\alpha(\tau) > 0$ , and  $q^2(\tau) - p^2(\tau) > 0$ , it follows that  $(H_1)$  holds and so  $\omega_i(\tau)$  is positive (i=1,2). As in (i),  $\theta(\tau)$  is defined and  $0 \leq \theta(\tau) \leq \pi$ . Since  $q(\tau) > 0$  and  $\omega_i(\tau) > \sqrt{\alpha(\tau)}$ ,  $h_1(\omega_i(\tau), \tau) > 0$ . The rest of the proof is similar to (i).

1.(iv) Conditions  $c(\tau) = 0$ ,  $\alpha(\tau) > 0$ , and  $q^2(\tau) - p^2(\tau) > 0$  imply that  $(H_1)$ holds and so  $\omega_i(\tau)$  is positive. Since  $q(\tau) < 0$  and  $\omega_i(\tau) < \sqrt{\alpha(\tau)}$ ,  $h_1(\omega_i(\tau), \tau) > 0$ . The rest of the proof is similar to (i).

To prove that  $\theta(\tau) \neq 0$ , we use the method of contradiction. Suppose that  $\theta(\tau) = 0$  for some  $\tau$ . By (4.2.17),  $h_2(\tau) = 1$ . From (4.2.16), we have  $q^2(\tau) - p^2(\tau) = 0$ . This contradicts  $q^2(\tau) - p^2(\tau) > 0$  in (i), (iii), or (iv). For (ii),  $\alpha(\tau) < 0$  and  $q^2(\tau) - p^2(\tau) + 4\alpha(\tau) > 0$  also implies that  $q^2(\tau) - p^2(\tau) > 0$ , another contradiction. Therefore  $\theta(\tau) \in (0, \pi]$ .

**Theorem 4.9.** Assume that  $\omega_i(\tau) > 0$  and  $\theta(\tau)$  is a solution of (4.2.18) for  $\tau \in I_i$ , where  $I_i$  is a closed interval including 0. Let  $M_i = \max_{\tau \in I_i} \tau \omega_i(\tau)$ . If  $(2n+1)\pi < 0$   $M_i < 2(n+1)\pi$ , there is at least one intersection of  $\theta(\tau) + 2k\pi$  and  $\tau\omega_i(\tau)$ , where  $1 \leq k \leq n$ , and n = 1, 2, ...

#### 4.3 Application

In this section, we apply our analytical results about (4.0.1) to single patch in the model studied in Brauer, van den Driessche, and Wang [6]:

$$\begin{cases} \dot{S}(t) = A - dS(t) - \beta S(t)I(t) + \gamma e^{-d\tau}I(t-\tau), \\ \dot{I}(t) = \beta S(t)I(t) - (\gamma + \epsilon + d)I(t), \\ \dot{R}(t) = \gamma I(t) - \gamma e^{-d\tau}I(t-\tau) - dR(t). \end{cases}$$
(4.3.19)

>From [6], we know if  $R_0 = \frac{A\beta}{d(\gamma+\epsilon+d)} > 1$ , model (4.3.19) has a unique endemic equilibrium  $E^* = (S^*, I^*, R^*)$  given by

$$S^* = \frac{A}{dR_0}, \quad I^* = \frac{A(1 - \frac{1}{R_0})}{(1 - e^{-d\tau})\gamma + \epsilon + d}, \quad R^* = \frac{\gamma}{d}(1 - e^{-d\tau})I^*.$$

The characteristic equation of system (4.3.19) at  $E^*$  has the same form as (4.0.1) with

$$p(\tau) = d + \beta I^*, \quad q(\tau) = 0, \quad \alpha(\tau) = \beta(\gamma + \epsilon + d)I^*, \quad c(\tau) = -\gamma\beta I^* e^{-d\tau}.$$
(4.3.20)

Since  $\alpha^2(\tau) - c^2(\tau) > 0$  for any  $\tau$ , only condition  $(H_1)$  is possible. Note that  $c(\tau) \neq 0$ and  $q(\tau) = 0$ , was considered in Section 4.1.

Applying Lemma 4.1, Theorem 4.3, and Theorem 4.4.(iv.b) to model (4.3.19), we obtain the following theorem.

**Theorem 4.10.** Assume that  $R_0 = \frac{A\beta}{d(\gamma+\epsilon+d)} > 1$  and the coefficients of (4.0.1) satisfy (4.3.20). Consider hypotheses,

$$i) \ A\beta - 2d(\gamma + \epsilon + d) \ge 0, \ \frac{4(\gamma + \epsilon + d)(A\beta - d(\gamma + \epsilon + d))}{\gamma^2(\epsilon + d)} < 1, \ \tau \in [0, \frac{-1}{2d} \ln \frac{4(\gamma + \epsilon + d)(A\beta - d(\gamma + \epsilon + d))}{\gamma^2(\epsilon + d)}],$$
$$ii) \ A\beta - d(\gamma + 2\epsilon + 2d) \le 0, \ \frac{4d^2(\gamma + \epsilon + d)^2}{\gamma^2(A\beta - d(\gamma + \epsilon + d))} < 1, \ \tau \in [0, \frac{-1}{2d} \ln \frac{4d^2(\gamma + \epsilon + d)^2}{\gamma^2(A\beta - d(\gamma + \epsilon + d))}].$$

If either i) or ii) holds, condition  $(H_1)$  holds and so both  $\omega_1(\tau)$  and  $\omega_2(\tau)$  are positive. Moreover  $2\pi - \theta_i(\tau) \in [\pi, 2\pi]$  and satisfies (4.0.9). If there exists an integer  $k \ge 0$ such that  $2\pi - \theta_i(\tau) + 2k\pi$  intersects  $\tau \omega_i(\tau)$  at some  $\bar{\tau}_i$ , then (4.0.1) has a pair of pure imaginary roots  $\pm \omega_i(\bar{\tau}_i)$  where i = 1, 2.

#### **Proof.** See Appendix C.

Lemma 3.1 in [6] can be rephrased as follows: If  $q^2(\tau) - p^2(\tau) + 2\alpha(\tau) \ge 2\sqrt{\alpha^2(\tau) - c^2(\tau)}$ , there exists an interval  $(\tau_l, \tau_u)$  such that  $q^2(\tau) - p^2(\tau) + 2\alpha(\tau) > 0$ and  $\Delta(\tau) = (q^2(\tau) - p^2(\tau) + 2\alpha(\tau))^2 - 4(\alpha^2(\tau) - c^2(\tau)) \ge 0$ , where either  $\tau_l = 0$  and  $\Delta(\tau_u) = 0$ , or  $\Delta(\tau_l) = \Delta(\tau_u) = 0$ . This lemma gives the existence of the interval  $[\tau_l, \tau_u]$  on which pure imaginary roots are possible. In Theorem 4.10, we define this interval explicitly in terms of the original parameters of the model. We have  $\tau_l = 0$ ,  $\frac{-1}{2d} \ln \frac{4(\gamma + \epsilon + d)(A\beta - d(\gamma + \epsilon + d))}{\gamma^2(\epsilon + d)} < \tau_u$  for case i, and  $\frac{-1}{2d} \ln \frac{4d^2(\gamma + \epsilon + d)^2}{\gamma^2(A\beta - d(\gamma + \epsilon + d))} < \tau_u$  for case ii.

Lemma 3.2 in [6] states that (4.0.1) has a pair of pure imaginary roots  $\pm \omega_i(\bar{\tau}_i)$ at  $\tau = \bar{\tau}_i$  if and only if there exists an integer k such that the graph of  $\delta_k(\tau)$ intersects  $\tau \omega_i(\tau)$  at some  $\bar{\tau}_i$ , where  $\delta_k(\tau)$  is implicitly defined as the unique solution of  $\cot(\eta) = \frac{h_2(\frac{\eta}{\tau},\tau)}{h_1(\frac{\eta}{\tau},\tau)}$  in the interval  $[2(k-1)\pi, 2k\pi]$  (k = 1, 2, 3...). In Theorem 4.10, though our results also depend on the assumption that  $2\pi - \theta_i(\tau) + 2k\pi$  and  $\tau \omega_i(\tau)$ intersect, the function  $\theta_i(\tau)$  is explicitly defined by (4.1.10). If condition i) or iiholds, from  $2\pi - \theta_i(\tau) \in [\pi, 2\pi]$ . Therefore  $2\pi - \theta_i(\tau) + 2k\pi \in [2k\pi + \pi, 2(k+1)\pi]$ , which implies that pure imaginary roots can only take values in  $[2k\pi + \pi, 2(k+1)\pi]$ .

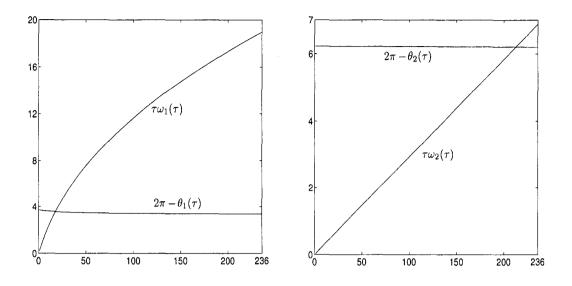


Figure 4.3: Intersection of  $2\pi - \theta_i(\tau)$  and  $\tau \omega_i(\tau)$  for i = 1, 2.

As pointed out in [6], since  $e^{-d\tau} \to 0$  as  $\tau \to \infty$  and  $P(\lambda) = \lambda^2 + (d + \beta I^*) + \beta(\gamma + \epsilon + d)I^* = 0$  with  $I^* = \frac{A(1-1/R_0)}{\gamma+\epsilon+d}$  has all roots with negative real parts, complex eigenvalues with positive real parts of (4.0.1) with coefficients satisfying (4.3.20) cannot enter the right half plane of the complex plane from infinity. The only way that a pair of complex eigenvalues with positive real part can appear is by a pair of roots crossing the imaginary axis. If  $\frac{dRe(\lambda(\tau))}{d\tau}|_{\tau=\bar{\tau}_i} \neq 0$ , by Theorem (A.2), system (4.3.19) has a Hopf bifurcation at  $\tau = \bar{\tau}_i$ .

For numerical simulations, we chose A = 0.045, d = 0.001,  $\epsilon = 0.01$ ,  $\gamma = 0.5$ ,  $\beta = 0.032$ , and hence  $R_0 = 2.64 > 1$ . For such parameters, Theorem 4.10.*i*) can be used, since  $A\beta - 2d(\gamma + \epsilon + d) \approx 0.0003 > 0$ ,  $\frac{4(\gamma + \epsilon + d)(A\beta - d(\gamma + \epsilon + d))}{\gamma^2(\epsilon + d)} = 0.62 < 1$ , and  $\tau \in [0, \frac{-1}{2d} \ln \frac{4(\gamma + \epsilon + d)(A\beta - d(\gamma + \epsilon + d))}{\gamma^2(\epsilon + d)}] \approx [0, 236]$ . Plotting  $\tau \omega_1(\tau)$  and  $2\pi - \theta_1(\tau)$  in one figure (see Figure 4.3 (Left)), we know there is one intersection at  $\bar{\tau}_1 \approx 16$ . Figure 4.3 (Right) indicates that  $2\pi - \theta_1(\tau)$  intersects  $\tau \omega_1(\tau)$  at  $\bar{\tau}_2 \approx 212$ . We chose constant initial data S(t) = 15, I(t) = 2.5, and R(t) = 20 for  $t \in [-\tau, 0]$ . For  $\tau = 15 < \overline{\tau}_1$ , the solution converges to the endemic equilibrium  $E_*$  (see Figure 4.4). For  $\tau = 17 > \overline{\tau}_1$ , numerical simulation indicates there is a stable periodic solution (see Figure 4.5). This confirms that Hopf bifurcation occurs at  $\overline{\tau}_1$  and the endemic equilibrium loss stability resulting a stable periodic solution as  $\tau$  increases past  $\overline{\tau}_1$ . For the bifurcation at  $\tau = \overline{\tau}_2$ . Simulations (not shown) confirm that a secondary Hopf bifurcation occurs resulting in the disappearance of periodic solution.

#### 4.4 Discussion

Beretta and Kuang [5] considered the general characteristic equation with delay dependent coefficients

$$P_n(\lambda,\tau) + Q_m(\lambda,\tau)e^{-\lambda\tau} = 0, \qquad (4.4.21)$$

where n > m are nonnegative integers and

$$P_n(\lambda,\tau) = \sum_{k=0}^n p_k(\tau)\lambda^k, \qquad Q_m(\lambda,\tau) = \sum_{k=0}^m q_k(\tau)\lambda^k.$$

Coefficients  $q_k(\tau)$  and  $p_k(\tau)$  are assumed to be continuously differentiable functions for  $\tau \ge 0$ . Assume that  $\omega(\tau)$  is a positive root of

$$|P_n(i\omega,\tau)|^2 - |Q_m(i\omega,\tau)|^2 = 0, \qquad (4.4.22)$$

and  $\theta(\tau) \in [0, 2\pi]$  is a solution of

$$\begin{cases} \sin \theta(\tau) = Im \left( \frac{P_n((i\omega, \tau))}{Q_m(i\omega, \tau)} \right), \\ \cos \theta(\tau) = -Re \left( \frac{P_n((i\omega, \tau))}{Q_m(i\omega, \tau)} \right). \end{cases}$$
(4.4.23)

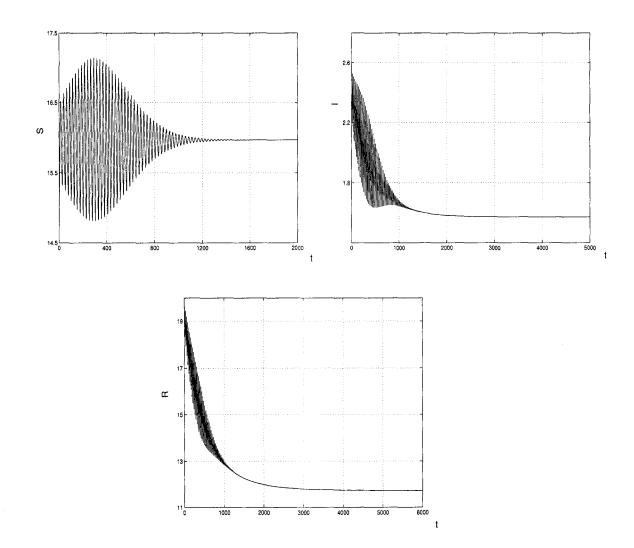


Figure 4.4: Time series showing that the endemic equilibrium is stable for  $\tau = 15$ 

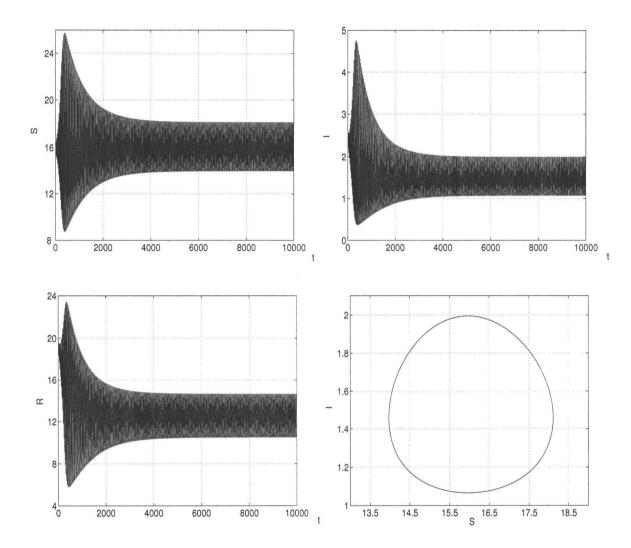


Figure 4.5: There is a stable periodic solution for  $\tau = 17$ .

Define

$$S_l(\tau) = \tau - \frac{\theta(\tau) + 2l\pi}{\omega(\tau)}, \qquad l = 0, 1, 2\cdots.$$

They claimed that if there exists  $\tau^* > 0$  such that  $S_l(\tau_*) = 0$  for some l, then a simple pair of pure imaginary roots  $\pm i\omega(\tau^*)$  of (4.4.21) exists. However, the definition of  $S_l(\tau)$  involves functions  $\omega(\tau)$  and  $\theta(\tau)$ , where  $\omega(\tau)$  has an analytical expression, but  $\theta(\tau)$  is implicitly defined as a solution of (4.4.23). They do not provide analytic criteria to determine whether or not a solution of (4.4.23) exists.

In this chapter we considered (4.4.21) with n = 2 and m = 1, i. e., the second order transcendental equation. In system (4.4.23),

$$Im\left(\frac{P_2((i\omega,\tau))}{Q_1(i\omega,\tau)}\right) = h_1(\omega,\tau), \qquad -Re\left(\frac{P_2((i\omega,\tau))}{Q_1(i\omega,\tau)}\right) = h_2(\omega,\tau) \tag{4.4.24}$$

where  $h_1(\omega, \tau)$  and  $h_2(\omega, \tau)$  are defined in (4.0.7) and (4.0.8), respectively. In this case, to distinguish between two potential positive roots of (4.4.22), we denote them as  $\omega_i(\tau)$  (i = 1, 2), defined in (4.0.5) or (4.0.6). Condition ( $H_1$ ) or ( $H_2$ ) guarantees that either  $\omega_1(\tau)$ , or  $\omega_2(\tau)$ , or both are positive (see Lemma 4.1). We define  $\theta_i(\tau)$ explicitly in (4.1.10) in term of  $\omega_i(\tau)$ . We obtain conditions in term of the coefficients of (4.4.21) that tell when a solution  $\theta_i(\tau)$  of (4.4.23) exists with  $\omega = \omega_i(\tau)$  and show that  $\theta_i(\tau) \in [0, \pi]$  provided it is a solution. These conditions were given in Theorems 4.4, 4.8, and Corollary 4.5. If  $\theta_i(\tau) + 2k\pi$  and  $\tau \omega_i(\tau)$  have intersections, then (4.4.21) has a pair of pure imaginary roots (see Theorem 4.3). But determining whether or not there are intersections is also of importance in applications. We showed that  $\theta_i(\tau) \in [0, \pi]$  and so  $\theta_i(\tau) + 2k\pi \in [2k\pi, 2k\pi + \pi]$ . If the maximum of  $\tau \omega_i(\tau)$  is greater than  $2k\pi + \pi$  and the minimum is less than  $2k\pi$ , then we know that there are intersections of  $\theta_i(\tau) + 2k\pi$  and  $\tau \omega_i(\tau)$ . This is summarized in theorem 4.7. We applied our method to a single patch of the model in [6] and showed that there is a Hopf bifurcations for appropriate parameters. In applications, if all parameters are fixed except the delay  $\tau$ , it would be useful to to be able to determine whether either of conditions  $(H_1)$  or  $(H_2)$  holds, for  $\tau$  in some interval. We have shown that in most cases one can find such an interval explicitly, and if not one can at least find an approximation to that interval. Once this interval is determined, it is easier to search for delay values at which Hopf bifurcations occur, using numerical simulations.

## Appendix A

### **Preliminary Results**

In example 5.1 of Kuang ([35], p.32), he studied the stability of the equilibrium x = 0 of the differential equation

$$\dot{x}(t) = -a(t)x(t) - b(t)x(t - \rho(t)), \tag{A.0.1}$$

where a(t), b(t) and r(t) are bounded continuous functions, and a(t) > 0,  $0 < \rho(t) < \rho_{max}$ , and  $\dot{\rho}(t) < 1$ .

**Lemma A.1.** Considering the scalar equation (A.0.1). If there exists  $\alpha > 0$  such that

$$b^{2}(t) < 4 (a(t) - \alpha) (1 - \rho'(t)) \alpha, \qquad (A.0.2)$$

then the equilibrium x = 0 of (A.0.1) is globally asymptotically stable. If a, b and  $\rho$  are constants, (A.0.2) reduces to

$$b^2 < 4(a-\alpha)\alpha \leqslant a^2,$$

which implies that if |b| < a, then the equilibrium x = 0 is globally asymptotically stable.

To establish the existence of periodic solutions in autonomous delay differential equations, one of the simplest ways is through Hopf Bifurcation. Below is a general Hopf Bifurcation theorem for delay differential equations due to De Oliveira [43]. Before stating the theorem we require some notation.

Consider a one parameter family of neutral delay differential equations:

$$\frac{\mathrm{d}}{\mathrm{d}t}[D(\alpha, x_t) - g(\alpha, x_t)] = L(\alpha, x_t) + f(\alpha, x_t), \quad \alpha \in \mathbb{R},$$
(A.0.3)

where D, L, f, and g are continuously differentiable in  $\alpha$  and  $x_t \in \mathbb{C}([-r, 0], \mathbb{R}^n)$ (r is a constant),  $f(\alpha, 0) = g(\alpha, 0), \partial f(\alpha, 0)/\partial x_t = \partial g(\alpha, 0)/\partial x_t = 0, D(\alpha, x_t)$  and  $L(\alpha, x_t)$  are linear in  $x_t$ , and

$$D(\alpha, x_t) = \sum_{k=0}^{\infty} A_k(\alpha) x(t - r_k(\alpha)) + \int_{-1}^{0} A(\alpha, \theta) x(t + \theta) d\theta,$$
$$L(\alpha, x_t) = \sum_{k=0}^{\infty} A_k(\alpha) x(t - r_k(\alpha)) + \int_{-1}^{0} A(\alpha, \theta) x(t + \theta) d\theta,$$

for  $x_t \in \mathbb{C}([-r, 0], \mathbb{R}^n)$ . Assume  $\alpha \in \mathbb{R}$ , where  $r_0(\alpha) = 0$ ,  $r_k(\alpha) \in (0, 1]$ , and  $A_k(\alpha)$ ,  $B_k(\alpha)$ ,  $A(\alpha, \theta)$ , and  $B(\alpha, \theta)$  satisfy

$$\sum_{k=0}^{\infty} (|A_k(\alpha)| + B_k(\alpha)|) + \int_{-1}^{0} (|A(\alpha,\theta)| + |B(\alpha,\theta)|) \mathrm{d}\theta < \infty.$$

It is easy to see that the characteristic matrix

$$\Delta(\alpha, \lambda) = \lambda D(\alpha, e^{\lambda} I) - L(\alpha, e^{\lambda} I)$$

is continuously differentiable in  $\alpha \in \mathbb{R}$  and  $\Delta(\alpha, \lambda)$  is an entire function of  $\lambda$ . Making the following assumptions on (A.0.3):

 $(S_1)$  There exist constants a > 0, b > 0 such that, for all complex values  $\lambda$ 

such that  $|Re\lambda| < a$  and all  $\alpha \in \mathbb{R}$ , the following inequalities hold:

$$\left| \det \left( \sum_{k=0}^{\infty} A_k(\alpha) e^{-\lambda r_k(\alpha)} \right) \right| \ge b,$$
$$\left| \det \left( \sum_{k=0}^{\infty} A_k(\alpha) e^{-\lambda r_k(\alpha)} + \int_{-1}^{0} A(\alpha, \ \theta) e^{\lambda \theta} \mathrm{d}\theta \right) \right| \ge b.$$

 $(S_2)$  The characteristic equation  $\det \Delta(\alpha, \lambda) = 0$  has, for  $\alpha = \alpha_0$ , a simple purely imaginary root  $\lambda_0 = iv_0, v_0 > 0$ , and no root of  $\det \Delta(\alpha_0, \lambda) = 0$ , other than  $\pm iv_0$ , is an integral multiple of  $\lambda_0$ .

(S<sub>3</sub>) 
$$Re\frac{\partial\lambda(\alpha_0)}{\partial\alpha} \neq 0.$$

Now we are ready to state the Hopf bifurcation Theorem for (A.0.3).

**Theorem A.2.** (Hopf Bifurcation Theorem, see Kuang [35] p.60). In (A.0.3), assume that  $(S_1) - (S_3)$  hold. Then there is an  $\epsilon > 0$  such that, for  $a \in \mathbb{R}$ ,  $|a| \leq \epsilon$ , there are functions  $\alpha(a) \in \mathbb{R}$ ,  $\omega(a) \in \mathbb{R}$ ,  $\alpha(0) = \alpha_0$ ,  $\omega(0) = 2\pi/v_0$ , such that (A.0.3) has an  $\omega(\alpha)$ -periodic solution  $x^*(a)(t)$ , that is continuously differentiable in t, and a with  $x^*(0) = 0$ . Furthermore, for  $|\alpha - \alpha_o| < \epsilon$ ,  $|\omega - (2\pi/v_0)| < \epsilon$ , every  $\omega$ -periodic solution x(t) of (A.0.3) with  $|x(t)| < \epsilon$  must be of this type, except for a translation in phase; that is, there exists  $a \in (-\epsilon, \epsilon)$  and  $b \in \mathbb{R}$  such that  $x(t) = x^*(a)(t+b)$  for all  $t \in \mathbb{R}$ .

In the study of differential equations, one must often estimate a function that satisfies a differential inequality. An important technique to address that problem is the following Comparison Theorem (see [38] or [41]). Before proceeding to the Comparison Theorem, we require the following notation for Dini derivatives:

$$D^{+}u(t) = \lim_{h \to 0^{+}} \sup h^{-1}[u(t+h) - u(t)],$$
  

$$D_{+}u(t) = \lim_{h \to 0^{+}} \inf h^{-1}[u(t+h) - u(t)],$$
  

$$D^{-}u(t) = \lim_{h \to 0^{-}} \sup h^{-1}[u(t+h) - u(t)],$$
  

$$D_{-}u(t) = \lim_{h \to 0^{-}} \inf h^{-1}[u(t+h) - u(t)],$$

where  $u \in |C[(t_0, t_0 + a), \mathbb{R}]$ . Let E be an open set of (t, u) in  $\mathbb{R}^2$  and  $g \in \mathbb{C}(E, \mathbb{R})$ . Consider the scalar initial value differential equation

$$\dot{u}(t) = g(t, u),$$
  $u(t_0) = u_0.$  (A.0.4)

The concepts of maximal and minimal solutions of (A.0.4) are now introduced.

**Definition A.3.** Let v(t) be a solution of the scalar differential equation (A.0.4) on  $[t_0, t_0+a)$ . Then v(t) is said to be a maximal solution of (A.0.4) if, for every solution u(t) of (A.0.4) existing on  $[t_0, t_0 + a)$ , the inequality

$$u(t) \le v(t), \qquad t \in [t_0, t_0 + a)$$
 (A.0.5)

holds. A minimal solution  $\omega(t)$  may be defined similarly by reversing the inequality (A.0.5).

**Theorem A.4.** (Comparison Theorem, Theorem 1.4.1 in [38], p.15) Let E be an open set of (t, u) in  $\mathbb{R}^2$  and  $g \in \mathbb{C}(E, \mathbb{R})$ . Suppose that  $[t_0, t_0 + a]$  is the largest interval in which the maximal solution r(t) of (A.0.4) exists, and S is an at-most countable subset of  $[t_0, t_0 + a)$ . Let  $m(t) \in \mathbb{C}[(t_0, t_0 + a), \mathbb{R}], (t, m(t)) \in E$  for  $t \in$  $[t_0, t_0 + a), m(t_0) \leq u_0$ , and for a fixed Dini derivative,

$$Dm(t) \leq g(t, m(t)), \qquad t \in [t_0, t_0 + a) - S.$$

Then,

$$m(t) \leq r(t)$$
 for  $t \in [t_0, t_0 + a)$ .

We now states the Basic Implicit Function Theorem taken from [1].

Consider maps  $F : \Lambda \times U \to Y$ , where  $\Lambda$  and U are open subsets of Banach space T and X, respectively, and Y is a Banach space.

**Theorem A.5.** Let  $(\lambda^*, u^*) \in \Lambda \times U$ . Suppose that

- (i) F is continuous and F has the u-partial derivative in  $\Lambda \times U$  and  $F_u : \Lambda \times U \rightarrow L(X,Y)$  is continuous.
- (ii)  $F_u(\lambda^*, u^*) \in L(X, Y)$  is invertible.

Then the map  $\Psi : \Lambda \times U \to T \times Y$ , given by  $\Psi(\lambda, u) = (\lambda, F(\lambda, u))$ , is locally invertible at  $(\lambda^*, u^*)$  with continuous inverse  $\Phi$ . If, in addition,  $F \in C^1(\Lambda \times U, Y)$ , then  $\Phi$  is  $C^1$ .

The following lemma is usually called the Fluctuation Lemma. For a proof, see Hirsh, Hanisch, and Gabrial [26].

**Lemma A.6.** Let  $f : \mathbb{R}^+ \to \mathbb{R}$  be a differentiable function. If  $\liminf_{t\to\infty} f(t) < \limsup_{t\to\infty} f(t)$ , then there are sequences  $t_m \uparrow \infty$  and  $s_m \uparrow \infty$  such that for all m

$$\dot{f}(t_m) = 0$$
, and  $f(t_m) \to \limsup_{t \to \infty} f(t)$  as  $m \to \infty$ ,  
 $\dot{f}(s_m) = 0$ , and  $f(s_m) \to \limsup_{t \to \infty} f(t)$  as  $m \to \infty$ ,.

The proof of the following useful lemma can be found in [20].

**Theorem A.7.** Let  $a \in (-\infty, \infty)$  and  $f : [a, \infty) \to \mathbb{R}$  be a differentiable function. If  $\lim_{t\to\infty} f(t)$  exists (finite) and the derivative function  $\dot{f}(t)$  is uniformly continuous on  $(a, \infty)$ , then  $\lim_{t\to\infty} \dot{f}(t) = 0$ .

## Appendix B

# Existence and Uniqueness of Solutions for a Class of DDEs with Simplified Initial Data.

In (1.2.4), s(t) does not involve a delay term, thus it is only necessary to know s(0), rather than s(t) for  $t \in [-\tau, 0]$  to obtain the existence and uniqueness of solutions. We prove a more general form of this result in Theorem B.1.

Consider the following system of delay differential equations with initial data

$$\begin{cases} \dot{u}(t) = F(u(t), v(t), v(t - \tau)), \\ \dot{v}(t) = G(u(t), v(t), v(t - \tau)) \\ u(t_0) = u_0 \in \mathbb{R}^m, \quad v(\theta) = \phi(\theta) \in \mathbb{C}([t_0 - \tau, t - 0], \mathbb{R}^n), \end{cases}$$
(B.0.1)

where u(t) is a vector function mapping t to  $\mathbb{R}^m$ , v(t) is a vector function mapping t to  $\mathbb{R}^n$ , and both functions F and G are continuous in each of their arguments and map to  $\mathbb{R}^m$  or  $\mathbb{R}^n$ , respectively. Note that in system (B.0.1), u(t) does not involve

delay. By simplified initial data, only those functions (e.g. v(t)) that involve delay require initial data on  $\in [t_0 - \tau, t_0]$ . The other functions (e.g. u(t)) need only be specified at  $t_0$ .

Without loss of generality, in the following theorem, we assume  $t_0 = 0$ .

**Theorem B.1.** Suppose D is an open subset of  $\mathbb{R}^m \times \mathbb{R}^n \times C([-\tau, 0], \mathbb{R}^n)$  and functions F and G are both continuous on D. If  $(u_0, \phi(0), \phi(\theta)) \in D$ , then there exists a solution (u(t), v(t)) of (B.0.1) passing through  $(u_0, \phi(0), \phi(\theta))$  for  $t \ge 0$ . If F and Gare both  $C^1$  on D, the solution is unique.

**Proof.** For  $t \in [0, \tau]$ , one has  $t - \tau \in [-\tau, 0]$  and  $v(t - \tau) = \phi(t - \tau)$ . System (B.0.1) becomes

$$\begin{cases} \dot{u} = F(u(t), v(t), \phi(t - \tau)), \\ \dot{v} = G(u(t), v(t), \phi(t - \tau)), \\ u(0) = u_0 \in \mathbb{R}^m, \quad v(0) = \phi(0) \in \mathbb{R}^n. \end{cases}$$
(B.0.2)

This changes the original problem to the existence of solutions of ordinary differential equations (B.0.2) with initial conditions  $u(0) = u_0$  and  $v(0) = \phi(0)$ . Since F and G are continuous, by Theorem 2.3 and 3.1 in Miller and Michel [41], there exists a solution (u(t), v(t)) defined on  $[0, \tau]$  satisfying (B.0.2). If F and G are both  $C^1$ , by Corollary 4.3 in Miller and Michel [41], the solution is unique. Similarly, using the method of steps in Bellman and Cooke [4], we can prove the existence and uniqueness of solutions for any  $t \ge \tau$ .

# Appendix C

# Proof of Theorem 4.10

First assume that i) holds. From  $A\beta-2d(\gamma+\epsilon+d)\geqslant 0,$ 

$$A\beta - 2d(\gamma + \epsilon + d) > -d\gamma e^{-d\tau}.$$

Adding  $d(\gamma + \epsilon + d)$  to both sides and noting  $\gamma - \gamma e^{-d\tau} > 0$  gives

$$A\beta - d(\gamma + \epsilon + d) > d(\gamma + \epsilon + d - \gamma e^{-d\tau}) > 0.$$

Therefore,

$$\frac{A\beta - d(\gamma + \epsilon + d)}{\gamma + \epsilon + d - \gamma e^{-d\tau}} > d,$$

which is equivalent to

$$\beta I^{\star} > d. \tag{C.0.1}$$

From

$$\tau \leqslant -\frac{1}{2d} \ln \bigg( \frac{4(\gamma+\epsilon+d)(A\beta-d(\gamma+\epsilon+d))}{\gamma^2(\epsilon+d)} \bigg),$$

we have

$$\frac{4(\gamma+\epsilon+d)(A\beta-d(\gamma+\epsilon+d))}{\epsilon+d}\leqslant \gamma^2 e^{-2d\tau}$$

Since  $\gamma + \epsilon + d - \gamma e^{-d\tau} > \epsilon + d$ ,

$$\frac{4(\gamma+\epsilon+d)(A\beta-d(\gamma+\epsilon+d))}{\gamma+\epsilon+d-\gamma e^{-d\tau}} < \frac{4(\gamma+\epsilon+d)(A\beta-d(\gamma+\epsilon+d))}{\epsilon+d} \leqslant \gamma^2 e^{-2d\tau}.$$

Noting  $\beta I^{\star} = \frac{A\beta - d(\gamma + \epsilon + d)}{\gamma + \epsilon + d - \gamma e^{-d\tau}}$ , we have

$$4\beta I^{\star} \leqslant \frac{\gamma^2 e^{-2d\tau}}{\gamma+\epsilon+d}.$$

Multiplying  $\beta I^{\star}$  on both sides and rearranging gives

$$(2\beta I^{\star})^2 \leqslant \frac{(\gamma\beta I^{\star}e^{-d\tau})^2}{\beta I^{\star}(\gamma+\epsilon+d)}.$$

From (C.0.1),

$$p^{2}(\tau) = (d + \beta I^{\star})^{2} \leqslant (2\beta I^{\star})^{2} \leqslant \frac{(\gamma\beta I^{\star}e^{-d\tau})^{2}}{\beta I^{\star}(\gamma + \epsilon + d)} = \frac{c^{2}(\tau)}{\alpha(\tau)}.$$
 (C.0.2)

It follows that  $-4p^2(\tau)\alpha(\tau) + 4c^2(\tau) \ge 0$ . Therefore,

$$\begin{aligned} (q^{2}(\tau) - p^{2}(\tau) + 2\alpha(\tau))^{2} &- 4\left(\alpha^{2}(\tau) - c^{2}(\tau)\right) \\ &= (-p^{2}(\tau) + 2\alpha(\tau))^{2} - 4\left(\alpha^{2}(\tau) - c^{2}(\tau)\right) \\ &= p^{4}(\tau) - 4p^{2}(\tau)\alpha(\tau) + 4c^{2}(\tau) \\ &\geqslant -4p^{2}(\tau)\alpha(\tau) + 4c^{2}(\tau) \geqslant 0. \end{aligned}$$

By (4.3.20),  $\alpha^2(\tau) - c^2(\tau) > 0$ . By (C.0.2),

$$p^{2}(\tau) < \frac{c^{2}(\tau)}{\alpha(\tau)} < \frac{\alpha^{2}(\tau)}{\alpha(\tau)} = \alpha(\tau) < 2\alpha(\tau).$$

Hence

$$q^{2}(\tau) - p^{2}(\tau) + 2\alpha(\tau) = 2\alpha(\tau) - p^{2}(\tau) > 0.$$

Therefore, condition  $(H_1)$  holds.

Now assume that *ii*) holds. From  $A\beta - d(\gamma + 2\epsilon + 2d) \leq 0$ ,

$$A\beta - 2d(\gamma + \epsilon + d) \leqslant -d\gamma e^{-d\tau}.$$

Adding  $d(\gamma + \epsilon + d)$  to both sides and noting that  $R_0 = \frac{A\beta}{d(\gamma + \epsilon + d)} > 1$ , we obtain

$$d(\gamma + \epsilon + d - \gamma e^{-d\tau}) \ge A\beta - d(\gamma + \epsilon + d) > 0.$$

Therefore,

$$d \geqslant \frac{A\beta - d(\gamma + \epsilon + d)}{\gamma + \epsilon + d - \gamma e^{-d\tau}} > 0,$$

which is equivalent to

$$d \geqslant \beta I^{\star}.\tag{C.0.3}$$

From

$$\tau \leqslant -\frac{1}{2d} \ln \left( \frac{4d^2(\gamma + \epsilon + d)^2}{\gamma^2 (A\beta - d(\gamma + \epsilon + d))} \right),$$

we have

$$\frac{4d^2(\gamma+\epsilon+d)^2}{A\beta-d(\gamma+\epsilon+d)}\leqslant \gamma^2 e^{-2d\tau}.$$

Since  $\gamma + \epsilon + d > \gamma + \epsilon + d - \gamma e^{-d\tau}$ ,

$$\gamma^2 e^{-2d\tau} \geqslant \frac{4d^2(\gamma + \epsilon + d)^2}{A\beta - d(\gamma + \epsilon + d)} \geqslant \frac{4d^2(\gamma + \epsilon + d)(\gamma + \epsilon + d - \gamma e^{-d\tau})}{A\beta - d(\gamma + \epsilon + d)}.$$

Noting  $\beta I^{\star} = \frac{A\beta - d(\gamma + \epsilon + d)}{\gamma + \epsilon + d - \gamma e^{-d\tau}}$ , we have

$$\beta I^{\star} \gamma^2 e^{-2d\tau} \ge 4d^2(\gamma + \epsilon + d).$$

Multiplying  $\beta I^{\star}$  on both sides and rearranging gives

$$\frac{(\gamma\beta I^{\star}e^{-d\tau})^2}{\beta I^{\star}(\gamma+\epsilon+d)} \ge 4d^2.$$

From (C.0.3),

$$p^{2}(\tau) = (d + \beta I^{\star})^{2} \leqslant 4d^{2} \leqslant \frac{(\gamma \beta I^{\star} e^{-d\tau})^{2}}{\beta I^{\star}(\gamma + \epsilon + d)} = \frac{c^{2}(\tau)}{\alpha(\tau)}.$$
 (C.0.4)

It follows that  $-4p^2(\tau)\alpha(\tau) + 4c^2(\tau) \ge 0$ . Therefore,

$$\begin{aligned} (q^{2}(\tau) - p^{2}(\tau) + 2\alpha(\tau))^{2} &- 4\left(\alpha^{2}(\tau) - c^{2}(\tau)\right) \\ &= (-p^{2}(\tau) + 2\alpha(\tau))^{2} - 4\left(\alpha^{2}(\tau) - c^{2}(\tau)\right) \\ &= p^{4}(\tau) - 4p^{2}(\tau)\alpha(\tau) + 4c^{2}(\tau) \\ &\geqslant -4p^{2}(\tau)\alpha(\tau) + 4c^{2}(\tau) \geqslant 0. \end{aligned}$$

By (4.3.20),  $\alpha^2(\tau) - c^2(\tau) > 0$ . By (C.0.4),

$$p^{2}(\tau) < \frac{c^{2}(\tau)}{\alpha(\tau)} < \frac{\alpha^{2}(\tau)}{\alpha(\tau)} = \alpha(\tau) < 2\alpha(\tau).$$

Hence

$$q^{2}(\tau) - p^{2}(\tau) + 2\alpha(\tau) = 2\alpha(\tau) - p^{2}(\tau) > 0.$$

Therefore condition  $(H_1)$  holds.

In either case,  $(H_1)$  holds. By Lemma 4.1, both  $\omega_1(\tau)$  and  $\omega_2(\tau)$  are positive. By Theorem 4.4 (iv.b),  $2\pi - \theta_i(\tau) \in [\pi, 2\pi]$  satisfies (4.0.9).

If  $2\pi - \theta_i(\tau) + 2k\pi$  intersects  $\tau \omega_i(\tau)$  at some  $\bar{\tau}_i$ , by Theorem 4.3, (4.0.1) has a pair of pure imaginary roots  $\pm \omega_i(\bar{\tau}_i)$ .

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