

## CHAPTER IV

### ANALYSIS OF THE POPULATION MODELS WITH STAGE-STRUCTURE

From Chapter III, we have studied the general population model with a constant delay of the form

$$N'(t) = -\gamma N(t) + \beta f(N(t - \tau))N(t - \tau). \quad (4-1)$$

Equation (4-1) represents the rate of change of the total population size, and there is only one stage or age-group of population. In general, an individual population has more than one stage and it can be changed its stage. For examples, each human population may be divided into two stages, i.e. mature stage and immature stage. Many types of insects have more than two stages in their life-cycle. The study of DDEs with age-structure or stage-structure has been extensively applied in many areas such as biology, networks, robot engineering, control of signals [2, 8, 10, 16].

In this chapter we add a term of stage-structure into (4-1), which will be described later in the next section. The dynamical properties of this problem are more complicated compare with the previous one. We also use the linearisation technique to determine stability properties of equilibria of the population model with stage-structure.

The main aim in this chapter is to determine sufficient conditions for the asymptotic stability and the existence of a *smallest* Hopf bifurcation point of the population model with stage-structure. In addition, to support the analytical results, we use Matlab<sup>®</sup> to illustrate numerical solutions and dynamical behaviours of the selected problems through the Mackey-Glass equation and the Nicholson's blowflies equation.

#### 4.1 The Population Model with Stage-Structure

In this part, we are interested in the population models with age-structure. Our work will be focused on two stages of age-structures, namely immature stage and mature stage. The stage-structure cannot be ignore in cases that the delay has an effect only one stage, i.e. the model can be explained some types of epidemics, which are spread in only children (immature stage), such as measles, mumps and chickenpox. In our considered model, the age to maturity is represented by a time delay, leading to a DDE with an age-structure term. More details on the modeling of the population model with age-structure are provided in the Appendix.

Suppose that  $N(t)$  is the population size at present time  $t$ . The relation between both groups is expressed as follow

$$\frac{dN}{dt} = -(\text{death rate}) + (\text{stage} - \text{structure})(\text{growth rate})$$

Here, we are interested in the population models with stage-structure. We analyse the general model of the form:

$$N'(t) = -\gamma N(t) + \beta e^{-\delta\tau} f(N(t-\tau))N(t-\tau), \quad (4-2)$$

where  $N(t)$  denotes the total population size,  $e^{-\delta\tau}$  represents term of stage-structure,  $f(N)$  is a birth-rate function,  $\beta > 0$  represents a birth-rate constant,  $\gamma > 0$  refers to the death-rate constant, and  $\tau$  is a positive delay. In population problems, delay  $\tau$  may represents the time in the past state or time delay. In this chapter, we are interested population problem with two stages.

#### 4.2 The Equilibria

In this part we aim to find the equilibria of (4-2). Let  $\tilde{N}$  be an equilibrium of (4-2). We can find the equilibrium of (4-2) by setting  $N'(t) = 0$ , then equation (4-2) becomes

$$-\gamma\tilde{N} + \beta e^{-\delta\tau} f(\tilde{N})\tilde{N} = 0,$$

or

$$\tilde{N}(-\gamma + \beta e^{-\delta\tau} f(\tilde{N})) = 0. \quad (4-3)$$

Then, the equilibria  $\tilde{N}$  must satisfy

$$\tilde{N}_0 = 0 \quad \text{or} \quad \tilde{N}_+ = f^{-1}\left(\frac{\gamma}{\beta e^{-\delta\tau}}\right), \quad (4-4)$$

where  $\gamma$ ,  $\beta$  and  $\delta$  are positive constants. The equilibrium  $\tilde{N}_0 = 0$  is called trivial equilibrium of (4-2). The second equilibrium  $\tilde{N}_+$  occurs provided that  $f^{-1}\left(\frac{\gamma}{\beta e^{-\delta\tau}}\right)$  can be determined. Moreover the function  $f$  must satisfy the following assumptions:

- (H1) function  $f$  is continuous and  $f^{-1}$  can be determined,
- (H2) function  $f(x)$  is positive for  $x \geq 0$ ,
- (H3) function  $f(x)$  is a decreasing function for  $x \geq 0$ .

Note that, throughout our study in this chapter, we assume that the selected function satisfies assumptions (H1)-(H3).

### 4.3 Stability Properties of the Selected Model

We study local stability properties of the equilibria of (4-2) by the linearisation method. Hence we restate (4-2),

$$N'(t) = -\gamma N(t) + \beta e^{-\delta\tau} f(N(t-\tau))N(t-\tau).$$

Under the assumption (H1)-(H3), suppose that  $\tilde{N}$  is an equilibrium of (4-2) and let  $y(t) = N(t) - \tilde{N}$ , then the linearised equation of (4-2) becomes

$$y'(t) = -\gamma y(t) + a(\tau)y(t-\tau), \quad (4-5)$$

where

$$a(\tau) = \beta e^{-\delta\tau} (f(\tilde{N}) + \tilde{N}f'(\tilde{N})). \quad (4-6)$$

Note that, for the zero equilibrium  $\tilde{N} = 0$ , we have  $a(\tau) = \beta e^{-\delta\tau} f(0)$ . Moreover it is not difficult to show that

$$a'(\tau) = -\delta a(\tau). \quad (4-7)$$

Next, we find the characteristic equation of (4-5). Let  $\lambda$  be an eigenvalue and  $y(t) = e^{\lambda t}$  be a solution of (4-5). Then the characteristic equation is

$$\lambda e^{\lambda t} = -\gamma e^{\lambda t} + a(\tau) e^{\lambda(t-\tau)}. \quad (4-8)$$

Divided both sides of equation (4-8) by  $e^{\lambda t}$ . Hence, the eigenvalues  $\lambda$  must satisfy

$$\lambda = -\gamma + a(\tau) e^{-\lambda\tau}. \quad (4-9)$$

Equation (4-9) is the characteristic equation of the linearised equation (4-5).

In our problem, we focus on the stability properties of (4-2) with the linearised equation (4-5). From Lemma 2-7, we compare the general linear DDE: (2-15) in Lemma 2-7 with (4-5). Hence, we can see that if  $A = -\gamma$  and  $B = a(\tau)$ , then the linear stability of (4-2) are shown as follows.

*Theorem 4-1*

*Suppose that  $\tau > 0$  and  $a(\tau)$  is defined in (4-6). Let  $\tilde{N}$  be an equilibrium of (4-2). Then the stability properties are as follows.*

- (1) If  $\gamma > |a(\tau)|$ , then  $\tilde{N}$  is asymptotically stable.*
- (2) If  $\gamma < a(\tau)$ , then  $\tilde{N}$  is unstable.*
- (3) If  $a(\tau) < 0$  and  $-\gamma > a(\tau)$ , then  $\tilde{N}$  is asymptotically stable for  $\tau \in [0, \tau_0)$ , and it is unstable for  $\tau > \tau_0$ .*

Theorem 4-1 provides the sufficient conditions for the equilibrium  $\tilde{N}$  of (4-2) to be stable or unstable. In addition condition (3) in Theorem 4-1 shows that the delay can switch stability properties of the system. Let  $\tau$  be the bifurcation parameter. We can see that  $\tau = \tau_0$  is a bifurcation point. Hence, the condition (3) in Theorem 4-1,  $0 < -a(\tau) < \gamma$ , is the sufficient conditions for the value  $\tau_0$  to be the smallest bifurcation point. In the next section we will evaluate the value of  $\tau_0$  and the conditions in which it becomes the Hopf bifurcation point.

#### 4.4 Analysis of the Hopf Bifurcation

From the Chapter II, we have shown the definitions of Hopf bifurcation and related theorems for the occurrence of the Hopf bifurcation. Then, in this section, we will apply them to find sufficient conditions for the existence of the Hopf bifurcation. From (4-9), we restate the characteristic equation of (4-5) as

$$\lambda = -\gamma + a(\tau)e^{-\lambda\tau}.$$

For  $\omega > 0$ , suppose that  $\lambda = i\omega$  is a root of the characteristic equation. It follows that

$$\begin{aligned} i\omega &= -\gamma + a(\tau)e^{-i\omega\tau} \\ &= -\gamma + a(\tau)(\cos \omega\tau - i \sin \omega\tau), \end{aligned}$$

or

$$\gamma + i\omega = a(\tau)\cos \omega\tau - ia(\tau)\sin \omega\tau. \quad (4-10)$$

Equate the real and imaginary parts from both-side of (4-10), we have

$$\gamma = a(\tau)\cos \omega\tau, \quad (4-11)$$

$$\omega = -a(\tau)\sin \omega\tau. \quad (4-12)$$

It is not difficult to show that

$$\gamma^2 + \omega^2 = a^2(\tau). \quad (4-13)$$

Since  $\omega > 0$ , equation (4-13) can be simplified as

$$\omega = \sqrt{a^2(\tau) - \gamma^2}. \quad (4-14)$$

Hence,  $\omega > 0$  is valid only if  $a^2(\tau) > \gamma^2$ , i.e.

$$|a(\tau)| > \gamma. \quad (4-15)$$

Note that condition (4-15) is a condition for the existence of a Hopf bifurcation. From condition (3) in Theorem 4-1, we can see that the condition (4-15) will be limited to  $-\gamma > a(\tau)$ , where  $a(\tau) < 0$ .

From (4-11), we see that

$$\tau = \frac{\theta}{\omega}, \quad (4-16)$$

where

$$\theta = \arccos\left(\frac{\gamma}{a(\tau)}\right). \quad (4-17)$$

To find a Hopf bifurcation point, we need to find the value of  $\tau$  in which  $\lambda = i\omega$  is a root of (4-9), where  $\omega$  is defined in (4-14). It follows from (4-16) that

$$\frac{\theta}{\tau} = \sqrt{a^2(\tau) - \gamma^2}. \quad (4-18)$$

From (4-16), suppose that  $\tau_0$  is the smallest bifurcation point, then

$$\tau_0 = \frac{\theta}{\omega_0}. \quad (4-19)$$

From (4-11) and (4-14), simplify the parameter  $\omega$ . Then there exists  $\tau_0$  satisfying

$$\frac{1}{\tau_0} \cos^{-1}\left(\frac{\gamma}{a(\tau_0)}\right) = \sqrt{a^2(\tau_0) - \gamma^2}. \quad (4-20)$$

Note that (4-20) is a nonlinear equation which will be used to calculate  $\tau_0$ , when all parameters are provided. The bifurcation can be occurred provided that the value of  $\tau_0$  in (4-20) can be determined.

According to Theorem 2-10, the parameter value  $\tau_0$  is the Hopf bifurcation point if  $\lambda(\tau_0)$  has simple purely imaginary part, and  $\text{Re}(\lambda'(\tau_0)) \neq 0$ .

**Theorem 4-2**

Let  $\lambda_0(\tau) = \alpha_0(\tau) + i\omega_0(\tau)$  be a root of (4-9) near  $\tau = \tau_0$  satisfying  $\alpha_0(\tau_0) = 0$  and  $\omega_0(\tau_0) = \omega_0$ , where  $\omega_0 \in \mathbb{R} \setminus \{0\}$  and  $\tau_0$  is the smallest positive root of (4-20).

If all parameters of (4-2) meet the conditions

$$0 < -a(\tau_0) < \gamma \quad \text{and} \quad a^2(\tau_0) > \frac{\gamma(\delta + \gamma)}{1 - \delta\tau_0},$$

then  $\text{Re}(\lambda'_0(\tau_0)) = \alpha'_0(\tau_0) > 0$ , and hence  $\tau = \tau_0$  is the Hopf bifurcation points of (4-2).

**Proof** The parameter condition  $0 < -a(\tau_0) < \gamma$  comes directly from condition (3) in Theorem 4-1. To prove additional conditions in Theorem 4-2, consider the characteristic equation

$$\lambda = -\gamma + a(\tau)e^{-\lambda\tau}. \quad (4-21)$$

Let  $\lambda$  be a function of  $\tau$ , i.e.  $\lambda = \lambda(\tau)$ . Differentiating both sides of (4-21) with respect to  $\tau$ , it follows that

$$\begin{aligned} \frac{d\lambda}{d\tau} &= a(\tau)e^{-\lambda\tau}(-\lambda - \tau \frac{d\lambda}{d\tau}) + e^{-\lambda\tau}a'(\tau) \\ &= -\lambda a(\tau)e^{-\lambda\tau} - \tau a(\tau)e^{-\lambda\tau} \frac{d\lambda}{d\tau} + e^{-\lambda\tau}a'(\tau). \end{aligned}$$

Simplify the equation above, we have

$$(e^{\lambda\tau} + \tau a(\tau))e^{-\lambda\tau} \frac{d\lambda}{d\tau} = e^{-\lambda\tau} (-\lambda a(\tau) + a'(\tau)),$$

or

$$\frac{d\lambda}{d\tau} = \frac{-\lambda a(\tau) + a'(\tau)}{e^{\lambda\tau} + \tau a(\tau)}. \quad (4-22)$$

Let  $\text{Re}(\lambda_0(\tau_0)) = 0$  and  $\text{Im}(\lambda_0(\tau_0)) = \omega_0$ . Suppose that

$$\lambda_0(\tau) = \alpha_0(\tau) + i\omega_0(\tau),$$

then  $\alpha_0(\tau_0) = 0$  and  $\lambda_0(\tau_0) = i\omega_0$ . From (4-22) and (4-6) we can show that

$$\begin{aligned} \left. \frac{d\lambda}{d\tau} \right|_{\tau=\tau_0} &= \frac{-i\omega_0 a(\tau_0) + a'(\tau_0)}{e^{i\omega_0 \tau} + \tau_0 a(\tau_0)} \\ &= \frac{-i\omega_0 a(\tau_0) + a'(\tau_0)}{\cos \omega_0 \tau_0 + i \sin \omega_0 \tau_0 + \tau_0 a(\tau_0)}. \end{aligned}$$

From (4-7),  $a'(\tau) = -\delta a(\tau)$ , it yields

$$\left. \frac{d\lambda}{d\tau} \right|_{\tau=\tau_0} = \frac{-i\omega_0 a(\tau_0) - \delta a(\tau_0)}{\cos \omega_0 \tau_0 + i \sin \omega_0 \tau_0 + \tau_0 a(\tau_0)}.$$

In addition, simplifying above equation, we then have

$$\begin{aligned} \left. \frac{d\lambda}{d\tau} \right|_{\tau=\tau_0} &= \frac{-i\omega_0 a(\tau_0) - \delta a(\tau_0)}{(\cos \omega_0 \tau_0 + \tau_0 a(\tau_0)) + i \sin \omega_0 \tau_0} \times \frac{(\cos \omega_0 \tau_0 + \tau_0 a(\tau_0)) - i \sin \omega_0 \tau_0}{(\cos \omega_0 \tau_0 + \tau_0 a(\tau_0)) - i \sin \omega_0 \tau_0} \\ &= \frac{-i\omega_0 a(\tau_0)(\cos \omega_0 \tau_0 + \tau_0 a(\tau_0)) - \omega_0 a(\tau_0) \sin \omega_0 \tau_0}{\cos^2 \omega_0 \tau_0 + 2\tau_0 a(\tau_0) \cos \omega_0 \tau_0 + \tau_0^2 a^2(\tau_0) + \sin^2 \omega_0 \tau_0} \\ &\quad - \frac{\delta a(\tau_0)(\cos \omega_0 \tau_0 + \tau_0 a(\tau_0))}{\cos^2 \omega_0 \tau_0 + 2\tau_0 a(\tau_0) \cos \omega_0 \tau_0 + \tau_0^2 a^2(\tau_0) + \sin^2 \omega_0 \tau_0} \\ &\quad + \frac{i\delta a(\tau_0) \sin \omega_0 \tau_0}{\cos^2 \omega_0 \tau_0 + 2\tau_0 a(\tau_0) \cos \omega_0 \tau_0 + \tau_0^2 a^2(\tau_0) + \sin^2 \omega_0 \tau_0}, \end{aligned}$$

or

$$\begin{aligned} \lambda'_0(\tau) &= \alpha'_0(\tau) + i\omega'_0(\tau) \\ &= \frac{-\omega_0 a(\tau_0) \sin \omega_0 \tau_0 - \delta a(\tau_0)(\cos \omega_0 \tau_0 + \tau_0 a(\tau_0))}{\cos^2 \omega_0 \tau_0 + 2\tau_0 a(\tau_0) \cos \omega_0 \tau_0 + \tau_0^2 a^2(\tau_0) + \sin^2 \omega_0 \tau_0} \\ &\quad + \frac{i\delta a(\tau_0) \sin \omega_0 \tau_0 - i\omega_0 a(\tau_0)(\cos \omega_0 \tau_0 + \tau_0 a(\tau_0))}{\cos^2 \omega_0 \tau_0 + 2\tau_0 a(\tau_0) \cos \omega_0 \tau_0 + \tau_0^2 a^2(\tau_0) + \sin^2 \omega_0 \tau_0}. \end{aligned}$$

Consider only the real part of  $\lambda'_0(\tau)$ . It follows that

$$\begin{aligned} \text{Re}(\lambda'_0(\tau_0)) &= \alpha'_0(\tau_0) \\ &= \frac{-\omega_0 a(\tau_0) \sin \omega_0 \tau_0 - \delta a(\tau_0)(\cos \omega_0 \tau_0 + \tau_0 a(\tau_0))}{\cos^2 \omega_0 \tau_0 + 2\tau_0 a(\tau_0) \cos \omega_0 \tau_0 + \tau_0^2 a^2(\tau_0) + \sin^2 \omega_0 \tau_0}. \end{aligned} \quad (4-23)$$



From (4-11) and (4-12), we can see that (4-23) becomes

$$\begin{aligned} \operatorname{Re}(\lambda'_0(\tau_0)) &= \frac{-\omega_0 a(\tau_0) \sin \omega_0 \tau_0 - \delta a(\tau_0) (\cos \omega_0 \tau_0 + \tau_0 a(\tau_0))}{\cos^2 \omega_0 \tau_0 + 2\tau_0 a(\tau_0) \cos \omega_0 \tau_0 + \tau_0^2 a^2(\tau_0) + \sin^2 \omega_0 \tau_0} \\ &= \frac{\omega_0^2 - \delta(\gamma + \tau_0 a^2(\tau_0))}{1 + 2\tau_0 \gamma + \tau_0^2 a^2(\tau_0)}. \end{aligned}$$

We can see that  $\operatorname{Re}(\lambda'_0(\tau_0)) > 0$  when

$$\omega_0^2 - \delta(\gamma + \tau_0 a^2(\tau_0)) > 0.$$

From (4-13), we know that  $\gamma^2 + \omega^2 = a(\tau)^2$ . Then the inequality above becomes

$$(1 - \delta\tau_0) a^2(\tau_0) > \gamma(\delta + \gamma).$$

As the results, if the condition  $a^2(\tau_0) > \gamma(\delta + \gamma) / (1 - \delta\tau_0)$ , which is stated in Theorem 4-2, then  $\operatorname{Re}(\lambda'_0(\tau_0))$  is positive. Thus  $\tau_0$  is the Hopf bifurcation point. This completes the proof. ■

From Theorem 4-2, we can see that  $\tau_0$  which is defined by (4-19) is a Hopf bifurcation point of (4-2).

#### 4.5 Applications and Numerical Results

For applications, we will apply the results with some birth-rate functions. To support the analytical results, we use Matlab<sup>®</sup> to show behaviours of the results and present the existence of a Hopf bifurcation point. The general equation which we will consider in this part has the form:

$$N'(t) = -\gamma N(t) + \beta e^{-\delta\tau} f(N(t - \tau)) N(t - \tau). \quad (4-24)$$

Next, we apply the obtained results to the Mackey-Glass equation and the Nicholson's blowflies equation.

#### 4.5.1 The Mackey-Glass equation

Consider the reduced Mackey-Glass equation provided in [11],

$$x'(t) = -\gamma x(t) + \frac{\beta e^{-\delta\tau} x(t-\tau)}{1 + x^n(t-\tau)}; \quad t > 0, \quad (4-25)$$

and the initial condition

$$x(t) = \varphi(t), \quad -\tau \leq t \leq 0,$$

where parameters  $\beta$ ,  $\delta$ ,  $\gamma$  and  $n$  are positive and the delay  $\tau \geq 0$ . Comparing equation (4-25) with (4-24), we see that

$$f(x) = \frac{1}{1 + x^n}. \quad (4-26)$$

The derivative of  $f$  from (4-26) is given by

$$f'(x) = -\frac{nx^{n-1}}{(1 + x^n)^2}. \quad (4-27)$$

The equilibrium  $\tilde{x}$  of (4-25) can be determined by setting  $x'(t) = 0$ . It is obvious that  $\tilde{x} = 0$  is an equilibrium.

In addition, if  $\beta e^{-\delta\tau} > \gamma$ , then there exists only the positive equilibrium:

$$\tilde{x}_+ = \left( \frac{\beta e^{-\delta\tau} - \gamma}{\gamma} \right)^{\frac{1}{n}}. \quad (4-28)$$

Substituting  $\tilde{x}_+$  from (4-28) into (4-26), we have

$$f(\tilde{x}_+) = \frac{\gamma}{\beta e^{-\delta\tau}}. \quad (4-29)$$

Next, we can solve  $f'(\tilde{x}_+)$  by substituting  $\tilde{x}_+$  from (4-28) into (4-27). Then,

$$f'(\tilde{x}_+) = -n \left( \frac{\gamma}{\beta e^{-\delta\tau}} \right)^2 \left( \frac{\beta e^{-\delta\tau} - \gamma}{\gamma} \right)^{\frac{n-1}{n}}. \quad (4-30)$$

Replacing  $\tilde{x}_+$ ,  $f(\tilde{x}_+)$  and  $f'(\tilde{x}_+)$  from (4-28)-(4-30) to (4-6), we have

$$a(\tau) = \beta e^{-\delta\tau} (f'(\tilde{x}_+)\tilde{x}_+ + f(\tilde{x}_+)) = \gamma \left( \frac{n\gamma}{\beta e^{-\delta\tau}} - (n-1) \right). \quad (4-31)$$

Substituting  $a(\tau)$  from (4-31) into (4-14) and (4-19), we have a system of nonlinear equations with  $\beta e^{-\delta\tau} > \gamma$ ,

$$\begin{aligned} \omega &= \gamma \sqrt{\left( \frac{n\gamma}{\beta e^{-\delta\tau}} - (n-1) \right)^2 - 1}, \\ \tau &= \frac{\theta}{\omega}, \end{aligned} \quad (4-32)$$

where

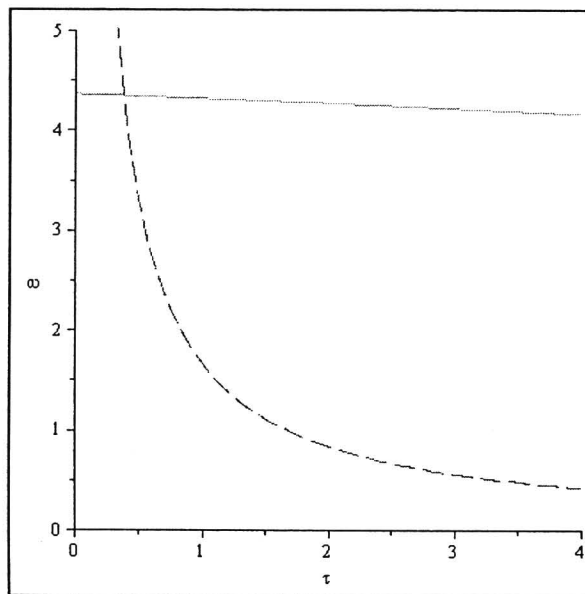
$$\theta = \arccos \left( \frac{\gamma}{a(\tau)} \right) \text{ and } \tau_0 = \frac{\theta}{\omega_0}. \quad (4-33)$$

In this study, we are interested only in the smallest positive bifurcation point  $\tau_0$ . To solve the nonlinear system (4-32), we use the mathematical software to plot the solution of the system.

Note that, in Figure 4.1, the solid line (—) refers to the first equation of (4-32), i.e.

$$\omega = \gamma \sqrt{\left( \frac{n\gamma}{\beta e^{-\delta\tau}} - (n-1) \right)^2 - 1},$$

and the dash line (---) represents the second equation of (4-32), i.e.  $\omega = \theta / \tau$ . The intersection between two curves is the solution of the system. In Figure 4-1, we can see that equation (4-32) has at least one solution. The value of  $\tau_0$  can be investigated from the Figure 4-1, or using a numerical technique.



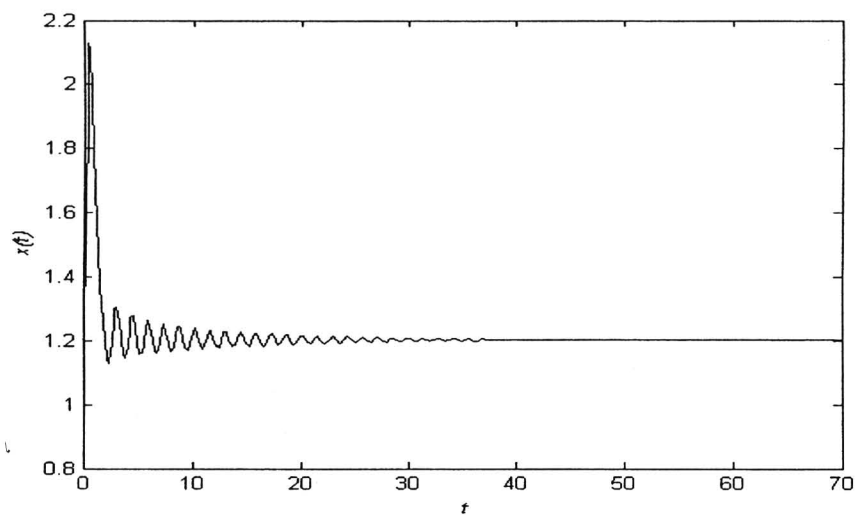
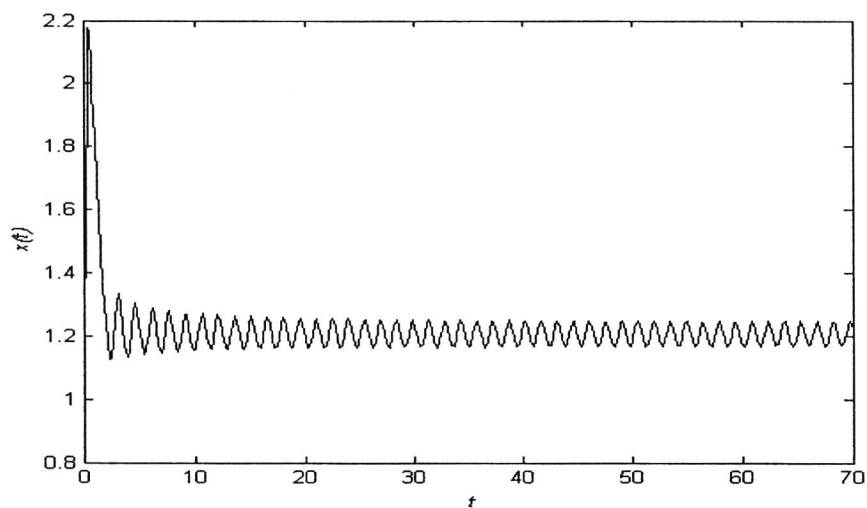
**FIGURE 4-1** Graph shows the intersection between two curves from the nonlinear system (4-32).

Finally, to support the results, we present some numerical results generated by Matlab<sup>®</sup>. The parameter values of (4-25) are followed by [27], which are placed as  $\beta = 5.0$ ,  $\gamma = 0.4$ ,  $\delta = 0.1$  and  $n = 13$ , and the initial function  $\varphi(t) = 0.8$ , where  $t \in [-\tau, 0]$ . The Hopf bifurcation point  $\tau_0$  is evaluated by (4-32) and (4-33). Then, we have

$$\tau_0 \approx 0.38. \quad (4-34)$$

We show numerical solutions of (4-25) with different values of  $\tau$  in Figure 4-2.

Figure 4-2 illustrates the numerical results of (4-25) near the bifurcation point  $\tau_0 \approx 0.38$ . We can see that the solution in Figure 4-2(a) converges to the positive equilibrium  $\tilde{x}_+ \approx 1.2$  when  $\tau = 0.37 < \tau_0$ . On the other hand, in Figure 4-2(b), the equilibrium  $\tilde{x}_+$  is unstable (with periodic solutions) when we set  $\tau = 0.39 > \tau_0$ .

(a)  $\tau = 0.37$ (b)  $\tau = 0.39$ .**FIGURE 4-2** Numerical solutions of (4-25) with different values of delays.

#### 4.5.2 The Nicholson's blowflies equation

In this part, we consider the Nicholson's blowflies equation which introduced by Gurney *et al.* [13]. Adding the stage-structure term, the delay equation with an age-class becomes

$$N'(t) = -\gamma N(t) + \beta e^{-\delta\tau} N(t-\tau) e^{-aN(t-\tau)}; \quad t \geq 0, \quad (4-35)$$

where the parameters  $\beta$ ,  $\delta$ ,  $\gamma$  and  $a$  are positive and the delay  $\tau \geq 0$ . Comparing equation (4-35) with (4-24), we see that

$$f(N) = e^{-aN}. \quad (4-36)$$

The inverse of  $f$  from (4-36) is given by

$$f^{-1}(N) = -\frac{1}{a} \ln N. \quad (4-37)$$

Then, it is not difficult to show that the positive equilibrium is

$$\tilde{N}_+ = f^{-1}\left(\frac{\gamma}{\beta e^{-\delta\tau}}\right) = -\frac{1}{a} \ln\left(\frac{\gamma}{\beta e^{-\delta\tau}}\right), \quad (4-38)$$

where  $\beta e^{-\delta\tau} > \gamma$ . Substituting  $\tilde{N}_+$  from (4-38) into (4-36) and (4-37), we have

$$f(\tilde{N}_+) = \frac{\gamma}{\beta e^{-\delta\tau}}, \quad (4-39)$$

and

$$f'(\tilde{N}_+) = -a \frac{\gamma}{\beta e^{-\delta\tau}}. \quad (4-40)$$

Replacing the values of  $\tilde{N}_+$ ,  $f(\tilde{N}_+)$  and  $f'(\tilde{N}_+)$  from (4-38)-(4-40) to (4-11):

$$a(\tau) = \beta e^{-\delta\tau} (f'(\tilde{N}_+) \tilde{N}_+ + f(\tilde{N}_+)).$$

Thus

$$a(\tau) = \gamma \left( \ln \left( \frac{\gamma}{\beta e^{-\delta\tau}} \right) + 1 \right). \quad (4-41)$$

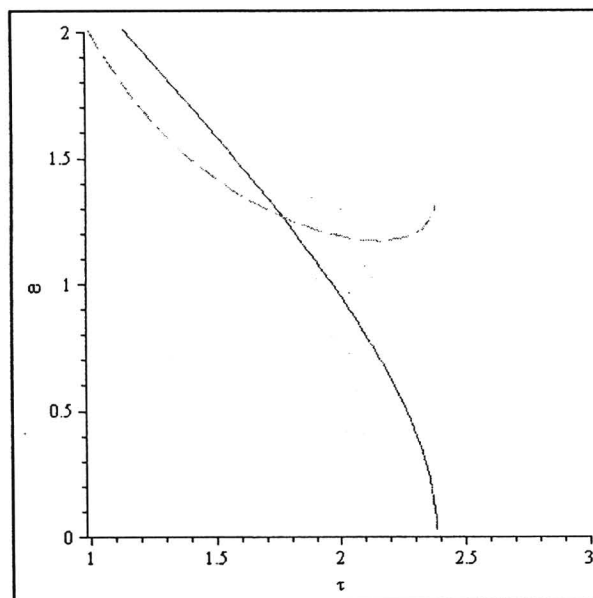
Substituting  $a(\tau)$  from (4-41) into (4-38) and (4-40), we have a system of non-linear equation with  $\beta e^{-\delta\tau} > \gamma$ . The nonlinear system for this problem is

$$\begin{aligned} \omega &= \gamma \sqrt{\left( \ln \left( \frac{\gamma}{\beta e^{-\delta\tau}} \right) + 1 \right)^2 - 1}, \\ \tau &= \frac{\theta}{\omega}, \end{aligned} \quad (4-42)$$

where

$$\theta = \arccos \left( \frac{\gamma}{a(\tau)} \right) \quad \text{and} \quad \tau_0 = \frac{\theta}{\omega_0}. \quad (4-43)$$

In this example, we are interested only in the case of the smallest positive Hopf bifurcation point  $\tau_0$ .



**FIGURE 4-3** Graph shows the intersection between two curves from the nonlinear system (4-42).

Note that, in Figure 4-3, the solid line (—) refers to the first equation of (4-42), i.e.

$$\omega = \gamma \sqrt{\left( \ln \left( \frac{\gamma}{\beta e^{-\delta\tau}} \right) + 1 \right)^2 - 1},$$

and the dash line (---) represents the second equation of (4-42), i.e.  $\tau = \theta/\omega$ .

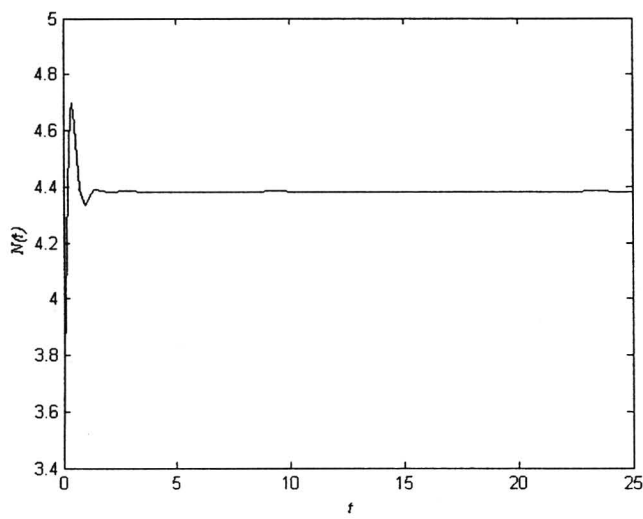
From Figure 4-3, we can see that equation (4-42) with suitable parameter values has at least one solution. We can investigate the solution  $\tau_0$  from the Figure 4-3.

Finally, to support the results, we present numerical results generated by Matlab®. The parameter values of (4-35), as presented in [7], are set as  $\beta = 80$ ,  $\gamma = 1.0$ ,  $\delta = 1.0$  and  $a = 1.0$ , and the initial function  $\varphi(t) = 3.5$ , where  $t \in [-\tau, 0]$ . The Hopf bifurcation point  $\tau_0$  is evaluated numerically from (4-42) and (4-43). By solving the nonlinear system, we have

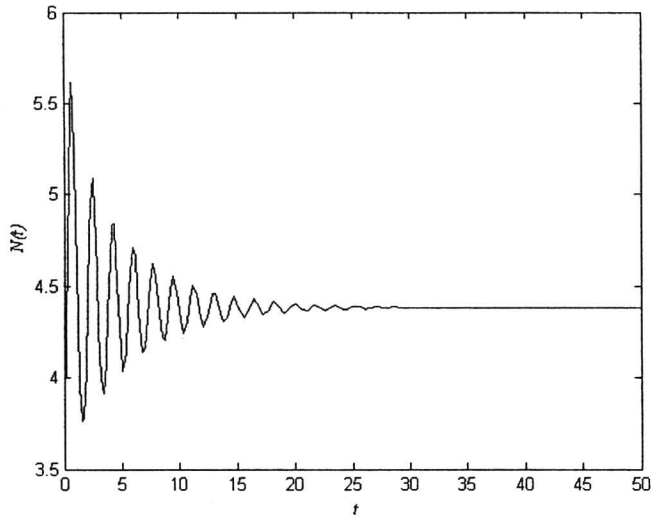
$$\tau_0 \approx 1.76. \quad (4-44)$$

From (4-44), the Hopf bifurcation point of (4-35) is  $\tau_0 \approx 1.76$ . In the numerical examples, we show the solutions for various cases of the bifurcation parameter  $\tau$ . In Figure 4-4, the graphs show asymptotic stability of the numerical solutions in the case that the bifurcation parameter is less than the bifurcation point  $\tau_0$ : (a)  $\tau = 0.2$  and (b)  $\tau = 1.5$ . On the contrary, the periodic solutions are illustrated in Figure 4-5. The bifurcation values are chosen as (a)  $\tau = 1.8$  and (b)  $\tau = 2.4$ , which they are larger than the bifurcation point  $\tau_0$ .



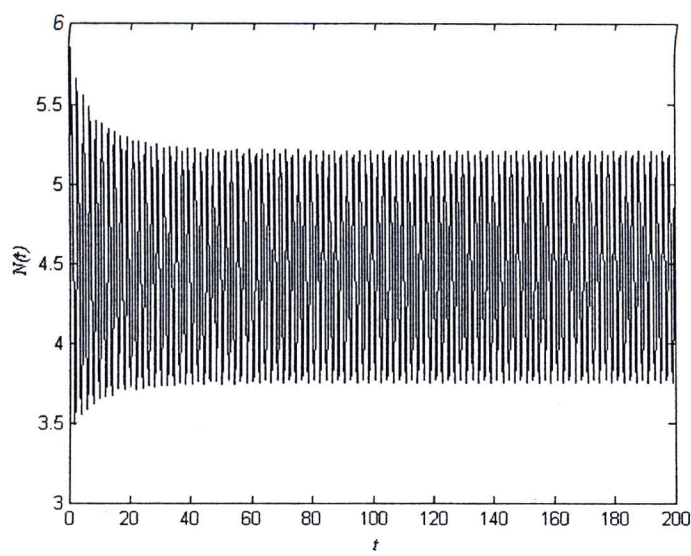


(a)  $\tau = 0.2$

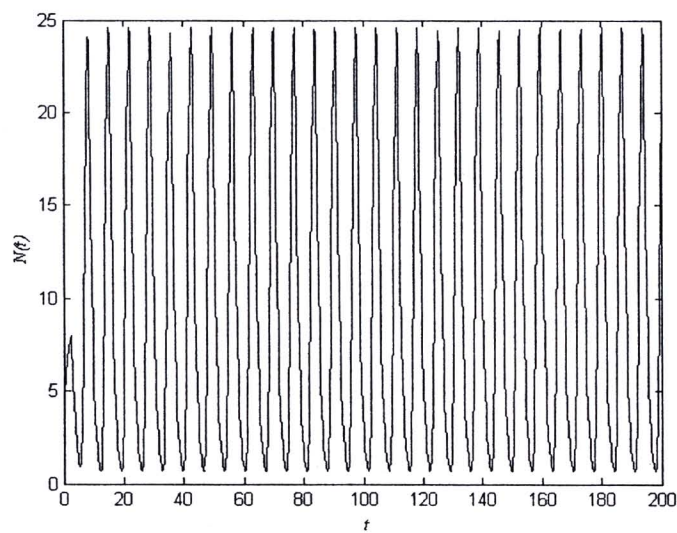


(b)  $\tau = 1.5$

**FIGURE 4-4** Numerical solutions of (4-35) showing the asymptotic stability of equilibria with different values of  $\tau$ .



(a)  $\tau = 1.80$



(b)  $\tau = 2.40$

**FIGURE 4-5** Numerical solutions of (4-35) present the periodic solutions about equilibria with different values of  $\tau$ .