

# DELAY DIFFERENTIAL EQUATIONS IN SINGLE SPECIES DYNAMICS

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O. Arino et al. (eds.), *Delay Differential Equations and Applications*, Springer, Berlin, 2006, pp.477-517.

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## 1. INTRODUCTION

Time delays of one type or another have been incorporated into biological models to represent resource regeneration times, maturation periods, feeding times, reaction times, etc. by many researchers. We refer to the monographs of Cushing (1977a), Gopalsamy (1992), Kuang (1993) and MacDonald (1978) for discussions of general delayed biological systems. In general, delay differential equations exhibit much more complicated dynamics than ordinary differential equations since a time delay could cause a stable equilibrium to become unstable and cause the populations to fluctuate. In this survey, we shall review various delay differential equations models arising from studying single species dynamics.

Let  $x(t)$  denote the population size at time  $t$ ; let  $b$  and  $d$  denote the birth rate and death rate, respectively, on the time interval  $[t, t + \Delta t]$ , where  $\Delta t > 0$ . Then

$$x(t + \Delta t) - x(t) = bx(t)\Delta t - dx(t)\Delta t.$$

Dividing by  $\Delta t$  and letting  $\Delta t$  approach zero, we obtain

$$(1.1) \quad \frac{dx}{dt} = bx - dx = rx,$$

where  $r = b - d$  is the intrinsic growth rate of the population. The solution of equation (1.1) with an initial population  $x(0) = x_0$  is given by

$$(1.2) \quad x(t) = x_0 e^{rt}.$$

The function (1.2) represents the traditional exponential growth if  $r > 0$  or decay if  $r < 0$  of a population. Such a population growth, due to Malthus (1798), may be valid for a short period, but it cannot go on forever. Taking the fact that resources are limited into account, Verhulst (1836) proposed the logistic equation

$$(1.3) \quad \frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right),$$

where  $r(> 0)$  is the *intrinsic growth rate* and  $K(> 0)$  is the *carrying capacity* of the population. In model (1.3), when  $x$  is small the population grows as in the Malthusian model (1.1); when  $x$  is large the members of the species compete with each other for the limited resources. Solving (1.3) by separating the variables, we obtain ( $x(0) = x_0$ )

$$(1.4) \quad x(t) = \frac{x_0 K}{x_0 - (x_0 - K)e^{-rt}}.$$

If  $x_0 < K$ , the population grows, approaching  $K$  asymptotically as  $t \rightarrow \infty$ . If  $x_0 > K$ , the population decreases, again approaching  $K$  asymptotically as  $t \rightarrow \infty$ . If  $x_0 = K$ , the population remains in time at  $x = K$ . In fact,  $x = K$  is called an *equilibrium* of equation (1.3). Thus, the positive equilibrium  $x = K$  of the logistic equation (1.3) is globally stable; that is,  $\lim_{t \rightarrow \infty} x(t) = K$  for solution  $x(t)$  of (1.3) with any initial value  $x(0) = x_0$ .

## 2. HUTCHINSON'S EQUATION

In the above logistic model it is assumed that the growth rate of a population at any time  $t$  depends on the relative number of individuals at that time. In practice, the process of reproduction is not instantaneous. For example, in a *Daphnia* a large clutch presumably is determined not by the concentration of unconsumed food available when the eggs hatch, but by the amount of food available when the eggs were forming, some time before they pass into the brood pouch. Between this time of determination and the time of hatching many newly hatched animals may have been liberated from the brood pouches of other *Daphnia* in the culture, so increasing the population. In fact, in an extreme case all the vacant spaces  $K - x$  might have been filled well before reproduction stops. Hutchinson (1948) assumed egg formation to occur  $\tau$  units of time before hatching and proposed the following more realistic logistic equation

$$(2.1) \quad \frac{dx}{dt} = rx(t) \left[ 1 - \frac{x(t - \tau)}{K} \right],$$

where  $r$  and  $K$  have the same meaning as in the logistic equation (1.3),  $\tau > 0$  is a constant. Equation (2.1) is often referred to as the *Hutchinson's equation* or *delayed logistic equation*.

**2.1. Stability and Bifurcation.** The initial value of equation (2.1) is given by

$$x(\theta) = \phi(\theta) > 0, \quad \theta \in [-\tau, 0],$$

where  $\phi$  is continuous on  $[-\tau, 0]$ . An equilibrium  $x = x^*$  of (2.1) is *stable* if for any given  $\epsilon > 0$  there is a  $\delta > 0$  such that  $|\phi(t) - x^*| \leq \delta$  on  $[-\tau, 0]$  implies that all solutions  $x(t)$  of (2.1) with initial value  $\phi$  on  $[-\tau, 0]$  satisfy  $|x(t) - x^*| < \epsilon$  for all  $t \geq 0$ . If in addition there is a  $\delta_0 > 0$  such that  $|\phi(t) - x^*| \leq \delta_0$  on  $[-\tau, 0]$  implies  $\lim_{t \rightarrow \infty} x(t) = x^*$ , then  $x^*$  is called *asymptotically stable*.

Notice that equation (2.1) has equilibria  $x = 0$  and  $x = K$ . Small perturbations from  $x = 0$  satisfy the linear equation  $\frac{dx}{dt} = rx$ , which shows that  $x = 0$  is unstable with exponential growth. We thus only need to consider the stability of the positive equilibrium  $x = K$ . Let  $X = x - K$ . Then,

$$\frac{dX}{dt} = -rX(t - \tau) - \frac{r}{K}X(t)X(t - \tau).$$

Thus, the linearized equation is

$$(2.2) \quad \frac{dX}{dt} = -rX(t - \tau).$$

We look for solutions of the form  $X(t) = ce^{\lambda t}$ , where  $c$  is a constant and the eigenvalues  $\lambda$  are solutions of the characteristic equation

$$(2.3) \quad \lambda + re^{-\lambda\tau} = 0,$$

which is a transcendental equation. By the linearization theory,  $x = K$  is asymptotically stable if all eigenvalues of (2.3) have negative real parts.

Set  $\lambda = \mu + i\nu$ . Separating the real and imaginary parts of the characteristic equation (2.3), we obtain

$$(2.4) \quad \begin{aligned} \mu + re^{-\mu\tau} \cos \nu\tau &= 0, \\ \nu - re^{-\mu\tau} \sin \nu\tau &= 0. \end{aligned}$$

Notice that when  $\tau = 0$ , the characteristic equation (2.3) becomes  $\lambda + r = 0$  and the eigenvalue  $\lambda = -r < 0$  is a negative real number. We seek conditions on  $\tau$  such that  $\operatorname{Re}\lambda$  changes from negative to positive. By the continuity, if  $\lambda$  changes from  $-r$  to a value such that  $\operatorname{Re}\lambda = \mu > 0$  when  $\tau$  increases, there must be some value of  $\tau$ , say  $\tau_0$ , at which  $\operatorname{Re}\lambda(\tau_0) = \mu(\tau_0) = 0$ . In other words, the characteristic equation (2.3) must have a pair of purely imaginary roots  $\pm i\nu_0$ ,  $\nu_0 = \nu(\tau_0)$ . Suppose such is the case. Then we have

$$\cos \nu_0\tau = 0,$$

which implies that

$$\nu_0\tau_k = \frac{\pi}{2} + 2k\pi, \quad k = 0, 1, 2, \dots$$

Noting that  $\nu_0 = r$ , we have

$$\tau_k = \frac{\pi}{2r} + \frac{2k\pi}{r}, \quad k = 0, 1, 2, \dots$$

Therefore, when

$$\tau = \tau_0 = \frac{\pi}{2r},$$

equation (2.3) has a pair of purely imaginary roots  $\pm ir$ , which are simple and all other roots have negative real parts. When  $0 < \tau < \frac{\pi}{2r}$ , all roots of (2.3) have strictly negative real parts.

Denote  $\lambda(\tau) = \mu(\tau) + i\nu(\tau)$  the root of equation (2.3) satisfying  $\mu(\tau_k) = 0$ ,  $\nu(\tau_k) = \nu_0$ ,  $k = 0, 1, 2, \dots$ . We have the transversality condition

$$\left. \frac{d\mu}{d\tau} \right|_{\tau=\tau_k} = r^2 > 0, \quad k = 0, 1, 2, \dots$$

We have just shown the following conclusions.

- Theorem 1.**
- (i) If  $0 \leq r\tau < \frac{\pi}{2}$ , then the positive equilibrium  $x = K$  of equation (2.1) is asymptotically stable.
  - (ii) If  $r\tau > \frac{\pi}{2}$ , then  $x = K$  is unstable.
  - (iii) When  $r\tau = \frac{\pi}{2}$ , a Hopf bifurcation occurs at  $x = K$ ; that is, periodic solutions bifurcate from  $x = K$ . The periodic solutions exist for  $r\tau > \frac{\pi}{2}$  and are stable.

The above theorem can be illustrated by Fig. 1, where the solid curves represent stability while the dashed lines indicated instability.

By (iii), the Hutchinson's equation (2.1) can have periodic solutions for a large range of values of  $r\tau$ , the product of the birth rate  $r$  and the delay  $\tau$ . If  $T$  is the period then  $x(t+T) = x(t)$  for all  $t$ . Roughly speaking, the stability of a periodic solution means that if a perturbation is imposed the solution returns to the original periodic solution as  $t \rightarrow \infty$  with possibly a phase shift. The period of the solution

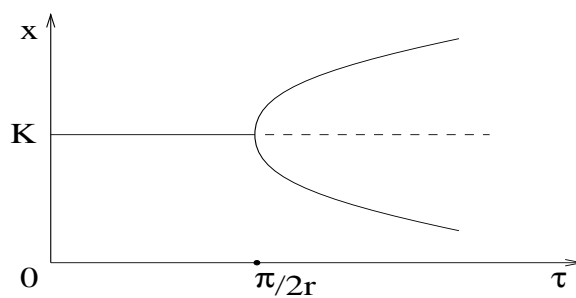


FIGURE 1. The bifurcation diagram for equation (2.1).

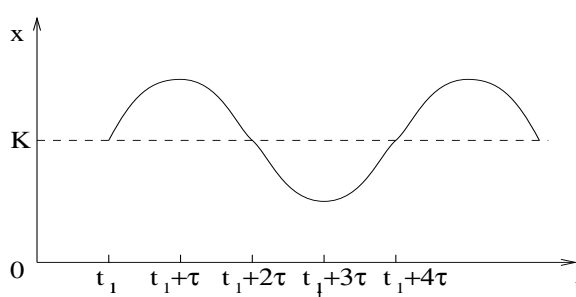


FIGURE 2. The periodic solution of the Hutchinson's equation (2.1).

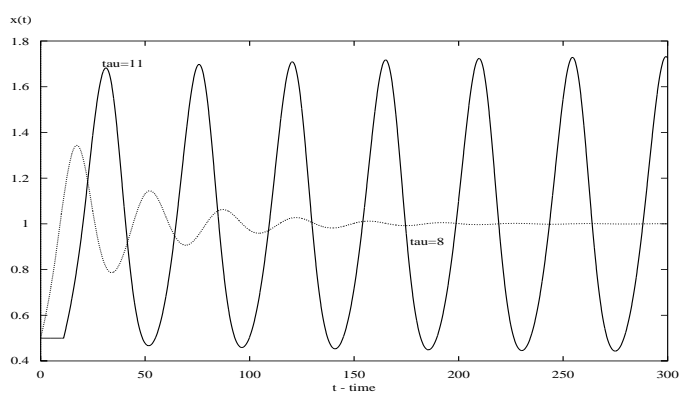


FIGURE 3. Numerical simulations for the Hutchinson's equation (2.1). Here  $r = 0.15$ ,  $K = 1.00$ . (i) When  $\tau = 8$ , the steady state  $x^* = 1$  is stable; (ii) When  $\tau = 11$ , a periodic solution bifurcated from  $x^* = 1$ .

at the critical delay value is  $\frac{2\pi}{\nu_0}$  (Hassard et al. (1981)), thus, it is  $4\tau$  (see Fig. 2). Numerical simulations are given in Fig. 3.

**2.2. Wright Conjecture.** The Hutchinson's equation (2.1) can be written as

$$\frac{dy}{dt} = -ry(t - \tau)[1 + y(t)]$$

by assuming  $y(t) = -1 + x(t)/K$ . Letting  $t = \tau\bar{t}$ ,  $\bar{y}(\bar{t}) = y(t)$ , we have

$$\frac{d}{d\bar{t}}\bar{y}(\bar{t}) = -r\tau\bar{y}(\bar{t} - 1)[1 + \bar{y}(\bar{t})].$$

Denoting  $\alpha = r\tau$  and dropping the bars, we obtain

$$(2.5) \quad \frac{dy}{dt} = -\alpha y(t - 1)[1 + y(t)].$$

By Theorem 1, we know that the zero solution of (2.5) is asymptotically stable if  $\alpha < \pi/2$  and unstable if  $\alpha > \pi/2$ . Wright (1955) showed that the zero solution of (2.5) is globally stable of  $\alpha < 3/2$ . Wright then conjectured that the zero solution of (2.5) is globally stable if  $\alpha < \pi/2$ , which is still open.

Kakutani and Markus (1958) proved that all solutions of (2.5) oscillate if  $\alpha > 1/e$  and do not oscillate if  $\alpha < 1/e$ . Jones (1962a, 1962b) studied the global existence of periodic solutions for  $\alpha > \pi/2$ . For further research on existence of non-constant periodic solutions, see Haderler and Tomiuk (1977), Hale and Verduyn Lunel (1993), Kaplan and York (1975), Naussbaum (1974), Walther (1975), etc. See also Kuang (1993) for further results and more references.

Recently, some attention has been paid to the study of equation (2.5) when  $\alpha = \alpha(t)$  is a positive continuous function. For example, Sugie (1992) showed that the zero solution of (2.5) with  $\alpha = \alpha(t)$  is uniformly stable if there is a constant  $\alpha_0 > 0$  such that

$$(2.6) \quad \alpha(t) \leq \alpha_0 < \frac{3}{2} \text{ for all } t \geq 0.$$

Chen et al. (1995) improved condition (2.6) to the following:

$$(2.7) \quad \int_{t-1}^t \alpha(s)ds \leq \alpha_0 < \frac{3}{2} \text{ for } t \geq 1.$$

Stability conditions such as (2.6) and (2.7) are called  $\frac{3}{2}$ -*stability criteria*. For further related work, we refer to Kuang (1993), Yu (1996) and the references therein.

**2.3. Instantaneous Dominance.** Consider a logistic equation with a discrete delay of the form

$$(2.8) \quad \frac{dx}{dt} = rx(t)[1 - a_1x(t) - a_2x(t - \tau)],$$

where  $a_1$  and  $a_2$  are positive constants. There is a positive equilibrium  $x^* = \frac{1}{a_1 + a_2}$ , which is stable when there is no delay. Employing similar arguments, one can prove the following results.

**Theorem 2.** (i) *If  $a_1 \geq a_2$ , then the steady state  $x^* = \frac{1}{a_1 + a_2}$  is asymptotically stable for all delay  $\tau \geq 0$ .*

(ii) If  $a_1 < a_2$ , then there is a critical value  $\tau_0$  given by

$$\tau_0 = \frac{a_1 + a_2}{r\sqrt{a_2^2 - a_1^2}} \arcsin \frac{\sqrt{a_2^2 - a_1^2}}{a_2},$$

such that  $x^* = \frac{1}{a_1 + a_2}$  is asymptotically stable when  $\tau \in [0, \tau_0)$  and unstable when  $\tau > \tau_0$ . A Hopf bifurcation occurs at  $x^*$  when  $\tau$  passes through  $\tau_0$ .

The above result indicates that if  $a_1 \geq a_2$ , that is, if the instantaneous term is dominant, then the steady state  $x^* = \frac{1}{a_1 + a_2}$  is asymptotically stable for all delay  $\tau \geq 0$ . In fact, we can show that it is asymptotically stable for any initial value, that is, globally stable.

**Theorem 3.** If  $a_1 > a_2$ , then the steady state  $x^* = \frac{1}{a_1 + a_2}$  of (2.8) is globally stable.

*Proof.* Suppose  $x$  is a continuous function from  $[-\tau, r)$  to  $R$  and denote  $x_t(\theta) = x(t + \theta)$ ,  $\theta \in [-\tau, 0]$ . Choose a Liapunov function of the form

$$(2.9) \quad V(x(t), x_t(\theta)) = x - x^* - x^* \ln \frac{x}{x^*} + \xi \int_{-\tau}^0 [x_t(\theta)]^2 d\theta,$$

where  $\xi > 0$  is a constant to be determined. Rewrite equation (2.8) as follows:

$$(2.10) \quad \frac{dx}{dt} = rx(t)[-a_1(x(t) - x^*) - a_2(x(t - \tau) - x^*)].$$

Then we have

$$\begin{aligned} \left. \frac{dV}{dt} \right|_{(2.10)} &= \frac{dx}{dt} \frac{x - x^*}{x} + \xi [(x(t) - x^*)^2 - (x(t - \tau) - x^*)^2] \\ &= -\{(ra_1 - \xi)[x(t) - x^*]^2 + ra_2[x(t) - x^*][x(t - \tau) - x^*] \\ &\quad + \xi[x(t - \tau) - x^*]^2\}. \end{aligned}$$

If  $a_1 > a_2$ , choose  $\xi = \frac{1}{2}ra_1$ , so  $\left. \frac{dV}{dt} \right|_{(2.10)}$  is negatively definite and the result follows.  $\square$

### 3. RECRUITMENT MODELS

**3.1. Nicholson's Blowflies Model.** The Hutchinson's equation (2.1) can be used to explain several experimental situations, including Nicholson's (1954) careful experimental data of the Australian sheep-blowfly (*Lucila cuprina*). Over a period of nearly two years Nicholson recorded the population of flies and observed a regular basic periodic oscillation of about 35-40 days. To apply the Hutchinson's equation (2.1),  $K$  is set by the food level available,  $\tau$  is approximately the time for a larva to mature into an adult. The only unknown parameter is  $r$ , the intrinsic growth rate of the population. If we take the observed period as 40 days, then the delay is about 9 days: the actual delay is about 15 days.

To overcome the discrepancy in estimating the delay value, Gurney et al. (1980) tried to modified Hutchinson's equation. Notice that Nicholson's data on blowflies consist primarily of observations of the time variation of adult population. Let  $x(t)$  denote the population of sexually mature adults. Then the rate of change of  $x(t)$

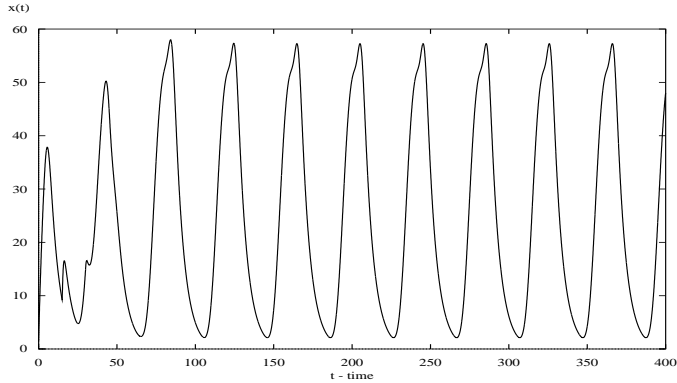


FIGURE 4. Oscillations in the Nicholson's blowflies equation (3.1). Here  $P = 8$ ,  $x_0 = 4$ ,  $\delta = 0.175$ , and  $\tau = 15$ .

is the instantaneous rate of recruitment to the adult population  $R(t)$  minus the instantaneous total death rate  $D(t)$  :

$$\frac{dx}{dt} = R(t) - D(t).$$

To express  $R(t)$  we have to consider the populations of all the various stages in the life-history of the species concerned and make the following assumptions:

- (i) all eggs take exactly  $\tau$  time units to develop into sexually mature adults;
- (ii) the rate at which the adult population produces eggs depends only on its current size;
- (iii) the probability of a given egg maturing into a viable adult depends only on the number of competitors of the same age.

These imply that the rate of recruitment at time  $t + \tau$  is a function only of the instantaneous size of the adult population at time  $t$ . Assume that the average per capita fecundity drops exponentially with increasing population, thus

$$R(t + \tau) = \theta(x(t)) = Px(t) \exp[-x(t)/x_0],$$

where  $P$  is the maximum per capita daily egg production rate,  $x_0$  is the size at which the blowflies population reproduces at its maximum rate, and  $\delta$  is the per capita daily adult death rate.

Assume that the per capita adult death rate has a time and density independent value  $\delta$ . The additional assumption that the total death rate  $D(t)$  is a function only of the instantaneous size of the adult population

$$D(t) = \phi(x(t)) = \delta x(t)$$

enables the entire population dynamics to be expressed in the delay differential equation

$$(3.1) \quad \frac{dx}{dt} = Px(t - \tau) \exp\left[-\frac{x(t - \tau)}{x_0}\right] - \delta x(t).$$



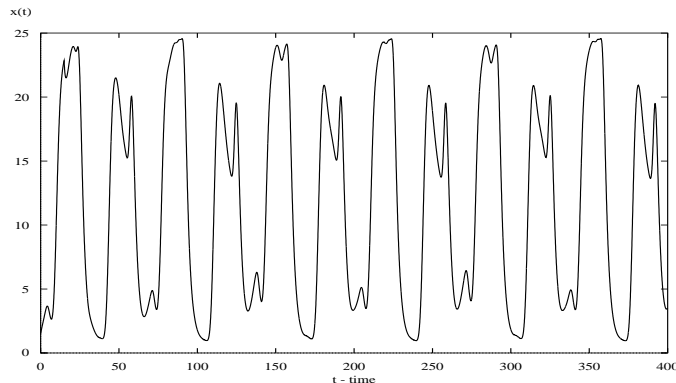


FIGURE 5. Aperiodic oscillations in the Nicholson's blowflies equation (3.1). Here  $P = 8$ ,  $x_0 = 4$ ,  $\delta = 0.475$ , and  $\tau = 15$ .

There is a positive equilibrium

$$x^* = x_0 \ln(P/\delta)$$

if the maximum possible per capita reproduction rate is greater than the per capita death rate, that is, if  $P > \delta$ . As in the Hutchinson's equation, there is a critical value of the time delay. The positive equilibrium is stable when the delay is less the critical value, becomes unstable when it is greater the value, and there are oscillations. Testing Nicholson's data, equation (3.1) not only provides self-sustaining limit cycles as the Hutchinson's equation did, but also gives an accurate measurement of the delay value as 15 days. Gurney et al. (1980) showed that the fluctuations observed by Nicholson are quite clear, of limit-cycle type (see Fig. 4). The period of the cycles is set mainly by the delay and adult death rate. High values of  $P\tau$  and  $\delta\tau$  will give large amplitude cycles. Moving deeper into instability produces a number of successive doublings of the repeated time until a region is reached where the solution becomes aperiodic (chaotic). See Fig. 5.

Equation (3.1) is now referred to as the *Nicholson's blowflies equation*, see Nisbet and Gurney (1982), Kulenović et al. (1992), So and Yu (1994), Smith (1995), Györi and Trofimchuk(2002), etc.

**3.2. Houseflies Model.** To describe the oscillations of the adult numbers in laboratory populations of houseflies *Musca domestica*, Taylor and Sokal (1976) proposed the delay equation

$$(3.2) \quad \frac{dx}{dt} = -dx(t) + bx(t - \tau)[k - bz x(t - \tau)],$$

where  $x(t)$  is the number of adults,  $d > 0$  denotes the death rate of adults, the time delay  $\tau > 0$  is the length of the developmental period between oviposition and eclosion of adults. The number of eggs laid is assumed to be proportional to the number of adults, so at time  $t - \tau$  the number of new eggs would be  $bx(t - \tau)$ , where  $b > 0$  is the number of eggs laid par adult.  $k - bz x(t - \tau)$  represents the egg-to-adult survival rate, where  $k > 0$  is the maximum egg-adult survival rate, and  $z$  is the

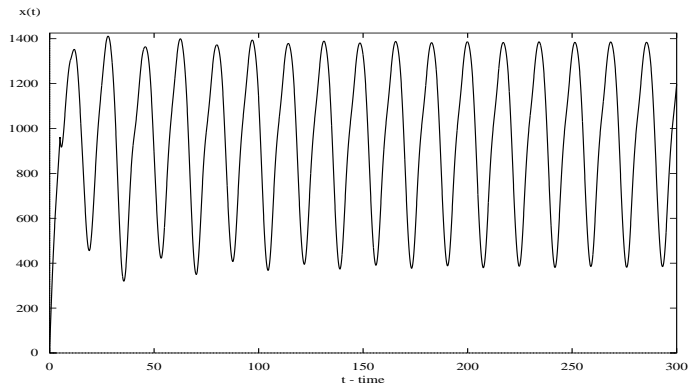


FIGURE 6. Numerical simulations in the houseflies model (3.2). Here the parameter values  $b = 1.81, k = 0.5107, d = 0.147, z = 0.000226, \tau = 5$  were reported in Taylor and Sokal (1976).

reduction in survival produced by each additional egg. Notice that when there is no time delay, i.e.,  $\tau = 0$ , then the equation becomes the familiar logistic equation.

Though analytical analysis of equation (3.2) has never been carried out, numerical simulations indicate that its dynamics are very similar to that of the Nicholson's blowflies equation (see Fig. 6). However, unlike the Nicholson's model, aperiodic oscillations have not been observed.

**3.3. Recruitment Models.** Blythe et al. (1982) proposed a general single species population model with a time delay

$$(3.3) \quad \frac{dx}{dt} = R(x(t - \tau)) - Dx(t),$$

where  $R$  and  $D$  represent the rates of recruitment to, and death rate from, an adult population of size  $x$ , and  $\tau > 0$  is the maturation period. For a linear analysis of the model, see Brauer and Castillo-Chávez (2001).

This equation could exhibit very complex dynamic behavior for some functions  $R$ , such as  $R(x(t - \tau)) = Px(t - \tau) \exp[-x(t - \tau)/x_0]$  in the Nicholson's blowflies equation. However, for some other functions, for example

$$R(x(t - \tau)) = \frac{bx^2(t - \tau)}{x(t - \tau) + x_0} \left[ 1 - \frac{x(t - \tau)}{K} \right]$$

as in Beddington and May (1975), the time delay is not necessarily destabilizing (see also Rodríguez (1998)).

Freedman and Gopalsamy (1986) studied three classes of general single species models with a single delay and established criteria for the positive equilibrium to be globally stable independent of the length of delay. See also Cao and Gard (1995), Karakostas et al. (1992).

## 4. THE ALLEE EFFECT

The logistic equation was based on the assumption that the density has a negative effect on the per-capita growth rate. However, some species often cooperate among themselves in their search for food and to escape from their predators. For example some species form hunting groups (packs, prides, etc.) to enable them to capture large prey. Fish and birds often form schools and flocks as a defense against their predators. Some parasitic insects aggregate so that they can overcome the defense mechanism of a host. A number of social species such as ants, termites, bees, etc., have developed complex cooperative behavior involving division of labor, altruism, etc. Such cooperative processes have a positive feedback influence since individuals have been provided a greater chance to survive and reproduce as density increase. Aggregation and associated cooperative and social characteristics among members of a species were extensively studied in animal populations by Allee (1931), the phenomenon in which reproduction rates of individuals decrease when density drops below a certain critical level is now known as the *Allee effect*.

Gopalsamy and Ladas (1990) proposed a single species population model exhibiting the Allee effect in which the per capita growth rate is a quadratic function of the density and is subject to time delays:

$$(4.1) \quad \frac{dx}{dt} = x(t)[a + bx(t - \tau) - cx^2(t - \tau)],$$

where  $a > 0, c > 0, \tau \geq 0$ , and  $b$  are real constants. In the model, when the density of the population is not small, the positive feedback effects of aggregation and cooperation are dominated by density-dependent stabilizing negative feedback effects due to intraspecific competition. In other words, intraspecific mutualism dominates at low densities and intraspecific competition dominates at higher densities.

Equation (4.1) has a positive equilibrium

$$x^* = \frac{b + \sqrt{b^2 + 4ac}}{2c}.$$

Gopalsamy and Ladas (1990) showed that under some restrictive assumptions, the positive equilibrium is globally attractive (see Fig. 7). If the delay is sufficiently large, solutions of equation (4.1) oscillate about the positive equilibrium. See also Cao and Gard (1995). The following result is a corollary of the main results of Liz et al. (2003).

**Theorem 4.** *If*

$$\tau x^*(2cx^* - b) \leq \frac{3}{2},$$

*then the equilibrium  $x^*$  attracts all positive solutions of (4.1).*

Ladas and Qian (1994) generalized (4.1) to the form

$$(4.2) \quad \frac{dx}{dt} = x(t)[a + bx^p(t - \tau) - cx^q(t - \tau)],$$

where  $p, q$  are positive constants, and discussed oscillation and global attractivity in the solutions.

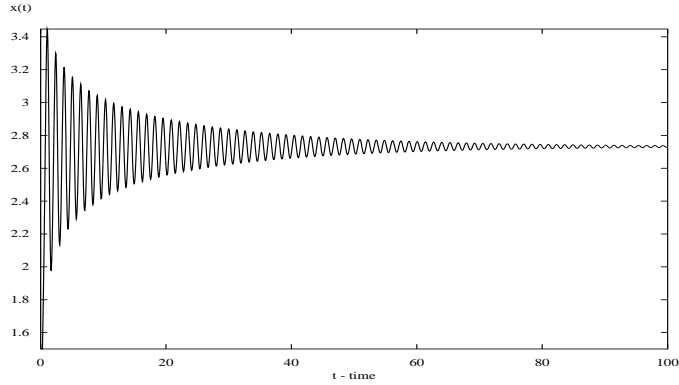


FIGURE 7. The steady state of the delay model (4.1) is attractive. Here  $a = 1, b = 1, c = 0.5, \tau = 0.2$ .

## 5. FOOD-LIMITED MODELS

Rewriting the logistic equation (2.1) as

$$\frac{1}{x(t)} \frac{dx}{dt} = r \left( 1 - \frac{x}{K} \right),$$

we can see that the average growth rate of a population is a linear function of its density. In experiments of bacteria cultures *Daphnia magna* Smith (1963) found that the average growth rate  $(1/x)(dx/dt)$  is not a linear function of the density. Smith argued that the per capita growth rate of a population is proportional to the rate of food supply not momentarily being used. This results in the model:

$$(5.1) \quad \frac{1}{x} \frac{dx}{dt} = r \left( 1 - \frac{F}{T} \right),$$

where  $F$  is the rate at which a population of biomass  $x$  consumes resources, and  $T$  is the rate at which the population uses food when it is at the equilibrium  $K$ . Note that  $F/T$  is not usually equal to  $x/K$ . It is assumed that  $F$  depends on the density  $x$  (that is being maintained) and  $dx/dt$  (the rate of change of the density) and takes the following form:

$$F = c_1 x + c_2 \frac{dx}{dt}, \quad c_1 > 0, \quad c_2 \geq 0.$$

When saturation is attained,  $dx/dt = 0, x = K$  and  $T = F$ . Thus,  $T = c_1 K$  and equation (5.1) becomes

$$\frac{1}{x} \frac{dx}{dt} = r \left[ 1 - \frac{c_1 x + c_2 \frac{dx}{dt}}{c_1 K} \right].$$

If we let  $c = c_2/c_1 \geq 0$ , the above equation can be simplified to the form

$$(5.2) \quad \frac{1}{x(t)} \frac{dx(t)}{dt} = r \left[ \frac{K - x(t)}{K + rcx(t)} \right],$$

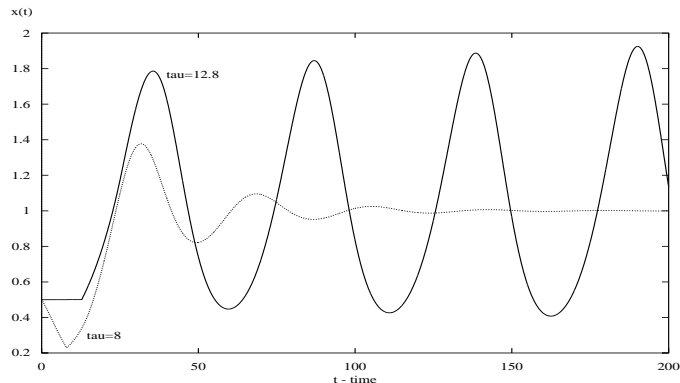


FIGURE 8. The steady state of the delay food-limited model (5.3) is stable for small delay ( $\tau = 8$ ) and unstable for large delay ( $\tau = 12.8$ ). Here  $r = 0.15$ ,  $K = 1.00$ ,  $c = 1$ .

which is referred to as the *food-limited* population model. Equation (5.2) has also been discussed by Hallam and DeLuna (1984) in studying the effects of environmental toxicants on populations.

Gopalsamy et al. (1988) introduced a time delay  $\tau > 0$  into (5.2) and obtained the delayed food-limited model

$$(5.3) \quad \frac{dx}{dt} = rx(t) \left[ \frac{K - x(t - \tau)}{K + rcx(t - \tau)} \right].$$

They studied global attractivity of the positive equilibrium  $x^* = K$  and oscillation of solutions about  $x^* = K$  (see Fig. 8). The dynamics are very similar to the Hutchinson's model.

For other related work on equation (5.3) and its generalizations, see Gopalsamy et al. (1990a), Grove et al. (1993), So and Yu (1995), Qian (1996), etc.

## 6. REGULATION OF HAEMATOPOIESIS

Haematopoiesis is the process by which primitive stem cells proliferate and differentiate to produce mature blood cells. It is driven by highly coordinated patterns of gene expression under the influence of growth factors and hormones. The regulation of haematopoiesis is about the formation of blood cell elements in the body. White and red blood cells are produced in the bone marrow from where they enter the blood stream. The principal factor stimulating red blood cell production is the hormone produced in the kidney, called erythropoiesin. About 90% of the erythropoiesin is secreted by renal tubular epithelial cells when blood is unable to deliver sufficient oxygen. When the level of oxygen in the blood decreases this leads to a release of a substance, which in turn causes an increase in the release of the blood elements from the marrow. There is a feedback from the blood to the bone marrow. Abnormalities in the feedback are considered as major suspects in causing periodic haematological disease.

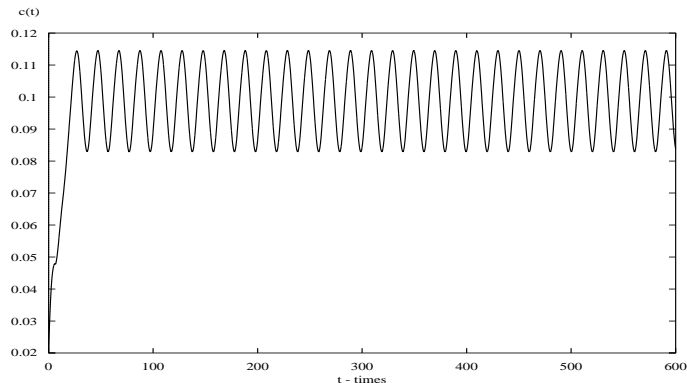


FIGURE 9. Oscillations in the Mackey-Glass model (6.1). Here  $\lambda = 0.2, a = 01, g = 0.1, m = 10$  and  $\tau = 6$ .

**6.1. Mackey-Glass Models.** Let  $c(t)$  be the concentration of cells (the population species) in the circulating blood with units  $\text{cells}/\text{mm}^3$ . Assume that the cells are lost at a rate proportional to their concentration, say,  $gc$ , where  $g$  has dimensions  $(\text{day}^{-1})$ . After the reduction in cells in the blood stream there is about a 6-day delay before the marrow releases further cells to replenish the deficiency. Assume the flux of cells into the blood stream depends on the cell concentration at an earlier time,  $c(t - \tau)$ , where  $\tau$  is the delay. Mackey and Glass (1977) suggested, among others, the following delay model for the blood cell population

$$(6.1) \quad \frac{dc}{dt} = \frac{\lambda a^m c(t - \tau)}{a^m + c^m(t - \tau)} - gc(t),$$

where  $\lambda, a, m, g$  and  $\tau$  are positive constants. The numerical simulations of equation (6.1) by Mackey and Glass (1977) (see also Mackey and Milton (1988)) indicate that there is a cascading sequence of bifurcating periodic solutions when the delay is increased (see Fig. 9). When the delay is further increased the periodic solutions becomes aperiodic and chaotic (see Fig. 10).

**6.2. Wazewska-Czyzewska and Lasota Model.** Another well-known model belongs to Wazewska-Czyzewska and Lasota (1976) which takes the form

$$(6.2) \quad \frac{dN}{dt} = -\mu N(t) + pe^{-\gamma N(t-\tau)},$$

where  $N(t)$  denotes the number of red-blood cells at time  $t$ ,  $\mu$  is the probability of death of a red-blood cell,  $p$  and  $\gamma$  are positive constants related to the production of red-blood cells per unit time and  $\tau$  is the time required to produce a red-blood cells. See also Arino and Kimmel (1986).

Global attractivity in the Mackey-Glass model (6.1) and the Lasota-Wazewska model (6.2) has been studied by Gopalsamy et al. (1990b), Karakostas et al. (1992), Kuang (1992) and Györi and Trofimchuk (1999). Liz et al. (2002) study these models when the delay is infinite.

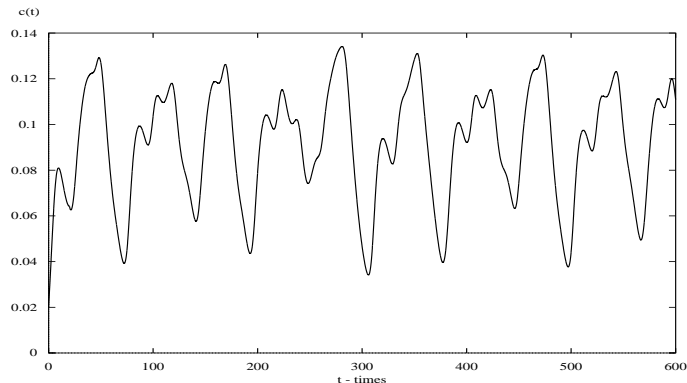


FIGURE 10. Aperiodic behavior of the solutions of the Mackey-Glass model (6.1). Here  $\lambda = 0.2, a = 0.1, g = 0.1, m = 10$  and  $\tau = 20$ .

Other types of delay physiological models can be found in Mackey and Milton (1988,1990) and Fowler and Mackey (2002).

## 7. A VECTOR DISEASE MODEL

Let  $y(t)$  denote the infected host population and  $x(t)$  be the population of uninfected human. Assume that the total host population is constant and is scaled so that

$$x(t) + y(t) = 1.$$

The disease is transmitted to the host by an insect vector, assumed to have a large and constant population, and by the host to that vector. Within the vector there is an incubation period  $\tau$  before the disease agent can infect a host. So the population of vectors capable of infecting the host is

$$z(t) = dy(t - \tau).$$

where  $d$  is the infective rate of the vectors. Infection of the host is assumed to proceed at a rate ( $e$ ) proportional to encounters between uninfected host and vectors capable of transmitting the disease,

$$ex(t) \cdot dy(t - \tau) = by(t - \tau)[1 - y(t)],$$

and recovery to proceed exponentially at a rate  $c$ . Thus,  $b$  is the contact rate. Infection leads neither to death, immunity or isolation. Based on these assumptions, Cooke (1978) proposed a delay model

$$(7.1) \quad \frac{dy}{dt} = by(t - \tau)[1 - y(t)] - cy(t).$$

Using the Liapunov functional method, he obtained the following results on global stability of the steady states.

**Theorem 5.** *For the vector disease model (7.1), we have the following:*

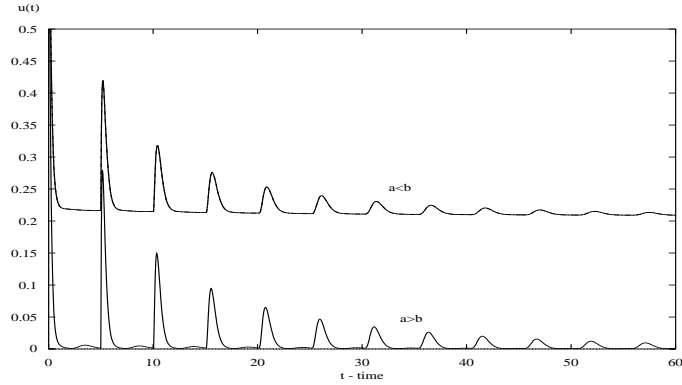


FIGURE 11. Numerical simulations for the vector disease equation (7.1). When  $a = 5.8, b = 4.8 (a > b)$ , the zero steady state  $u = 0$  is asymptotically stable; When  $a = 3.8, b = 4.8 (a < b)$ , the positive steady state  $u^*$  is asymptotically stable for all delay values; here for both cases  $\tau = 5$ .

- (i) If  $0 < b \leq a$ , then the steady state solution  $u_0 = 0$  is asymptotically stable and the set  $\{\phi \in ([-\tau, 0], R) : 0 \leq \phi(\theta) \leq 1 \text{ for } -\tau \leq \theta \leq 0\}$  is a region of attraction.
- (ii) If  $0 \leq a < b$ , then the steady state solution  $u_1 = (b - a)/b$  is asymptotically stable and the set  $\{\phi \in ([-\tau, 0], R) : 0 < \phi(\theta) \leq 1 \text{ for } -\tau \leq \theta \leq 0\}$  is a region of attraction.

The stability results indicate that there is a *threshold* at  $b = a$ . If  $b \leq a$ , then the proportion  $u$  of infectious individuals tends to zero as  $t$  becomes large and the disease dies out. If  $b > a$ , the proportion of infectious individuals tends to an endemic level  $u_1 = (b - a)/b$  as  $t$  becomes large. There is no non-constant periodic solutions in the region  $0 \leq u \leq 1$ . Numerical simulations are given in Fig. 11.

Busenberg and Cooke (1978) studied the existence of periodic solutions in the vector-host model (7.1) when  $b = b(t)$  is a positive periodic function.

## 8. MULTIPLE DELAYS

Kitching (1977) pointed out that the life cycle of the Australian blowfly *Lucila cuprina* has multiple time delay features which need to be considered in modelling its population. Based on this observation, Braddock and van den Driessche (1983) proposed the two delay logistic equation (see also Gopalsamy (1990))

$$(8.1) \quad \frac{dx}{dt} = rx(t)[1 - a_1x(t - \tau_1) - a_2x(t - \tau_2)],$$

where  $r, a_1, a_2, \tau_1$  and  $\tau_2$  are positive constants. Other equations with two delays appear in neurological models (Bélair and Campbell (1994)), physiological models (Beuter et al. (1993)), medical models (Bélair et al. (1995)), epidemiological models (Cooke and Yorke (1973)), etc. Very rich dynamics have been observed in such equations (Hale and Huang (1993), Mahaffy et al. (1995)).



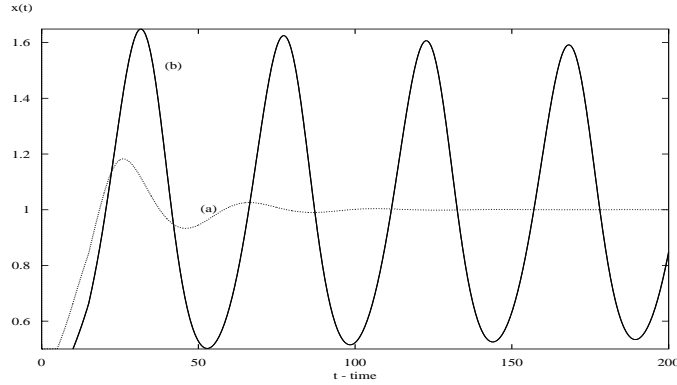


FIGURE 12. For the two delay logistic model (8.1), choose  $r = 0.15, a_1 = 0.25, a_2 = 0.75$ . (a) The steady state (a) is stable when  $\tau_1 = 15$  and  $\tau_2 = 5$  and (b) becomes unstable when  $\tau_1 = 15$  and  $\tau_2 = 10$ , a Hopf bifurcation occurs.

Equation (8.1) has a positive equilibrium  $x^* = 1/(a_1 + a_2)$ . Let  $x(t) = x^*(1 + X(t))$ . Then (8.1) becomes

$$(8.2) \quad \dot{X}(t) = -(1 + X(t))[A_1 X(t - \tau_1) + A_2 X(t - \tau_2)],$$

where  $A_1 = ra_1 x^*, A_2 = ra_2 x^*$ . The linearized equation of (8.2) at  $X = 0$  is

$$\dot{X}(t) = -A_1 X(t - \tau_1) - A_2 X(t - \tau_2).$$

Braddock and van den Driessche (1983) described some linear stability regions for equation (8.1) and observed stable limit cycles when  $\tau_2/\tau_1$  is large. Gopalsamy (1990) obtained stability conditions for the positive equilibrium. Using the results in Li et al. (1999), we can obtain the following theorem on the stability and bifurcation of equation (8.1).

**Theorem 6.** *If one of the following conditions is satisfied:*

- (i)  $A_1 < A_2$  and  $\tau_1 > 0$  such that  $\frac{\pi}{2\tau_1} < \sqrt{A_2^2 - A_1^2} < \frac{3\pi}{2\tau_1}$ ;
- (ii)  $A_2 < A_1$  and  $\bar{\tau}_1 > \frac{\pi}{2(A_1 + A_2)}$  such that  $\tau_1 \in [\frac{\pi}{2(A_1 + A_2)}, \bar{\tau}_1]$ , where

$$\bar{\tau}_1 = (A_1^2 - A_2^2)^{-\frac{1}{2}} \arcsin \sqrt{(A_1^2 - A_2^2)/A_1^2};$$

- (iii)  $A_1 = A_2$  and  $\tau_1 > \frac{1}{2A_1}$ ;

then there is a  $\tau_2^0 > 0$ , such that when  $\tau_2 = \tau_2^0$  the two-delay equation (8.1) undergoes a Hopf bifurcation at  $x^* = 1/(b + c)$ .

Lenhart and Travis (1986) studied the global stability of the multiple delay population model

$$(8.3) \quad \frac{dx}{dt} = x(t) \left[ r + ax(t) + \sum_{i=1}^n b_i x(t - \tau_i) \right].$$

Their global stability conditions very much depend on the negative, instantaneously dominated constant  $a$ . It would be interesting to determine the dynamics of the multiple-delay logistic equation without the negative instantaneously dominated term (see Kuang (1993))

$$(8.4) \quad \frac{dx}{dt} = rx(t) \left[ 1 - \sum_{i=1}^n \frac{x(t - \tau_i)}{K_i} \right].$$

## 9. VOLTERRA INTEGRODIFFERENTIAL EQUATIONS

The Hutchinson's equation (2.1) means that the regulatory effect depends on the population at a fixed earlier time  $t - \tau$ , rather than at the present time  $t$ . In a more realistic model the delay effect should be an average over past populations. This results in an equation with a *distributed delay* or an *infinite delay*. The first work using a logistic equation with distributed delay was by Volterra (1934) with extensions by Kostitzin (1939). In the 1930's, many experiments were performed with laboratory populations of some species of small organisms with short generation time. Attempts to apply logistic models to these experiments were often unsuccessful because populations died out. One of the causes was the pollution of the closed environment by waste products and dead organisms. Volterra (1934) used an integral term or a distributed delay term to examine a cumulative effect in the death rate of a species, depending on the population at all times from the start of the experiment. The model is an *integro-differential equation*

$$(9.1) \quad \frac{dx}{dt} = rx \left[ 1 - \frac{1}{K} \int_{-\infty}^t G(t-s)x(s)dx \right],$$

where  $G(t)$ , called the *delay kernel*, is a weighting factor which indicates how much emphasis should be given to the size of the population at earlier times to determine the present effect on resource availability. Usually the delay kernel is normalized so that

$$\int_0^{\infty} G(u)du = 1.$$

In this way we ensure that for equation (9.1) the equilibrium of the instantaneous logistic equation (1.3) remains an equilibrium in the presence of time delay. If  $G(u)$  is the Dirac function  $\delta(\tau - t)$ , where

$$\int_{-\infty}^{\infty} \delta(\tau - s)f(s)ds = f(\tau),$$

then equation (9.1) reduces to the discrete delay logistic equation

$$\frac{dx}{dt} = rx(t) \left[ 1 - \frac{1}{K} \int_{-\infty}^t \delta(t - \tau - s)x(s)dx \right] = rx(t) \left[ 1 - \frac{x(t - \tau)}{K} \right].$$

The *average delay* for the kernel is defined as

$$T = \int_0^{\infty} uG(u)du.$$

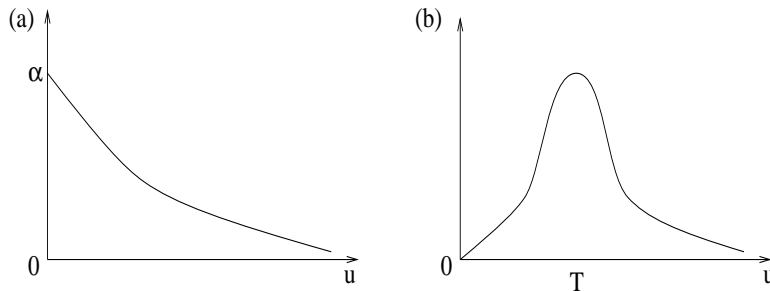


FIGURE 13. (a) Weak delay kernel and (b) strong delay kernel.

It follows that if  $G(u) = \delta(u - \tau)$ , then  $T = \tau$ , the discrete delay. We usually use the Gamma distribution delay kernel

$$(9.2) \quad G(u) = \frac{\alpha^n u^{n-1} e^{-\alpha u}}{(n-1)!}, \quad n = 1, 2, \dots$$

where  $\alpha > 0$  is a constant,  $n$  an integer, with the average delay  $T = n/\alpha$ . Two special cases,

$$G(u) = \alpha e^{-\alpha u} \quad (n = 1), \quad G(u) = \alpha^2 u e^{-\alpha u}; \quad (n = 2),$$

are called *weak delay kernel* and *strong delay kernel*, respectively. The weak kernel qualitatively indicates that the maximum weighted response of the growth rate is due to current population density while past densities have (exponentially) decreasing influence. On the other hand the strong kernel means that the maximum influence on growth rate response at any time  $t$  is due to population density at the previous time  $t - T$  (see Fig. 13).

The initial value for the integro-differential equation (9.1) is

$$(9.3) \quad x(\theta) = \phi(\theta) \geq 0, \quad -\infty < \theta \leq 0,$$

where  $\phi(\theta)$  is continuous on  $(-\infty, 0]$ . Following Volterra (1931) or Miller (1971), we can obtain existence, uniqueness, continuity and continuation about solutions to such a kind of integro-differential equations.

An equilibrium  $x^*$  of equation (9.1) is called *stable* if given any  $\epsilon > 0$  there exists a  $\delta = \delta(\epsilon) > 0$  such that  $|\phi(t) - x^*| \leq \delta$  for  $t \in (-\infty, 0]$  implies that any solution  $x(t)$  of (9.1) and (9.3) exists and satisfies  $|x(t) - x^*| < \epsilon$  for all  $t \geq 0$ . If in addition there exists a constant  $\delta_0 > 0$  such that  $|\phi(t) - x^*| \leq \delta_0$  on  $(-\infty, 0]$  implies  $\lim_{t \rightarrow \infty} x(t) = x^*$ , then  $x^*$  is called *asymptotically stable*.

**9.1. Weak Kernel.** To determine the stability of  $x^* = K$ , let us first consider the equation with a weak kernel, i.e.,

$$(9.4) \quad \frac{dx}{dt} = rx(t) \left[ 1 - \frac{1}{K} \int_{-\infty}^t \alpha e^{-\alpha(t-s)} x(s) ds \right].$$

Using the linear chain trick (Fargue (1973) and MacDonald (1978)), define

$$(9.5) \quad y(t) = \int_{-\infty}^t \alpha e^{-\alpha(t-s)} x(s) ds.$$

Then the scalar integro-differential equation (9.4) is equivalent to the following system of two ordinary differential equations

$$(9.6) \quad \begin{aligned} \frac{dx}{dt} &= rx(t) \left[1 - \frac{1}{K}y(t)\right], \\ \frac{dy}{dt} &= \alpha x(t) - \alpha y(t). \end{aligned}$$

Notice that the positive equilibrium of system (9.6) is  $(x^*, y^*) = (K, K)$ . To determine the stability of  $(x^*, y^*)$ , let  $X = x - x^*$ ,  $Y = y - y^*$ . The characteristic equation of the linearized system is given by

$$(9.7) \quad \lambda^2 + \alpha\lambda + \alpha r = 0,$$

which has roots

$$\lambda_{1,2} = -\frac{\alpha}{2} \pm \frac{1}{2}\sqrt{\alpha^2 - 4\alpha r}.$$

Therefore,  $\text{Re}\lambda_{1,2} < 0$ , which implies that  $x^* = K$  is locally asymptotically stable.

In fact,  $x^* = K$  is globally stable. Rewrite (9.1) as follows:

$$(9.8) \quad \begin{aligned} \frac{dx}{dt} &= -\frac{r}{K}x(t)(y(t) - y^*), \\ \frac{dy}{dt} &= \alpha(x(t) - x^*) - \alpha(y(t) - y^*). \end{aligned}$$

Choose a Liapunov function as follows

$$(9.9) \quad V(x, y) = x - x^* - x^* \ln \frac{x}{x^*} + \frac{r}{2\alpha K}(y - y^*)^2.$$

Along the solutions of (9.8), we have

$$\frac{dV}{dt} = \frac{dx}{dt} \frac{x - x^*}{x} + \frac{r}{\alpha K}(y - y^*) \frac{dy}{dt} = -\frac{r}{K}(y - y^*)^2 < 0.$$

Since the positive quadrant is invariant, it follows that solutions of system (9.8), and hence of (9.1), approach  $(x^*, y^*)$  as  $t \rightarrow \infty$ . Therefore,  $x(t) \rightarrow x^*$  as  $t \rightarrow \infty$ .

The above analysis can be summarized as the following theorem.

**Theorem 7.** *The positive equilibrium  $x^* = K$  of the logistic equation (9.1) with a weak kernel is globally stable (see Fig. 14).*

The result indicates that if the delay kernel is a weak kernel, the logistic equation with distributed delay has properties similar to the instantaneous logistic equation. We shall see that the logistic equation with a strong kernel exhibits richer dynamics similar to the logistic equation with a constant delay.

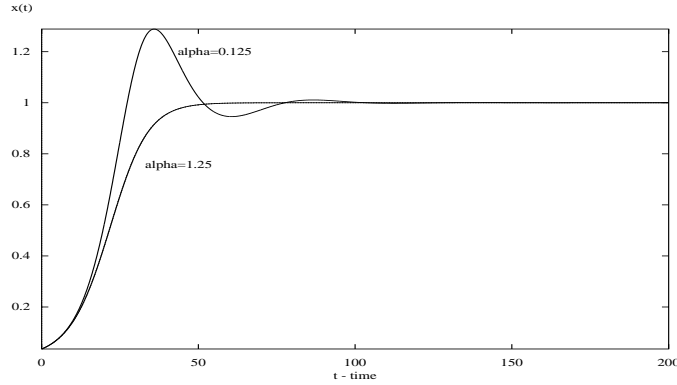


FIGURE 14. The steady state of the integrodifferential equation (9.1) is globally stable. Here  $r = 0.15$ ,  $K = 1.00$ .

9.2. **Strong Kernel.** Consider the logistic equation (9.1) with a strong kernel, i.e.,

$$(9.10) \quad \frac{dx}{dt} = rx(t) \left[ 1 - \frac{1}{K} \int_{-\infty}^t \alpha^2(t-s)e^{-\alpha(t-s)}x(t-s)ds \right].$$

To use the linear chain trick, define

$$y(t) = \int_{-\infty}^t \alpha e^{-\alpha(t-s)}x(s)ds, \quad z(t) = \int_{-\infty}^t \alpha^2(t-s)e^{-\alpha(t-s)}x(s)ds.$$

Then equation (9.10) is equivalent to the system

$$(9.11) \quad \begin{aligned} \frac{dx}{dt} &= rx(t) \left( 1 - \frac{1}{K}z(t) \right), \\ \frac{dy}{dt} &= \alpha x(t) - \alpha y(t), \\ \frac{dz}{dt} &= \alpha y(t) - \alpha z(t), \end{aligned}$$

which has a positive equilibrium  $(x^*, y^*, z^*) = (K, K, K)$ . Considering the linearization of (9.11) at  $(x^*, y^*, z^*)$ , we obtain the characteristic equation

$$(9.12) \quad \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0,$$

where

$$a_1 = 2\alpha, \quad a_2 = \alpha^2, \quad a_3 = r\alpha^2.$$

The Routh-Hurwitz criterion says that all roots of the equation (9.12) have negative real parts if and only if the following inequalities hold:

$$(9.13) \quad a_1 > 0, \quad a_3 > 0, \quad a_1a_2 - a_3 > 0.$$

Clearly,  $a_1 = 2\alpha > 0$ ,  $a_3 = r\alpha^2 > 0$ . The last inequality becomes

$$(9.14) \quad \alpha > \frac{r}{2}.$$

Thus, the equilibrium  $x^* = K$  is stable if  $\alpha > r/2$  and unstable if  $\alpha < r/2$ . Note that the average delay of the strong kernel is defined as  $T = 2/\alpha$ . Inequality (9.14)

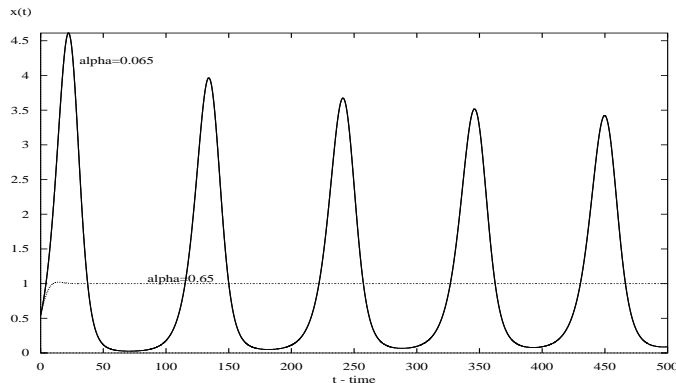


FIGURE 15. The steady state  $x^* = K$  of the integrodifferential equation (9.10) loses stability and a Hopf bifurcation occurs when  $\alpha$  changes from 0.65 to 0.065. Here  $r = 0.15$ ,  $K = 1.00$ .

then becomes

$$(9.15) \quad T < \frac{4}{r}.$$

Therefore, the equilibrium  $x^* = K$  is stable for “short delays” ( $T < 4/r$ ) and is unstable for “long delays” ( $T > 4/r$ ).

When  $T = T_0 = 4/r$ , (9.12) has a negative real root  $\lambda_1 = -r$  and a pair of purely imaginary roots  $\lambda_{2,3} = \pm i\frac{r}{2}$ . Denote by

$$\lambda(T) = \mu(T) + i\nu(T)$$

the complex eigenvalue of (9.12) such that  $u(T_0) = 0$ ,  $\nu(T_0) = r/2$ . We can verify that

$$(9.16) \quad \left. \frac{d\mu}{dT} \right|_{T=\frac{4}{r}} = \frac{8}{5}r^2 > 0.$$

The transversality condition (9.16) thus implies that system (9.11) and hence equation (9.10) exhibits a Hopf bifurcation as the average delay  $T$  passes through the critical value  $T_0 = 4/r$  (Marsden and McKraeken (1976)).

We thus have the following theorem regarding equation (9.10).

**Theorem 8.** *The positive equilibrium  $x^* = K$  of equation (9.10) is asymptotically stable if the average delay  $T = 2/\alpha < 4/r$  and unstable if  $T > 4/r$ . When  $T = 4/r$ , a Hopf bifurcation occurs at  $x^* = K$  and a family of periodic solutions bifurcates from  $x^* = K$ , the period of the bifurcating solutions is  $\frac{\pi}{\nu_0} = \frac{2\pi}{r}$ , and the periodic solutions exist for  $T > 4/r$  and are orbitally stable.*

Thus, the logistic equation with a strong delay kernel, just like the logistic equation with a discrete delay, exhibits a typical bifurcation phenomenon. As the (average) delay is increased through a critical value the positive equilibrium passes from stability to instability, accompanied by the appearance of stable periodic solutions (see Fig. 15).

**9.3. General Kernel.** Now consider the stability of the equilibrium  $x^* = K$  for the integrodifferential equation (9.1) with a general kernel. Let  $X = x - K$ . Then (9.1) can be written as

$$\frac{dX}{dt} = -r \int_{-\infty}^t G(t-s)X(s)ds + rX(t) \int_{-\infty}^t G(t-s)X(s)ds.$$

The linearized equation about  $x = K$  is given by

$$(9.17) \quad \frac{dX}{dt} = -r \int_{-\infty}^t G(t-s)X(s)ds$$

and the characteristic equation takes the form

$$(9.18) \quad \lambda + r \int_0^{\infty} G(s)e^{-\lambda s} ds = 0.$$

If all eigenvalues of the characteristic equation (9.18) have negative real parts, then the solution  $X = 0$  of (9.17), that is, the equilibrium  $x^* = K$  of (9.1), is asymptotically stable.

**Theorem 9.** *If*

$$\int_0^{\infty} sG(s)ds < \frac{1}{r},$$

*then  $x^* = K$  of (9.1) is asymptotically stable.*

*Proof.* Since the roots of (9.18) coincide with the zeros of the function

$$g(\lambda) = \lambda + r \int_0^{\infty} G(s)e^{-\lambda s} ds,$$

we may apply the argument principle to  $g(\lambda)$  along the contour  $\Gamma = \Gamma(a, \varepsilon)$  that constitutes the boundary of the region

$$\{\lambda \mid \varepsilon \leq \operatorname{Re}\lambda \leq a, \quad -a \leq \operatorname{Im}\lambda \leq a, \quad 0 < \varepsilon < a\}.$$

Since the zeros of  $g(\lambda)$  are isolated, we may choose  $a$  and  $\varepsilon$  so that no zeros of  $g(\lambda)$  lie on  $\Gamma$ . The argument principle now states that the number of zeros of  $g(\lambda)$  contained in the region bounded by  $\Gamma$  is equal to the number of times  $g(\lambda)$  wraps  $\Gamma$  around the origin as  $\lambda$  traverses  $\Gamma$ . (A zero of  $g(\lambda)$  of multiplicity  $m$  is counted  $m$  times.) Thus, it suffices to show for all small  $\varepsilon > 0$  and all large  $a > r$ , that  $g(\lambda)$  does not encircle 0 as  $\lambda$  traverses  $\Gamma(a, \varepsilon)$ .

Along the segment of  $\Gamma$  given by  $\lambda = a + i\nu$ ,  $-a \leq \nu \leq a$ , we have

$$g(a + i\nu) = a + i\nu + r \int_0^{\infty} G(s)e^{-(a+i\nu)s} ds.$$

Since  $a > 0$ , it follows that

$$\left| \int_0^{\infty} G(s)e^{-(a+i\nu)s} ds \right| \leq \int_0^{\infty} G(s)ds = 1.$$

Because  $a > r$ , we may conclude that every real value assumed by  $g(\lambda)$  along this segment must be positive. Along the segment of  $\Gamma$  given by  $\lambda = \mu + ia$ ,  $\varepsilon \leq \mu \leq a$ , we have

$$g(\mu + ia) = \mu + ia + r \int_0^{\infty} G(s)e^{-(\mu+ia)s} ds.$$

A similar argument shows  $g(\lambda)$  to assume no real value along this path. In fact,  $\text{Img}(\mu + ia)$  is always positive here. Similarly, one can show that  $\text{Img}(\mu - ia)$  is negative along the segment  $\lambda = \mu - ia$ ,  $\varepsilon \leq \mu \leq a$ . By continuity,  $g(\lambda)$  must assume at least one positive real value (and no negative values) as  $\lambda$  travels clockwise from  $\varepsilon + ia$  to  $\varepsilon - ia$  along  $\Gamma$ .

Finally, consider the path traced out as  $\lambda = \varepsilon + i\nu$  increases from  $\varepsilon - ia$  to  $\varepsilon + ia$ . Under the assumption,  $\text{Img}(\varepsilon + i\nu)$  is seen to increase monotonically with  $\nu$ . In fact,

$$\begin{aligned} \frac{d}{d\nu} \text{Img}(\varepsilon + i\nu) &= \frac{d}{d\nu} \left[ \nu + r \int_0^\infty G(s) e^{-\varepsilon s} \sin(\nu s) ds \right] \\ &= 1 + r \int_0^\infty s G(s) e^{-\varepsilon s} \cos(\nu s) ds \\ &\geq 1 - r \int_0^\infty s G(s) ds \\ &> 0. \end{aligned}$$

It follows immediately that  $g(\lambda)$  assumes precisely one real value along this last segment of  $\Gamma$ . Since no zero of  $g(\lambda)$  lies on  $\Gamma$ , that real value is non-zero. Assuming it to be negative,  $g(\lambda)$  would have wrapped  $\Gamma$  once about the origin, predicting exactly one zero  $\lambda_0$  of  $g(\lambda)$  inside the region bounded by  $\Gamma$ . Since  $\alpha$  and  $G$  are real, the zeros of  $g(\lambda)$  occur in complex conjugate pairs, forcing  $\lambda_0$  to be real. This, however, is a contradiction since the positivity of  $\alpha$  shows  $g(\lambda)$  to have no real positive zeros. Thus, the real value assumed by  $g(\lambda)$  along this last segment must be positive. Therefore,  $g(\lambda)$  does not encircle the origin. This completes the proof.  $\square$

**9.4. Remarks.** In studying the local stability of equation (9.1) with weak and strong kernels, we applied the so-called linear chain trick to transform the scalar integrodifferential equation into equivalent a system of first order ordinary differential equations and obtained the characteristic equations (9.7) and (9.12). It should be pointed out that these characteristic equations can be derived directly from the characteristic equation (9.18). If  $G$  is a weak kernel, then (9.18) becomes

$$\lambda + r \int_0^\infty \alpha e^{-(\lambda+\alpha)s} ds = \lambda + \frac{\alpha r}{\lambda + \alpha} = 0,$$

which is equation (9.7). If  $G$  is a strong kernel, then (9.18) becomes

$$\lambda + r \int_0^\infty \alpha^2 s e^{-(\lambda+\alpha)s} ds = \lambda + \frac{\alpha^2 r}{(\lambda + \alpha)^2} = 0,$$

which is equation (9.12).

One of the varieties of equation (9.1) is the following equation

$$(9.19) \quad \frac{dx}{dt} = x(t) \left[ a - bx(t) - c \int_{-\infty}^t G(t-s)x(s) ds \right].$$

where  $a > 0$ ,  $b \geq 0$ ,  $c \geq 0$ ,  $b + c \neq 0$ . Stability and bifurcation of equation (9.19) have been studied by many researchers. We refer to Miller (1966), Cushing (1977a), MacDonald (1978) and references cited therein. See Corollary 13.



It should be pointed out that bifurcations can occur in equation (9.19) when other coefficients (not necessarily the average delay) are chosen as bifurcation parameters. For example, Landman (1980) showed that there exists a positive  $a^*$  such that for  $a = a^*$ , a steady state becomes unstable and oscillatory solutions bifurcate for  $a$  near  $a^*$ . See also Simpson (1980).

## 10. PERIODICITY

If the environment is not temporally constant (e.g., seasonal effects of weather, food supplies, mating habits, etc.), then the parameters become time dependent. It has been suggested by Nicholson (1933) that any periodic change of climate tends to impose its period upon oscillations of internal origin or to cause such oscillations to have a harmonic relation to periodic climatic changes. Pianka (1974) discussed the relevance of periodic environment to evolutionary theory.

**10.1. Periodic Delay Models.** Nisbet and Gurney (1976) considered a periodic delay logistic equation and carried out a numerical study of the influence of the periodicity in  $r$  and  $K$  on the intrinsic oscillations of the equation such as those caused by the time delay. Rosen (1987) noted the existence of a relation between the period of the periodic carrying capacity and the delay of the logistic equation. Zhang and Gopalsamy (1990) assumed that the intrinsic growth rate and the carrying capacity are periodic functions of a period  $\omega$  and that the delay is an integer multiple of the period of the environment. Namely, they considered the periodic delay differential equation of the form

$$(10.1) \quad \frac{dx}{dt} = r(t)x(t) \left[ 1 - \frac{x(t - n\omega)}{K(t)} \right],$$

where  $r(t+\omega) = r(t)$ ,  $K(t+\omega) = K(t)$  for all  $t \geq 0$ . They proved the following result on the existence of a unique positive periodic solution of equation (10.1) which is globally attractive with respect to all other positive solutions.

**Theorem 10.** *Suppose that*

$$(10.2) \quad \int_0^{n\omega} r(s)ds \leq \frac{3}{2}.$$

*Then the periodic delay logistic equation (10.1) has a unique positive solution  $x^*(t)$  and all other solutions of (10.1) corresponding to initial conditions of the form*

$$x(\theta) = \phi(\theta) \geq 0, \quad \phi(0) > 0; \quad \phi \in C[-n\omega, 0]$$

*satisfy*

$$(10.3) \quad \lim_{t \rightarrow \infty} |x(t) - x^*(t)| = 0.$$

Following the techniques of Zhang and Gopalsamy (1990), quite a few papers have been produced by re-considering the delayed models which appeared in the previous sections with the assumption that the coefficients are periodic. See, for example, the periodic Nicholson's blowflies model (3.1) (Saker and Agarwal (2002)), the periodic Allee effect models (4.1) (Lalli and Zhang (1994)) and (4.2) (Yan and Feng (2003)), the periodic food-limited model (5.3) (Gopalsamy et al. (1990a)), the

periodic Wazewska-Czyzewska and Lasota model (6.2) (Grea et al. (1996)), etc. In all these papers, the delays are assumed to be integral multiples of periods of the environment. The coincidence degree theory (Gaines and Mawhin (1977)) has also been used to establish the existence of periodic solutions in periodic models with general periodic delays. However uniqueness is not guaranteed and stability can be obtained only when the delays are constant (Li (1998)).

Freedman and Wu (1992) considered the following single-species model with a general periodic delay

$$(10.4) \quad \frac{dx}{dt} = x(t)[a(t) - b(t)x(t) + c(t)x(t - \tau(t))],$$

where the net birth rate  $a(t) > 0$ , the self-inhibition rate  $b(t) > 0$ , the reproduction rate  $c(t) \geq 0$ , and the delay  $\tau(t) \geq 0$  are continuously differentiable,  $\omega$ -periodic functions on  $(-\infty, \infty)$ . This model represents the case that when the population size is small, growth is proportional to the size, and when the population size is not so small, the positive feedback is  $a(t) + c(t)x(t - \tau(t))$  while the negative feedback is  $b(t)x(t)$ . Such circumstance could arise when the resources are plentiful and the reproduction at time  $t$  is by individuals of at least age  $\tau(t)$  units of time. Using fixed point theorem and Razuminkin technique, they proved the following theorem.

**Theorem 11.** *Suppose that the equation*

$$a(t) - b(t)K(t) + c(t)K(t - \tau(t)) = 0$$

*has a positive,  $\omega$ -periodic, continuously differentiable solution  $K(t)$ . Then equation (10.4) has a positive  $\omega$ -periodic solution  $Q(t)$ . Moreover, if  $b(t) > c(t)Q(t - \tau(t))/Q(t)$  for all  $t \in [0, \omega]$ , then  $Q(t)$  is globally asymptotically stable with respect to positive solutions of (10.4).*

Notice that in equation (10.4),  $b(t)$  has to be greater than zero. So Theorem 11 does not apply to the periodic delay logistic equation

$$(10.5) \quad \frac{dx}{dt} = r(t)x(t) \left[ 1 - \frac{x(t - \tau(t))}{K(t)} \right]$$

where  $\tau(t)$  a positive periodic function. As Schley and Gourley (2000) showed, the periodic delays can have either a stabilizing effect or a destabilizing one, depending on the frequency of the periodic perturbation. It is still an open problem to study the dynamics, such as existence, uniqueness and stability of periodic solutions and bifurcations, for the periodic delay logistic equation (10.5).

**10.2. Integrodifferential Equations.** Periodic logistic equations with distributed delay have been systematically studied in Cushing (1977a). Bardi and Schiavino (1982) considered the integrodifferential equation (9.1) when the coefficients are periodic, that is,

$$(10.6) \quad \frac{dx}{dt} = x(t) \left[ a(t) - b(t)x(t) - c(t) \int_{-\infty}^t G(t-s)x(s)ds \right].$$

where  $a > 0$ ,  $b > 0$ ,  $c \geq 0$  are  $\omega$ -periodic continuous functions on  $R$  and  $G \geq 0$  is a normalized kernel. Let  $C_\omega = C_\omega(R, R)$  denote the Banach space of all  $\omega$ -periodic

continuous functions endowed with the usual supremum norm  $\|x\| = \sup |x(t)|$ . For  $a \in C_\omega$ , define the average of  $a$  as

$$\langle a \rangle = \frac{1}{\omega} \int_0^\omega a(s) ds.$$

The convolution of the kernel  $G$  and a bounded function  $f$  is defined by

$$(G * f)(t) = \int_{-\infty}^t G(t-s)f(s) ds.$$

Observe that an  $\omega$ -periodic solution of (10.6) is a fixed point of the operator  $B : \Gamma \rightarrow C_\omega$  defined by

$$(Bx)(t) = u(t), \quad t \in R,$$

where  $\Gamma = \{x \in C_\omega : \langle a - c(G * x) \rangle > 0\}$ . Since  $\langle a \rangle > 0$ ,  $x(t) \equiv 0$  belongs to  $\Gamma$ , that is,  $\Gamma$  is not empty. Define

$$u_0(t) = (B0)(t).$$

**Claim I.** If  $x_1$  and  $x_2$  belong to  $\Gamma$  with  $x_1 \leq x_2$ , then  $Bx_2 \leq Bx_1$ .

In fact, let  $\alpha_i(t) = a(t) - c(t)(G * x_i)(t)$  and  $u_i(t) = (Bx_i)(t)$  for  $t \in R$  ( $i = 1, 2$ ). Then  $\alpha_1(t) \geq \alpha_2(t)$ . Since  $\alpha_i(t) = \dot{u}_i(t)/u_i(t) + b(t)u_i(t)$ , we have  $\langle \alpha_i \rangle = \langle bu_i \rangle$  because  $u_i(t)$  ( $i = 1, 2$ ) are periodic. Thus, we deduce  $\langle bu_1 \rangle \geq \langle bu_2 \rangle$  and for some  $t_0 \in R$ ,  $u_2(t_0) \leq u_1(t_0)$ . Setting  $v(t) = u_1(t) - u_2(t)$ , we have

$$\dot{v}(t) \geq (\alpha_1(t) - b(t)(u_1(t) + u_2(t)))v(t),$$

which implies that  $v(t) \geq 0$  for all  $t \geq t_0$ . By the periodicity of  $v(t)$ , we have  $Bx_2 \leq Bx_1$ .

**Claim II.** If  $v$  and  $c$  belong to  $C_\omega$ , then  $\langle c(G * v) \rangle = \langle v(G * c) \rangle$ .

In fact, if we define  $G(t) = 0$  for  $t < 0$ , we have

$$\begin{aligned} \langle c(G * v) \rangle &= \sum_{j=-\infty}^{+\infty} \int_0^\omega c(t) \int_{j\omega}^{(j+1)\omega} G(t-s)v(s) ds dt \\ &= \sum_{j=-\infty}^{+\infty} \int_0^\omega c(t) \int_0^\omega G(t-s-j\omega)v(s) ds dt \\ &= \sum_{j=-\infty}^{+\infty} \int_0^\omega v(t) \int_{-j\omega}^{(1-j)\omega} G(t-s)c(s) ds dt \\ &= \langle v(G * c) \rangle. \end{aligned}$$

**Claim III.** Let  $z$  be a bounded continuous function on  $R$ . Then

$$\liminf_{t \rightarrow \infty} (G * z)(t) \geq \liminf_{t \rightarrow \infty} z(t); \quad \limsup_{t \rightarrow \infty} (G * z)(t) \leq \limsup_{t \rightarrow \infty} z(t).$$

We only prove the first inequality. Let  $l = \liminf_{t \rightarrow \infty} z(t)$ . Choose  $\epsilon > 0$  and pick  $t_\epsilon$  such that  $z(t) > l - \epsilon$  for any  $t > t_\epsilon$ . If  $t > t_\epsilon$ , we have

$$\begin{aligned} (G * z)(t) &= \int_{-\infty}^{t_\epsilon} G(t-s)z(s)ds + \int_{t_\epsilon}^t G(t-s)z(s)ds \\ &\geq \inf_t z(t) \int_{-\infty}^{t_\epsilon} G(t-s)ds + (l - \epsilon) \int_{t_\epsilon}^t G(t-s)ds. \end{aligned}$$

Hence,

$$\liminf_{t \rightarrow \infty} (G * z)(t) \geq l - \epsilon,$$

which implies the first inequality.

**Claim IV.** Let  $u \in \Gamma$  and let  $v(t) > 0$  be the solution of (10.6). Then

$$\begin{aligned} \liminf_{t \rightarrow \infty} (v(t) - u(t)) > 0 &\text{ implies } \liminf_{t \rightarrow \infty} ((Bu)(t) - v(t)) > 0, \\ \limsup_{t \rightarrow \infty} (v(t) - u(t)) < 0 &\text{ implies } \limsup_{t \rightarrow \infty} (Bu)(t) - v(t) < 0. \end{aligned}$$

We prove the first statement. Let  $w(t) = (Bu)(t)$ ,  $t \in R$ . Then  $w(t)$  is a solution of

$$\dot{w}(t) = a(t)w(t) - b(t)w(t)^2 - c(t)w(t)(G * u)(t)$$

while

$$\dot{v}(t) = a(t)v(t) - b(t)v(t)^2 - c(t)v(t)(G * v)(t).$$

Define  $z(t) = w(t) - v(t)$ . Then

$$\begin{aligned} \dot{z}(t) &= (a(t) - b(t)w(t) - c(t)(G * u))z(t) + c(t)v(t)(G * (v - u))(t) \\ &= (\dot{w}(t)/w(t) - b(t)v(t))z(t) + c(t)v(t)(G * (v - u))(t). \end{aligned}$$

Let  $l = \liminf_{t \rightarrow \infty} (v(t) - u(t))$ . Because of Claim III, there exists a  $t_0 \in R$ , such that

$$\dot{z}(t) > (\dot{w}(t)/w(t) - b(t)v(t))z(t) + lc(t)v(t)/2$$

for all  $t > t_0$ , that is,

$$z(t) > z(t_0) \exp\left\{\int_{t_0}^t \beta(s)ds\right\} + \frac{1}{2} \int_{t_0}^t \exp\left\{\int_s^t \beta(\theta)d\theta\right\} c(s)v(s)ds,$$

where  $\beta = \dot{w}(t)/w(t) - b(t)v(t)$ . Because  $\dot{w}(t)/w(t)$  is periodic and its average is zero,  $b(t)v(t)$  is positive and bounded, we can see that  $\int_{t_0}^t \beta(s)ds > \gamma_1 - t\gamma_2$ , where  $\gamma_1$  and  $\gamma_2 > 0$  are constants. Thus,

$$z(t) > \gamma_3 \int_{t_0}^t \exp((s-t)\gamma)ds = (\gamma_3/\gamma)(1 - \exp((t_0 - t)\gamma_2)),$$

where  $\gamma_3 > 0$  is a suitable constant. Then  $\liminf_{t \rightarrow \infty} z(t) \geq \gamma_3/\gamma$  which implies the first statement.

**Theorem 12.** Suppose  $\langle a \rangle > 0$ . If

$$(10.7) \quad b(t) > (G * c)(t)$$

for any  $t \in [0, \omega]$ , then equation (10.6) has a unique positive  $\omega$ -periodic solution  $x^*(t)$  which is globally asymptotically stable with respect to all solutions of equation (10.6) under initial condition  $x(\theta) = \phi(\theta)$ ,  $\theta \in (-\infty, 0]$ ,  $\phi(0) > 0$ .

*Proof.* Since

$$\dot{u}_0(t)/u_0(t) = a(t) - b(t)u_0(t),$$

the periodicity of  $u_0(t)$  and Claim II imply that  $\langle a \rangle = \langle bu_0 \rangle > \langle c(G * u_0) \rangle$ . As  $u_0 > 0$ , we have  $Bu_0 \leq u_0$ . Therefore, for any  $v \in C_\omega$  satisfying  $0 < v \leq u_0$ , we have  $0 < Bu_0 \leq Bv \leq u_0$ . Hence, the set  $\Gamma_0 = \{v \in C_\omega : 0 < v \leq u_0\} \subset \Gamma$  is invariant under  $B$ . Moreover,

$$Bu_0 \leq Bv \leq u_0 \Rightarrow Bu_0 \leq B^2v \leq B^2u_0 \Rightarrow B^3u_0 \leq B^3v \leq B^2u_0$$

and by induction

$$B^{2n+1}u_0 \leq B^{2n+1}v \leq B^{2n}u_0, \quad B^{2n+1}u_0 \leq B^{2n+2}v \leq B^{2n+2}u_0, \quad n = 0, 1, 2, \dots$$

Since  $0 < B^20 = Bu_0$ , by Claim I, we know that  $\{B^{2n+1}u_0\}$  is increasing and  $\{B^{2n}u_0\}$  is decreasing. Define

$$u_n(t) = (B^n u_0)(t) = (Bu_{n-1})(t).$$

Then

$$u^-(t) = \lim_{n \rightarrow \infty} u_{2n+1}(t) \quad \text{and} \quad u^+(t) = \lim_{n \rightarrow \infty} u_{2n}(t)$$

exist with  $0 < u^-(t) \leq u^+(t)$ . If we can show that  $u^-(t) = u^+(t) = u^*(t)$ , it is easy to see that  $u^*(t)$  is the unique fixed point of  $B$ . By the definition, we have

$$\dot{u}_n(t) = (a(t) - c(t)(G * u_{n-1})(t))u_n(t) - b(t)u_n(t)^2.$$

By the monotonicity and uniform boundedness of  $\{u_n\}$  we have the  $L^2$ -convergence of both  $u_{2n+1}$  and  $u_{2n}$  and their derivatives. Taking the limits, we have

$$\begin{aligned} \dot{u}^-(t) &= (a(t) - c(t)(G * u^+)(t))u^-(t) - b(t)u^-(t)^2, \\ \dot{u}^+(t) &= (a(t) - c(t)(G * u^-)(t))u^+(t) - b(t)u^+(t)^2. \end{aligned}$$

Dividing them by  $u^-(t)$  and  $u^+(t)$  respectively, we have

$$\langle a - c(G * u^+) - bu^- \rangle = \langle a - c(G * u^-) - bu^+ \rangle$$

followed by the fact that  $\ln u^+$  and  $\ln u^-$  are periodic. Let  $v(t) = u^+(t) - u^-(t)$ . Then we have  $\langle c(G * v) \rangle = \langle bv \rangle$ . Now by Claim II we have  $\langle c(G * v) \rangle = \langle v(G * c) \rangle$ . Hence,  $\langle v(b - G * c) \rangle = 0$ , which implies that  $v \equiv 0$  by the assumption (10.7). Therefore,  $u^*(t)$  is a unique periodic solution of the equation (10.6).

To prove the global stability, first we show that any solution  $v(t)$  of equation (10.6) satisfies  $\liminf_{t \rightarrow \infty} v(t) > 0$ . In fact, we have

$$\dot{v}(t) < a(t)v(t) - b(t)v(t)^2$$

and

$$\limsup_{t \rightarrow \infty} (v(t) - (Bu)(t)) \leq 0.$$

Choose  $\epsilon > 0$  so that  $u(t) = u_0(t) + \epsilon \in \Gamma$ . By Claim IV we have

$$\liminf_{t \rightarrow \infty} (v(t) - (Bu)(t)) \geq \epsilon.$$

Since  $(Bu)(t)$  is strictly positive and periodic, we have  $\liminf_{t \rightarrow \infty} v(t) > 0$ . Thus, by Claim III,  $\liminf_{t \rightarrow \infty} (u_0(t) - v(t)) > 0$  and by induction,

$$\liminf_{t \rightarrow \infty} (v(t) - (B^{2n+1}u_0)(t)) > 0, \quad \limsup_{t \rightarrow \infty} (v(t) - (B^{2n}u_0)(t)) < 0.$$

Given  $\varepsilon > 0$ , choose  $n$  such that

$$u^*(t) - \varepsilon < (B^{2n+1}u_0)(t) < (B^{2n}u_0)(t) < u^*(t) + \varepsilon.$$

Since  $(B^{2n+1}u_0)(t) < v(t) < (B^{2n}u_0)(t)$  for large  $t$ , it follows that the sequence  $\{B^j u\}$  tends to  $u^*$  uniformly as  $j \rightarrow \infty$ .  $\square$

If  $a, b$  and  $c$  are real positive constants, then condition (10.7) becomes  $b > c$ . This is the main result in Miller (1966).

**Corollary 13.** *If  $b > c$  and  $G$  satisfies the above assumptions, then the positive equilibrium  $x^* = a/(b + c)$  of equation (9.19) (with constant coefficient) is globally stable with respect to positive solutions of (9.19).*

For other related work on periodic logistic equations with distributed delay, we refer to Bardi (1983), Cohen and Rosenblat (1982), Cushing (1977a), Karakostas (1982) and the references therein.

## 11. STATE-DEPENDENT DELAYS

Let  $x(t)$  denote the size of a population at time  $t$ . Assume that the number of births is a function of the population size only. The birth rate is thus density dependent but not age dependent. Assume that the lifespan  $L$  of individuals in the population is variable and is a function of the current population size. If we take into account the crowding effects, then  $L(\cdot)$  is a decreasing function of the population size.

Since the population size  $x(t)$  is equal to the total number of living individuals, we have (Bélair (1991))

$$(11.1) \quad x(t) = \int_{t-L[x(t)]}^t b(x(s)) ds.$$

Differentiating with respect to the time  $t$  on both sides of equation (11.1) leads to a state-dependent delay model of the form

$$(11.2) \quad \frac{dx}{dt} = \frac{b(x(t)) - b(x(t - L[x(t)]))}{1 - L'[x(t)] b(x(t - L[x(t)]))}.$$

Note that state-dependent delay equation (11.2) is not equivalent to the integral equation (11.1). It is clear that every solution of (11.1) is a solution of (11.2) but the reverse is not true. In fact, any constant function is a solution of (11.2) but clearly it may not necessarily be a solution of (11.1). The asymptotic behavior of the solutions of 11.2) has been studied by Bélair (1991). See also Cooke and Huang (1996).

State-dependent delay models have also been introduced by Kirk et al. (1970) to model the control of the bone marrow stem cell population which supplies the circulating red blood cell population. See also Mackey and Milton (1990).

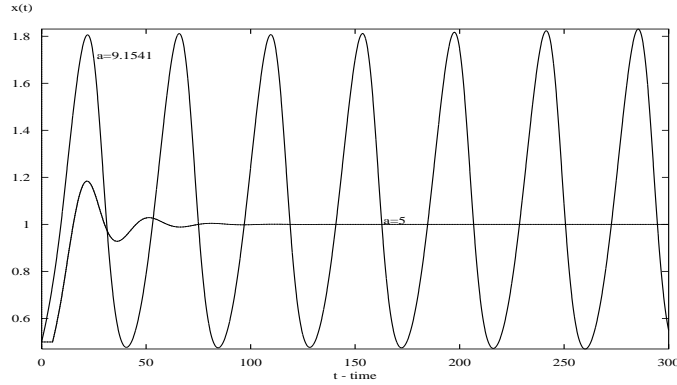


FIGURE 16. Numerical simulations for the state-dependent delay model (11.3) with  $r = 0.15, K = 1.00$  and  $\tau(x) = a + bx^2$ . (i)  $a = 5, b = 1.1$ ; and (ii)  $a = 9.1541, b = 1.1$ .

Numerical simulations (see Fig. 16) show that the logistic model with a state-dependent delay

$$(11.3) \quad x'(t) = rx(t) \left[ 1 - \frac{x(t - \tau(x(t)))}{K} \right],$$

has similar dynamics to the Hutchinson's model (2.1). Choose  $r = 0.15, K = 1.00$  as in Fig. 3 for the Hutchinson's model (2.1) and  $\tau(x) = a + bx^2$ . We observe stability of the equilibrium  $x = K = 1$  for small amplitude of  $\tau(x)$  and oscillations about the equilibrium for large amplitude of  $\tau(x)$  (see Fig. 16).

Recently, great attention has been paid on the study of state-dependent delay equations. Consider

$$(11.4) \quad \varepsilon x'(t) = -x(t) + f(x(t - r(x(t))))$$

and assume that

- (H1)  $A$  and  $B$  are given positive real numbers and  $f : [-B, A] \rightarrow [-B, A]$  is a Lipschitz map with  $xf(x) < 0$  for all  $x \in [-B, A], x \neq 0$ ;
- (H2) For  $A$  and  $B$  in (H1),  $r : [-B, A] \rightarrow R$  is a Lipschitz map with  $r(0) = 1$  and  $r(u) \geq 0$  for all  $u \in [-B, A]$ ;
- (H2')  $B$  is a positive real number and  $r : [-B, \infty) \rightarrow R$  is a locally Lipschitz map with  $r(0) = 1, r(u) \geq 0$  for all  $u \geq -B$  and  $r(-B) = 0$ ;
- (H1')  $f : R \rightarrow R$  is a locally Lipschitz map, and if  $B$  is as in (H1') and  $A = \sup\{|f(u)| : -B \leq u \leq 0\}$ , then  $uf(u) < 0$  for all  $u \in [-B, A], u \neq 0$ .

A periodic solution  $x(t)$  of (11.4) is called an *slowly oscillating periodic* (SOP) solution if there exist numbers  $q_1 > 1$  and  $q_2 > q_1 + 1$  such that

$$x(t) \begin{cases} = 0, & t = 0, \\ < 0, & 0 < t < q_1, \\ = 0, & t = q_1, \\ > 0, & q_1 < t < q_2, \\ = 0, & t = q_2 \end{cases}$$

and  $x(t + q_2) = x(t)$  for all  $t$ . Mallet-Paret and Nussbaum (1992) proved the following theorem.

**Theorem 14.** *Assume that  $f$  and  $r$  satisfy (H1)-(H2) or (H1')-(H2'). Suppose that  $f$  is in  $C^1$  near 0 and  $f'(0) = -k < -1$ . Let  $\nu_0$ ,  $\pi/2 < \nu_0 < \pi$ , be the unique solution of  $\cos \nu_0 = -1/k$  and define  $\lambda_0 = \nu_0/\sqrt{k^2 - 1}$ . Then for each  $\lambda > \lambda_0$  the equation*

$$x'(t) = -\lambda x(t) + \lambda f(x(t - r(x(t))))$$

*has an SOP solution  $x_\lambda(t)$  such that  $-B < x_\lambda(t) < A$  for all  $t$ .*

Mallet-Paret and Nussbaum (1996, 2003) studied the shape of general periodic solutions of the equation (11.4) and their limiting profile as  $\varepsilon \rightarrow 0^+$ . We refer to Arino et al. (1998), Bartha (2003), Kuang and Smith (1992a, 1992b), Mallet-Paret et al. (1994), Magal and Arino (2000), Walther (2002) for existence of periodic solutions; to Krisztin and Arino (2001) for the existence of two dimensional attractors; to Louihi et al. (2002) for semigroup property of the solutions; to Bartha (2001) and Chen (2003) for convergence of solutions, and to Ait Dads and Ezzinbi (2002) and Li and Kuang (2001) for almost periodic and periodic solutions to state-dependent delay equations. See also Arino et al. (2001) for a brief review on state-dependent delay models.

## 12. DIFFUSIVE MODELS WITH DELAY

Diffusion is a phenomenon by which a group of particles, for example animals, bacteria, cells, chemicals and so on, spreads as a whole according to the irregular motion of each particle. When this microscopic irregular movement results in some macroscopic regular motion of the group, the phenomenon is a *diffusion* process. In terms of randomness, diffusion is defined to be a basically irreversible phenomenon by which particles spread out within a given space according to individual random motion.

**12.1. Fisher Equation.** Let  $u(x, t)$  represent the population density at location  $x$  and time  $t$  and the source term  $f$  represents the birth-death process. With the logistic population growth  $f = ru(1 - u/K)$  where  $r$  is the linear reproduction rate and  $K$  the carrying capacity of the population, the one-dimensional scalar reaction-diffusion equation takes the form (Fisher (1937) and Kolmogorov et al. (1937))

$$(12.1) \quad \frac{\partial u}{\partial t} = D \frac{\partial^2 u}{\partial x^2} + ru \left(1 - \frac{u}{K}\right), \quad a < x < b, \quad 0 \leq t < \infty,$$



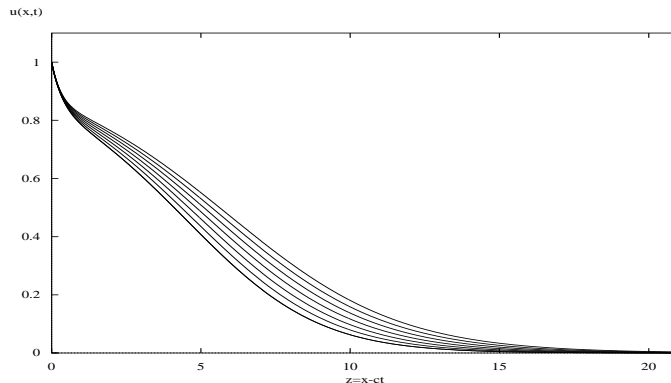


FIGURE 17. The traveling front profiles for the Fisher equation (12.1). Here  $D = r = K = 1$ ,  $c = 2.4 - 3.0$

which is called the *Fisher equation* or *diffusive logistic equation*. Fisher (1937) proposed the model to investigate the spread of an advantageous gene in a population.

Recall that for the spatially uniform logistic equation

$$\frac{\partial u}{\partial t} = ru \left(1 - \frac{u}{K}\right),$$

the equilibrium  $u = 0$  is unstable while the positive equilibrium  $u = K$  is globally stable. How does the introduction of the diffusion affect these conclusion? The answer depends on the domain and the boundary conditions. (a) In a finite domain with zero-flux (Neumann) boundary conditions, the conclusions still hold (Fife (1979) and Britton (1986)). (b) Under the Dirichlet conditions,  $u = K$  is no longer a solution to the problem. In this case the behaviour of solutions depends on the size of the domain. When the domain is small,  $u = 0$  is asymptotically stable, but it loses its stability when the domain exceeds a certain size and a non-trivial steady-state solution becomes asymptotically stable. (c) In an infinite domain the Fisher equation has travelling wave solutions (see Figure 17).

**12.2. Diffusive Equations with Delay.** In the last two decades, diffusive biological models with delays have been studied extensively and many significant results have been established. For instance, the diffusive logistic equations with a discrete delay of the form

$$(12.2) \quad \frac{\partial u(x,t)}{\partial t} = D \frac{\partial^2 u(x,t)}{\partial x^2} + ru(x,t) \left(1 - \frac{u(x,t-\tau)}{K}\right)$$

with either Neumann or Dirichlet boundary conditions have been investigated by Green and Stech (1981), Lin and Khan (1982), Yoshida (1982), Morita (1984), Luckhaus (1986), Busenberg and Huang (1996), Feng and Lu (1996), Huang (1998), Freedman and Zhao (1997), Faria and Huang (2002), etc. The diffusive logistic equations with a distributed delay of the form

$$(12.3) \quad \frac{\partial u(x,t)}{\partial t} = D \frac{\partial^2 u(x,t)}{\partial x^2} + ru(x,t) \left[1 - \frac{1}{K} \int_{-\infty}^t G(t-s)u(x,t-s)ds\right]$$

have been studied by Schiaffino (1979), Simpson (1980), Tesei (1980), Gopalsamy and Aggarwala (1981), Schiaffino and A. Tesei (1981), Yamada (1993), Bonilla and Liñán (1984), Redlinger (1985), Britton (1990), Gourley and Britton (1993), Pao (1997), etc.

Recently, researchers have studied the combined effects of diffusion and various delays on the dynamics of the models mentioned in previous sections. For example, for the food-limited model (5.3) with diffusion, Gourley and Chaplain (2002) considered the case when the delay is finite. Feng and Lu (2003) assumed that the time delay in an integral multiple of the period of the environment and considered the existence of periodic solutions. Davidson and Gourley (2001) studied the model with infinite delay, and Gourley and So (2002) investigated the dynamics when the delay is nonlocal.

The diffusive Nicholson's blowflies equation

$$(12.4) \quad \frac{\partial u}{\partial t} = d\Delta u - \tau u(\mathbf{x}, t) + \beta \tau u(\mathbf{x}, t-1) \exp[-u(\mathbf{x}, t-1)]$$

with Dirichlet boundary conditions has been investigated by So and Yang (1998). They studied the global attractivity of the positive steady state of the equation. Some numerical and bifurcation analysis of this model has been carried out by So, Wu and Yang (1999) and So and Zou (2001).

Gourley and Ruan (2000) study various local and global aspects of Nicholson's blowflies equation with infinite delay

$$(12.5) \quad \frac{\partial u}{\partial t} = d\Delta u - \tau u(\mathbf{x}, t) + \beta \tau \left( \int_{-\infty}^t F(t-s)u(\mathbf{x}, s) ds \right) \exp \left( - \int_{-\infty}^t F(t-s)u(\mathbf{x}, s) ds \right)$$

for  $(\mathbf{x}, t) \in \Omega \times [0, \infty)$  where  $\Omega$  is either all of  $R^n$  or some finite domain, and where the kernel satisfies  $F(t) \geq 0$  and the conditions

$$(12.6) \quad \int_0^{\infty} F(t) dt = 1 \quad \text{and} \quad \int_0^{\infty} t F(t) dt = 1.$$

Gourley (2000) discussed the existence of travelling waves in equation (12.5).

Ruan and Xiao (2003) considered the diffusive integro-differential equation modeling the host-vector interaction

$$(12.7) \quad \frac{\partial u}{\partial t}(t, x) = d\Delta u(t, x) - au(t, x) + b[1 - u(t, x)] \int_{-\infty}^t \int_{\Omega} F(t-s, x, y)u(s, y)dyds,$$

where  $u(t, x)$  is the normalized spatial density of infectious host at time  $t \in R_+$  in location  $x \in \Omega$ ,  $\Omega$  is an open bounded set in  $R^N$  ( $N \leq 3$ ), and the convolution kernel  $F(t, s, x, y)$  is a positive continuous function in its variables  $t \in R$ ,  $s \in R_+$ ,  $x, y \in \Omega$ , which is normalized so that

$$\int_0^{\infty} \int_{\Omega} F(t, s, x, y)dyds = 1.$$

Ruan and Xiao (2003) studied the stability of the steady states and proved the following results.

**Theorem 15.** *The following statements hold*

(i) If  $0 < b \leq a$ , then  $u_0 = 0$  is the unique steady state solution of (12.7) in

$$M = \{u \in E : 0 \leq u(x) \leq 1, x \in \bar{\Omega}\}$$

and it is globally asymptotically stable in  $C((-\infty, 0]; M)$ .

(ii) If  $0 \leq a < b$ , then there are two steady state solutions in  $M$ :  $u_0 = 0$  and  $u_1 = (b - a)/b$ , where  $u_0$  is unstable and  $u_1$  is globally asymptotically stable in  $C((-\infty, 0]; M)$ .

Notice that when  $F(t, s, x, y) = \delta(x - y)\delta(t - s - \tau)$ , where  $\tau > 0$  is a constant, and  $u$  does not depend on the spatial variable, then equation (12.7) becomes the vector disease model (7.1) and Theorem 15 reduces to Theorem 5 obtained by Cooke (1978).

When  $x \in (-\infty, \infty)$  and the kernel is a local strong kernel, i.e.

$$(12.8) \quad \frac{\partial u}{\partial t} = d\Delta u(t, x) - au(t, x) + b[1 - u(t, x)] \int_{-\infty}^t \frac{t-s}{\tau^2} e^{-\frac{t-s}{\tau}} u(s, x) ds,$$

where  $(t, x) \in R_+ \times \Omega$ , the existence of traveling waves has been established.

**Theorem 16.** For any  $\tau > 0$  sufficiently small there exist speeds  $c$  such that the system (12.8) has a traveling wave solution connecting  $u_0 = 0$  and  $u_1 = (b - a)/b$ .

The existence of traveling front solutions show that there is a moving zone of transition from the disease-free state to the infective state.

We refer to the monograph by Wu (1996) for a systematic treatment of partial differential equations with delay.

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