

5

Applications in the Life Sciences

In Chapter 1 we introduced simple advection and diffusion models to describe the motion of organisms, cells, and chemicals in a biological science context. In this chapter we extend these ideas to more complicated phenomena involving age structure of a population, the propagation of epidemic waves, and the relationship between spatial pattern formation and chemical instability. These advanced models show why PDEs have vast applications in the life sciences. The mathematical methods we introduce to analyze these problems extend the ideas and techniques presented in the earlier chapters. For collateral reading, extensive applications of PDEs in biology can be found in Edelstein-Keshet (2005), Kot (2001), Britton (2003), and Murray (2003).

5.1 Age-Structured Models

By an **age-structured model** we mean a demographic model where the population at time t has an age distribution superimposed on it. Thus, at time t we also consider ages of the individuals. Age-structured models are akin to more general **physiologically-structured models** where any other variable, say size or weight, could replace age. For example, in many non-mammalian populations the evolution of the population, especially the mortality rate, certainly depends upon the size of the animals; the survival probability is small for young fish or insects. Our modeling focuses on age structure, but similar ideas apply to any physiological structure.

We begin by considering a population of female organisms whose age-structure at time $t = 0$ is given by $f(a)$. That is, $f(a)da$ is approximately the number of females between age a and $a + da$. Generally, we use females in demographic models because they have a well-defined beginning and end to their reproductive capacity. For simplicity, we write the age range as $0 \leq a < \infty$ even though the age of death is finite. Given the initial age structure, the mortality rate, and the fecundity rate (average number of offspring produced per female), the problem is to determine the age structure $u = u(a, t)$ at any time $t > 0$. Here, $u(a, t)da$ represents the number of females at time t between the ages a and $a + da$. Then the total female population at time t is

$$N(t) = \int_0^{\infty} u(a, t)da.$$

What makes this problem more intractable than other problems is that $u(0, t)$, which is the number of newborns at time t , is not known *a priori*. Rather, $u(0, t)$ depends upon the population and age of reproducing females, which is the unknown in the problem. Specifically, we assume that the *per capita mortality rate* is given as a function of age as $m = m(a)$. And we assume that the fecundity rate is $b(a, t)$, which depends upon both time and age of the female. Precisely, $b(a, t)$ is the average number of offspring per female of age a at time t ; the function $b(a, t)$ is called the *maternity function*. We expect $b(a, t)$ to be zero until the age of onset of maturity and zero after menopause. In between these ages the fecundity rate varies according to age; for example, in humans, women of age 25 are more fertile than women of age 40. Figure 5.1 depicts the evolution of age structure profiles in a three-dimensional atu -space (age-time-density space).

The governing dynamics is given by the equation

$$u_t = -u_a - m(a)u.$$

Thus, the model equation is the advection equation with speed one and sink term given by the mortality rate; notice that the flux is $\phi = u$, or the number crossing the age a line at time t is just $u(a, t)$, the density at that age. This continuous time model has its origins in the work of McKendrick in 1926 and in subsequent studies by von Forester in 1959. The equation is often called the **McKendrick–von Forester equation**. Now we formulate the boundary condition $u(0, t)$, the number of newborns at time t . Because $u(a, t)da$ is the number of females between a and $a + da$, and $b(a, t)$ is the average reproduction rate, the number of offspring produced by females between age a and age $a + da$ is $b(a, t)u(a, t)da$. Thus, the total number of offspring produced by all females is the (sum) integral over all ages, or

$$u(0, t) = \int_0^{\infty} b(a, t)u(a, t)da.$$

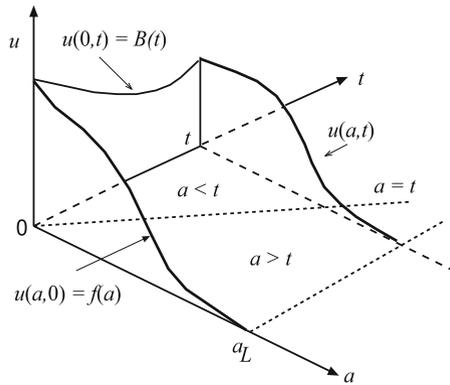


Figure 5.1 Age-structured model: $f(a)$ is the initial, known age structure, and $u(0, t) = B(t)$ is the unknown offspring at age $a = 0$ and time t . The age structure $u(a, t)$ for $a > t$ is affected only by the initial population $f(a)$, whereas for $a < t$ it is affected by the entire population and its fecundity; a_L is the maximum lifetime age. Individuals follow paths, or characteristics, $a = t + \text{constant}$ in age-time space

Therefore we have derived the age-structured model

$$u_t = -u_a - m(a)u, \quad a > 0, \quad t > 0, \tag{5.1}$$

$$u(0, t) = \int_0^\infty b(a, t)u(a, t)da, \quad t > 0, \tag{5.2}$$

$$u(a, 0) = f(a), \quad a \geq 0. \tag{5.3}$$

We emphasize again that the left boundary condition at age $a = 0$ is not known, but rather depends upon the solution $u(a, t)$, which is also unknown. This type of condition is called a **nonlocal boundary condition** because it depends upon the integrated unknown solution in the problem.

Age-structured models may be visualized as a conveyor belt of age length $0 \leq a \leq a_L$ moving at speed one year, per year. Individuals, representing a cohort, enter at age $a = 0$ and move forward along the belt in time. As they progress they are subject to mortality, and they reproduce between the ages of fertility, $a_m < a < a_M$. Those newborns then enter the belt at age $a = 0$.

Stable Age Structure

Rather than attempting to solve (5.1–5.3) directly, we take a different tack common in demographic models. We ignore the initial condition (5.3) and ask what happens over a long time. Births from the initial population $f(a)$ only

affect the solution for a finite time because those individuals and their offspring die. Therefore, in the case that the maternity function is independent of time, i.e., $b = b(a)$, we look for a **stable age structure** of the form

$$u(a, t) = U(a)e^{rt}, \quad t \text{ large}$$

where $U(a)$ is an unknown age structure and r is an unknown growth rate. Substituting into the PDE (5.1) and making reductions gives an ODE for $U(a)$,

$$U'(a) = -(m(a) + r)U(a).$$

This equation can be solved by separation of variables to get

$$U(a) = Ce^{-ra}e^{-\int_0^a m(s)ds},$$

where C is a constant. Letting $S(a) = \exp\left(-\int_0^a m(s)ds\right)$ denote the *survivorship function*, which is the probability of surviving to age a , we can write the long time solution as

$$u(a, t) = Ce^{rt-ra}S(a). \quad (5.4)$$

To determine the growth constant r , we substitute (5.4) into the nonlocal boundary condition (5.2) to obtain

$$1 = \int_0^\infty b(a)e^{-ra}S(a)da, \quad (5.5)$$

which is the **Euler–Lotka equation**. Using numerical methods this equation can be solved for r , and we will have determined, up to a constant, the long-time age structure $U(a)$ of the population and its growth rate r .

In the special case $m = \text{constant}$, the Euler–Lotka equation is

$$1 = \int_0^\infty b(a)e^{-(r+m)a}da.$$

This equation determines the growth rate r of the population. The exercises request calculations for specific population data.

The Renewal Equation

The method of characteristics introduced in Section 1.2 may be used to study (5.1–5.3) in the simple case when $b = b(a)$ and $m = \text{constant}$. The PDE (5.1) is

$$u_t = -u_a - mu, \quad a > 0, \quad t > 0. \quad (5.6)$$

If we change independent variables via the formulae

$$\xi = a - t, \quad \tau = t,$$

then the PDE (5.6) becomes

$$U_\tau = -mU, \quad \text{where } U = U(\xi, t).$$

This equation has general solution

$$U(\xi, \tau) = C(\xi)e^{-m\tau},$$

where C is an arbitrary function. In terms of the original variables,

$$u(a, t) = C(a - t)e^{-mt}.$$

To determine the arbitrary function C we consider two cases, $a > t$ and $a < t$. See Figure 5.1. The arbitrary function is different in each case. The solution in $a > t$ is determined by the initial age structure and we have

$$u(a, 0) = C(a) = f(a).$$

Therefore

$$u(a, t) = f(a - t)e^{-mt}, \quad a > t. \quad (5.7)$$

For $a < t$ we denote, for simplicity, $B(t) = u(0, t)$. Then, applying the boundary condition gives

$$u(0, t) = B(t) = C(-t)e^{-mt},$$

or

$$C(s) = B(-s)e^{-ms}.$$

Consequently

$$u(a, t) = B(t - a)e^{-ma}, \quad a < t. \quad (5.8)$$

The solution to (5.1–5.3) in the case $m(a) = m$ and $b(a, t) = b(a)$ is given by (5.7–5.8), but B is still unknown. To find B we substitute the expressions (5.7–5.8) into the yet unused nonlocal boundary condition (5.2). After breaking up the integral into two age domains, we obtain

$$\begin{aligned} B(t) &= \int_0^\infty b(a)u(a, t)da \\ &= \int_0^t b(a)u(a, t)da + \int_t^\infty b(a)u(a, t)da, \end{aligned}$$

or

$$B(t) = \int_0^t b(a)B(t - a)e^{-ma}da + \int_t^\infty b(a)f(a - t)e^{-mt}da. \quad (5.9)$$

Equation (5.9) is a *linear integral equation* for the unknown $B(t)$, and it is called the **renewal equation**. Once it is solved for $B(t)$, then (5.7–5.8) give the age structure for the population. In Exercise 2 the reader is asked to solve the renewal equation in a special case. Generally, (5.9), a nonhomogeneous

Volterra equation, is difficult to solve and must be dealt with numerically, or by successive approximation (iteration).

Structured Predator–Prey Model

The previous discussion illustrates how age structure leads to an advection equation that can be solved, in theory, by standard change of variable methods. Now we consider a more difficult nonlinear predator-prey problem where a different technique is illustrated. The method is called the **method of moments**, which is akin to an energy method. We can add this important technique to our analytic tool bag for dealing with PDEs.

We consider a population of prey with age density $u(a, t)$ and constant *per capita* mortality rate m . Then, as above, the governing age-time dynamics is given by

$$u_t = -u_a - mu, \quad a > 0, \quad t > 0, \quad (5.10)$$

where the initial number of prey is

$$u(a, 0) = f(a). \quad (5.11)$$

The total prey population is

$$N(t) = \int_0^\infty u(a, t) da.$$

We assume that the maternity function is

$$b(a) = b_0 a e^{-\gamma a}.$$

Then the prey produce offspring (eggs) given by

$$B(t) = \int_0^\infty b_0 a e^{-\gamma a} u(a, t) da.$$

Now let us introduce a total predator population $P = P(t)$; we shall not consider age-structure in the predator population, but only that the predators eat the eggs of the prey. (To stimulate thinking about this model, remember one of the theories posed for the extinction of the dinosaurs is that egg-eating predators caused the demise). Because predators eat only eggs ($a = 0$), the PDE is unaffected. What is affected is the actual number of offspring $u(0, t)$ produced. Thus we no longer have $u(0, t) = B(t)$, but rather we must include a predation term that decreases the egg population. The simplest model is the Lotka–Volterra model, which requires that the number eggs eaten is proportional to the product of the number of eggs and the number of predators. That is, we have

$$u(0, t) = B(t) - kB(t)P(t),$$

where k is a proportionality constant. But the right side can be negative, so we define $M(B, P) = \max(B - kBP, 0)$ and take the number of eggs at $a = 0$ to be

$$u(0, t) = M(B, P). \quad (5.12)$$

This equation provides the boundary condition to the problem. Finally, we ask how the predator population changes. We assume Lotka–Volterra dynamics

$$\frac{dP}{dt} = -\delta P + cBP, \quad (5.13)$$

where δ is the per capita mortality rate and c is the yield. Hence, in the absence of eggs, predators die out. Initially, we take $P(0) = P_0$.

We remark that if the predators consumed prey other than eggs, then a predation term would have to be included as a sink term on the right side of the dynamical equation (5.10).

The method of moments allows us to obtain a system of ordinary differential equations for the total prey and predator populations $N(t)$ and $P(t)$. In the analysis, we will also obtain equations for some additional auxiliary variables, but the overall end result is a system of ODEs, which is simpler than the mixed PDE-ODE system given by the model equations (5.10–5.13).

The idea is to multiply the PDE (5.10) by a *moment* function $g(a)$ and then integrate over $0 \leq a \leq \infty$. The only requirement is that $u(a, t)g(a) \rightarrow 0$ as $a \rightarrow \infty$. Upon taking g to be different functions, we can obtain equations that lead to the differential equations we seek. The reader will find it valuable to verify these calculations. Proceeding in a general way, we multiply the PDE by g and integrate to get

$$\frac{d}{dt} \int_0^\infty g(a)u(a, t)da = - \int_0^\infty g(a)u_a(a, t)da - m \int_0^\infty g(a)u(a, t)da.$$

The first integral on the right can be integrated by parts to get

$$\frac{d}{dt} \int_0^\infty g(a)u(a, t)da = M(B, P)g(0) + \int_0^\infty g'(a)u(a, t)da - m \int_0^\infty g(a)u(a, t)da. \quad (5.14)$$

Now we make different choices for g . If $g(a) = 1$ then (5.14) becomes simply

$$\frac{dN}{dt} = M(B, P) - mN, \quad (5.15)$$

an ODE involving N, P , and B . If we take $g(a) = b(a)$, the maternity function, then (5.14) becomes

$$\frac{dB}{dt} = -\gamma B + b_0H - mB, \quad (5.16)$$

where $H = H(t)$ is defined by

$$H(t) = \int_0^\infty e^{-\gamma a} u(a, t) da.$$

But now H is yet a new variable. To get another equation involving H we take $g(a) = e^{-\gamma a}$. Then (5.14) becomes

$$\frac{dH}{dt} = M(B, P) - (m + \gamma)H. \quad (5.17)$$

Therefore we have four ODEs (5.13), (5.15–5.17) for N , P , B , and H . Clearly the N equation decouples from the system and we can just consider the three ODEs

$$\frac{dP}{dt} = -\delta P + cBP, \quad \frac{dB}{dt} = -(m + \gamma)B + b_0H, \quad \frac{dH}{dt} = M(B, P) - (m + \gamma)H.$$

The initial conditions are $P(0) = P_0$, $B(0) = \int_0^\infty b_0 a e^{-\gamma a} f(a) da$, $H(0) = \int_0^\infty e^{-\gamma a} f(a) da$.

We can now proceed with a numerical method (e.g., the Runge–Kutta method) to solve the system and determine the dynamics. The reader is asked for such a calculation in Exercise 4.

EXERCISES

1. Consider a population of organisms whose *per capita* death rate is three percent per month and that the maternity function, in births per female per age in months, is given by $b(a) = 4$ for $3 \leq a \leq 8$, and $b(a) = 0$ otherwise. Use the Euler–Lotka equation to calculate the growth rate r .
2. Consider the age-structured model (5.1–5.3) in the case that the mortality rate is constant ($m(a) = \gamma$) and the maternity function is a constant ($b(a, t) = \beta$). At time $t = 0$ assume the age distribution is $f(a) = u_0$ for $0 < a \leq \delta$, and $f(a) = 0$ for $a > \delta$.

(a) Show that the renewal equation (5.9) takes the form

$$B(t) = \int_0^t \beta B(s) e^{-\gamma(t-s)} ds + \beta \delta u_0 e^{-\gamma t}.$$

(b) Show that $B(t)$ satisfies the differential equation

$$B' = (\beta - \gamma)B.$$

Hint: use Leibniz' rule to differentiate the integral.

(c) Determine $B(t)$ and the population density $u(a, t)$.

(d) What is the total size $N(t)$ of the population at any time t ?

3. Consider the structured model where the per capita mortality rate depends upon the total population $N = N(t)$ and the maternity function is $b(a) = b_0 e^{-\gamma a}$:

$$\begin{aligned}u_t &= -u_a - m(N)u, \quad a > 0, t > 0, \\u(0, t) &= \int_0^\infty b_0 e^{-\gamma a} u(a, t) da, \\u(a, 0) &= f(a), \quad a > 0.\end{aligned}$$

- (a) Use the method of moments to obtain the system of ODEs

$$\frac{dN}{dt} = B - m(N)N, \quad \frac{dB}{dt} = (b_0 - \gamma - m(N))B,$$

for $N(t)$ and the offspring $B(t) = u(0, t)$. (Note that the maternity function in this model is unreasonable because it predicts that newborns give birth; but it may be a good approximation when the females reproduce at a very young age).

- (b) Show that the relation $B = (b_0 - \gamma)N$ gives a solution to the ODEs in the NB -plane.
- (c) Show that the solution to the system cannot oscillate and, in fact, approaches a steady state.
4. Numerically solve equations (5.13), (5.15–5.17) and plot the prey and predator populations $N(t)$ and $P(t)$ for $0 \leq t \leq 125$. Take $b_0 = 5$ and the remaining constants to be one. Based upon your calculation, is there a basis for controlling pests by introducing predators that selectively eat their eggs?
5. Consider an age-structured population where $u = u(a, t)$ is the age density of people at age a at time t . In a model where no person survives past age $a = d$, the PDE for u is given by

$$u_t + u_a = -\frac{c}{d-a}u, \quad 0 < a < d, t > 0.$$

Interpret this model and use the methods in Chapter 1, or otherwise, to find the general solution. Then use analytical techniques to find the solution that satisfies the initial and boundary conditions

$$u(a, 0) = f(a), \quad 0 \leq a \leq d; \quad u(0, t) = B(t), \quad t > 0,$$

where $f(a)$ is the initial age structure and $B(t)$ is a given birth schedule.

6. This exercise presents an alternate derivation of the McKendrick-von Forester equation (5.1). If $u(a, t)$ is the density of females of age a at time t , then at a small time dt later, all females still alive will have aged an amount $da = dt$. Thus, the average number of females dying in this interval is

$$\frac{u(a + da, t + dt) - u(a, t)}{dt} = -m(a)u(a, t) + O(dt),$$

where $m(a)u(a, t)dt$ represents the probability of dying in the small time interval t to $t + dt$. Finish the derivation.

5.2 Traveling Waves Fronts

We observed in Chapter 1 that the advection equation $u_t = -cu_x$ and the wave equation $u_{tt} = c^2u_{xx}$ both admit **traveling wave solutions** of the form $u(x, t) = U(z)$, where U is any function (the shape of the wave), and $z = x - ct$ is a moving coordinate that travels with speed c . As it turns out, many nonlinear PDEs have these types of solutions. They model a signal, or disturbance, that moves with constant speed, and they can represent moving population fronts, infectious disease or epidemic waves, biological invasions, chemical reaction fronts, and many other interesting biological phenomena.

First consider the model diffusion-type equation having the general form

$$u_t = Du_{xx} + f(u, u_x), \quad (5.18)$$

where f is some fixed function, possibly nonlinear, depending the concentration u and its spatial gradient u_x . We are interested in finding solutions of the form $u(x, t) = U(z)$, where $z = x - ct$, where both the wave form U and the wave speed c are unknown. The spatial independent variable x is assumed to vary over all real numbers, that is, $-\infty < x < \infty$, and therefore $-\infty < z < \infty$. We can find an equation for the shape of the wave $U(z)$ by substituting this form into the PDE. First, we calculate the partial derivatives of u in order to make the substitution. Using the multi-variable chain rule, we get

$$\begin{aligned} u_t &= U'(z)z_t = -cU'(z), \\ u_x &= U'(z)z_x = U'(z), \\ u_{xx} &= U''(z)z_x = U''(z). \end{aligned}$$

Substituting into the PDE produces an ODE for the wave form $U(z)$:

$$-cU' = DU'' + f(U, U'), \quad -\infty < z < \infty. \quad (5.19)$$

Notice that the ODE has only two variables, the independent “moving” coordinate z and the dependent wave form U . The variables t and x dropped out of the problem, which is required if the method is to succeed. The constant wave speed is not known.

Ordinary differential equations are sometimes easier to deal with than PDEs. In the present case we have a second-order ODE where the independent variable is any real number. Solutions of such equations usually depend upon two arbitrary constants, and we need two auxiliary conditions to determine those constants. Therefore we impose conditions at $z = \pm\infty$ on the wave form, namely that $U(z)$ approach constant values, or densities, at both extremes:

$$U(-\infty) = u_l, \quad U(+\infty) = u_r, \quad (5.20)$$

where u_l and u_r are two fixed constants. We assume these two states are equilibrium states for the equation, i.e., $f(u_l, 0) = f(u_r, 0) = 0$. Thus we are not interested in any traveling wave, but only those that are bounded and approach constant, equilibrium states at $z = \pm\infty$. These special types of traveling wave solutions are called **wave front solutions**. See Figure 5.2.

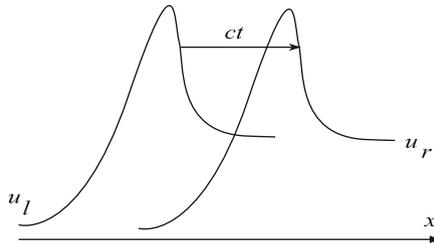


Figure 5.2 Plot of two successive wave profiles of a right, traveling wave front solution moving at speed c

To complicate matters, the wave speed c is also unknown and often acts as an *eigenvalue*; that is, wave front solutions will exist only for certain values of c . Hence, we often refer to (5.19–5.20) as a nonlinear eigenvalue problem.

Wave fronts can arise from natural settings as limiting, or long time, solutions to boundary value problems. As an illustration, consider the initial BVP for a toxic chemical of concentration $u = u(x, t)$ in a semi-infinite domain, e.g.,

a long canal:

$$\begin{aligned}u_t &= Du_{xx} + f(u, u_x), \quad x > 0, \quad t > 0, \\u(x, 0) &= 0, \quad x > 0, \\u(0, t) &= 1, \quad t > 0, \\u(\infty, t) &= 0.\end{aligned}$$

Here f is a term that contains advection and reaction processes. Intuitively, we reason as follows. For early times a concentration wave with unit magnitude at the left boundary ($x = 0$) begins to move into the medium; at these times the shape of the wave changes as it evolves. However, over a longer time the concentration wave can begin to approach a wave front with the same shape wave form. That is, the solution to the initial BVP may approach a wave front having the form $u = F(x - ct)$ for some wave speed c . Often we just look for the wave front. The issue of whether solutions to initial BVPs evolve into wave fronts is a question of whether the wave front attracts other solutions, i.e., it is one of stability of the front.

Generally we cannot find an explicit solution to (5.19) and we resort to numerical computation. Oftentimes we can prove there must be a unique solution without solving the equation in any manner. A standard technique is to transform (5.19) to a system of first order ODEs for the variables U and $V = U'$ in the UV phase plane. We obtain

$$\begin{aligned}U' &= V, \\V' &= -\frac{c}{D}V - \frac{1}{D}f(U, V).\end{aligned}$$

Assuming that V , or equivalently U' , goes to zero at $z = \pm\infty$, the problem of finding a wave front solution to (5.19) now consists of finding a solution (trajectory) in phase space that connects the two equilibrium points $(u_l, 0)$ and $(u_r, 0)$. A thorough discussion of the phase space method is beyond our scope and we refer the reader to other sources (e.g., Logan 2001, 2009, or the references given at the beginning of this chapter).

Example 5.1

Consider the diffusion equation

$$u_t = Du_{xx}.$$

Solutions of the form $u(x, t) = U(z)$, where $z = x - ct$, must satisfy the ODE

$$-cU' = DU''.$$

This is a linear second-order equation with characteristic equation $-cm = Dm^2$ having roots $m = 0$, $m = -c/D$. Therefore the independent solutions are 1 and $e^{-cz/D}$, and the general solution is therefore

$$U(z) = c_1 + c_2 e^{-cz/D},$$

or

$$u(x, t) = c_1 + c_2 e^{-c(x-ct)/D}.$$

Therefore the diffusion equation admits traveling wave solutions, but not (non-constant) wave front solutions because $e^{-cz/D}$ does not remain bounded at $z = +\infty$. \square

Example 5.2

(Epidemic waves) We consider a model for the spread of a rabies epidemic throughout a healthy population of foxes. We set up the problem in one-dimensional linear geometry, and we ignore natural mortality and births. Let $S = S(x, t)$ denote the density of the susceptible fox population and $I = I(x, t)$ the density of the infected foxes. We assume the rate that healthy foxes become infected is proportional to SI , the argument being that the number of contacts between members of the two groups is equal to their product; thus the rate of conversion of susceptibles to infecteds is bSI , where b is the constant infection rate, or the fraction of the contacts that lead to infection. Because rabies is fatal, we assume that infected foxes die at *per capita* rate r and they are removed from the susceptible and infected populations. Finally, we assume that healthy foxes are territorial and do not diffuse, while rabid foxes are disoriented and diffuse randomly with diffusion constant D . Thus we have the model equations

$$\begin{aligned} S_t &= -bSI, \\ I_t &= bSI - rI + DI_{xx}. \end{aligned}$$

By an epidemic wave we mean a wave of infecteds moving into a healthy population, and we model it by a wave front of unknown wave speed c . Letting $S = S(z)$, $I = I(z)$, $z = x - ct$, we get wave front equations

$$\begin{aligned} -cS' &= -bSI, \\ -cI' &= bSI - rI + DI''. \end{aligned}$$

At $z = +\infty$, ahead of the infection or epidemic wave, we assume there are only susceptibles, so $S(+\infty) = N$, where N is the total population of foxes, and $I(+\infty) = 0$. After the wave has passed, at $z = -\infty$, we assume no infecteds remain, or $I(-\infty) = 0$ (the epidemic has died out), and the number of susceptibles is $S(-\infty) = S_l$, which is not known *a priori*. We want to determine the

speed c of the epidemic wave and S_l , the number that will not get the disease. Figure 5.3 shows the shapes of the waves that we might expect.

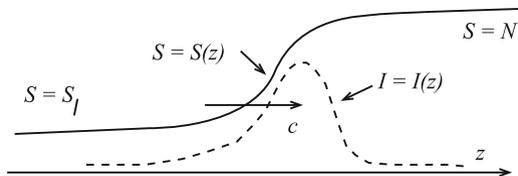


Figure 5.3 SI epidemic wave $S = S(x - ct)$

To make progress, note that $S'/S = (\ln S)'$, so the first equation becomes $I = (c/b)(\ln S)'$. We can substitute this into the second equation to obtain

$$-cI' = cS' - \frac{rc}{b}(\ln S)' + DI'',$$

which can be integrated with respect to z since every term is a derivative. Then

$$-cI = cS - \frac{rc}{b} \ln S + DI' + a,$$

where a is a constant of integration. Taking the limit as $z \rightarrow +\infty$ gives $a = c\left(\frac{r}{b} \ln N - N\right)$. Taking the limit as $z \rightarrow -\infty$ gives another equation relating a and c , namely $a = c\left(\frac{r}{b} \ln S_l - S_l\right)$. Therefore

$$\frac{r}{b} \ln N - N = \frac{r}{b} \ln S_l - S_l, \quad (5.21)$$

which is a relation between the number S_l that do not get the disease, the total initial population N , the infection rate b , and the death rate r . The relation is independent of the epidemic wave speed c . To simplify, we introduce parameters

$$R_0 = \frac{r}{Nb}, \quad F = \frac{S_l}{N},$$

where F is the fraction that do not contract rabies and R_0 is the reproductive ratio of the disease, representing the death rate divided by the infection rate. Then (5.21) can be written in the form

$$R_0 = \frac{F - 1}{\ln F}, \quad 0 < F < 1.$$

A plot of this function is shown in Figure 5.4, from which we infer that R_0 cannot exceed 1. Thus, no epidemic wave front can occur when $R_0 > 1$. This is reasonable since the death rate would be high compared to the rate of getting the disease; the epidemic dies out because the infecteds die out faster than they

are replaced. This case can occur if b is small or can be forced small, say, by inoculation. On the other hand, if $R_0 < 1$ then an epidemic wave can propagate; the smaller R_0 , the greater the number that get rabies. \square

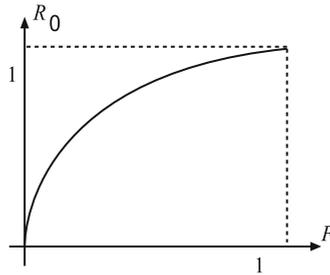


Figure 5.4 Plot of F vs R_0

Several questions remain in this example. We did not solve the wave front equations to find the wave forms or even show that such wave forms exist; nor did we determine the speed of the epidemic. The goal has been to derive certain properties of the epidemic wave under the assumption that it exists. A more thorough analysis, given in the references, shows that such solutions do exist.

EXERCISES

1. Show that the nonlinear advection-diffusion equation

$$u_t = Du_{xx} - uu_x$$

admits a wave front solution $U = U(z)$, satisfying the boundary conditions $U(-\infty) = 1$, $U(+\infty) = 0$. Find the wave speed and sketch the solution on a zu -coordinate system if $U(0) = \frac{1}{2}$.

2. Consider a reaction-diffusion equation with a nonlinear advection term given by

$$u_t = u_{xx} - u^2 u_x.$$

For which wave speeds c does a positive wave front solution exist with $u \rightarrow 0$ as $x \rightarrow \infty$? What are the possible states at $x = -\infty$?

3. Consider the system of reaction-advection-diffusion equations

$$\begin{aligned}u_t &= Du_{xx} - \gamma u_x - aF(u, v), \\v_t &= -bF(u, v),\end{aligned}$$

where a , b , D , and γ are positive constants. Find a system of ODEs for traveling wave forms $u = U(z)$, $v = V(z)$, $z = x - ct$. If boundary conditions are given by

$$U(-\infty) = u_l, \quad U(+\infty) = 0, \quad V(-\infty) = 0, \quad V(+\infty) = v_r,$$

what conditions must the reaction term F satisfy for wave front solutions to exist? Sketch possible wave front profiles. Assuming wave fronts exist, show that the speed c of the wave is less than the advection speed γ .

4. The following system of PDEs arises in the study of bioremediation of aquifer systems where immobile, indigenous microbes attached to the soil are stimulated to consume a contaminant and produce nontoxic products (see Logan 2001, p. 107):

$$RS_t = -vS_x - F, \quad A_t = -vA_x - rF, \quad M_t = yF - b(M - M_0),$$

where $M(x, t)$ is the density of the microbes, $S(x, t)$ is the density of the contaminant (e.g., a hydrocarbon), $A(x, t)$ is the density of a nutrient stimulant (e.g., oxygen), and $F = qSAM / \left[(K_s + S)(K_a + A) \right]$ is the biodegradation rate. $R > 1$ is the retardation constant, v is the average velocity of the subsurface flow, b is the decay rate of the bacteria, y is the yield, M_0 is a reference microbe density, and r is the mass of the nutrient used per mass contaminant degraded; q , K_s , and K_a are rate constants. Find the speed c of an assumed wave front that satisfies the boundary conditions $S = 0$, $A = A_0$ at $-\infty$, $S = S_r$, $A = 0$ at $+\infty$, and $M = M_0$ at $\pm\infty$. Without solving the wave front differential equations, sketch anticipated profiles of S , A , and M as a function of the variable $z = x - ct$.

5. The nonlinear PDE model

$$\left((1 + b)u - mu^2 \right)_t = u_{xx} - u_x$$

arises in the subsurface transport of a contaminant that is adsorbed to the soil. Assume $b > m$. Find a wave front solution $u = U(x - ct)$ satisfying the conditions $U(-\infty) = 1$, $U(+\infty) = 0$, $U(0) = 0.5$. The solution is

$$u(x, t) = \frac{1}{1 + e^{cm(x-ct)}}.$$

5.3 Equilibria and Stability

We already noted the broad occurrence of diffusion problems in biological systems. Now we investigate another aspect of such problems, namely the persistence of equilibrium states in systems governed by reaction-diffusion systems. At issue is the stability of those states: if a system is in an equilibrium state and it is slightly perturbed, or displaced, does the system return to that state, or does it evolve to a completely different state?

Underpinned by the seminal work of Alan Turing in 1952 on the chemical basis of morphogenesis, it has been shown in extensive research that diffusion induced instabilities can give rise to spatial patterns in all sorts of biological systems. Reaction-diffusion models have been used to explain the evolution of form and structure in developmental biology (morphogenesis), tumor growth, ecological spatial patterns, aggregation, patterns on animal coats, and many other processes in molecular and cellular biology.

In this section we introduce the basic idea of stability in reaction-diffusion models and we observe that such systems can have instabilities that lead to density variations and patterns. We refer the reader to Murray (2003) for an in-depth treatment of these models in the life sciences.

Stability

To illustrate the notion of stability of an equilibrium, or steady-state, to a PDE, we begin with a review of the stability issue for ODEs. For example, consider the logistics population model

$$\frac{du(t)}{dt} = ru(t) \left(1 - \frac{u(t)}{K} \right), \quad (5.22)$$

where r is the intrinsic growth rate and K is the carrying capacity, both positive. A steady-state, or *equilibrium solution*, is a constant solution $u = u_e$. For such a solution the left side of (5.22) must be zero, and so u_e satisfies the algebraic equation

$$ru_e \left(1 - \frac{u_e}{K} \right) = 0.$$

Therefore there are two equilibria, $u_e = 0$ and $u_e = K$. If at some time t the system is in an equilibrium state, it remains in that state for all time. That, if $u(t_0) = u_e$ for some t_0 , then $u(t) = u_e$ for all $t > t_0$ because $u(t) = u_e$ satisfies both the initial condition and the differential equation; uniqueness implies this. Natural “perturbations,” however, often disturb equilibrium and move the system a small amount away from its steady state. Does the system return to that state, or does it deviate significantly from that state, possible going to another equilibrium state? This is the question of stability. In the

present example, if the system is at carrying capacity $u = K$ and a small number of organisms are removed, does the system grow back to that original state or does it do something else? To answer this question we try to determine how a small deviation, or *perturbation*, will evolve by finding an equation for the deviation and solving it. Therefore, let $U(t)$ be a *small deviation* from the steady state $u = K$. That is, assume $u(t) = K + U(t)$. Then $u(t)$ must still solve the model equation. Substituting into (5.22) gives

$$\frac{d(K + U(t))}{dt} = r(K + U(t)) \left(1 - \frac{K + U(t)}{K} \right).$$

Simplifying the right side and noticing that $dK/dt = 0$ gives

$$\frac{dU(t)}{dt} = -\frac{r}{K} (KU(t) + U(t)^2), \quad (5.23)$$

which is called the **perturbation equation**. In general we cannot always solve the perturbation equation, so we make another argument. In (5.23) the perturbation $U(t)$ is small; therefore the $U(t)^2$ term is very small compared to the $U(t)$ term and we can discard it to obtain a **linearized perturbation equation**

$$\frac{dU(t)}{dt} = -rU(t).$$

This equation can be solved instantly to obtain $U(t) = Ce^{-rt}$, which shows that the perturbations decay, as long as they remain small.

This **linearization** procedure can be applied to any nonlinear autonomous equation

$$\frac{du}{dt} = f(u), \quad u = u(t).$$

Equilibrium solutions $u = u_e$ are solutions of the algebraic equation

$$f(u_e) = 0. \quad (5.24)$$

If $u(t) = u_e + U(t)$, where $U = U(t)$ is a small deviation from equilibrium, then it satisfies the perturbation equation

$$\frac{dU}{dt} = f(u_e + U).$$

Because U is assumed small, we may expand the right side in its Taylor series about u_e . Thus

$$f(u_e + U) = f(u_e) + f'(u_e)U + \frac{1}{2}f''(u_e)U^2 + \dots$$

Discarding the higher order nonlinear terms, while using (5.24), we obtain a linearized perturbation equation

$$\frac{dU}{dt} = f'(u_e)U.$$

This equation has general solution $U(t) = Ce^{\lambda t}$, where $\lambda = f'(u_e)$ is termed the *eigenvalue*; if $\lambda < 0$ the perturbation decays and the equilibrium u_e is stable, and if $\lambda > 0$ the perturbation grows and the equilibrium is unstable. If $\lambda = 0$ there is no information and we have to take into account additional terms in the Taylor series. In summary, the stability of an equilibrium state can be determined by examining the sign of the eigenvalue, i.e., the sign of the derivative of the right side of the differential equation, evaluated at that equilibrium state.

The linearization procedure is based upon the assumption that the perturbations are sufficiently small. The type of stability that results is called *local stability* since the deviations are not far from the equilibrium state. The procedure gives no results about *global stability*, i.e., how the system would evolve if any perturbation, regardless of its magnitude, were permitted.

Example 5.3

In the logistics equation (5.22) the right side is

$$f(u) = ru\left(1 - \frac{u}{K}\right).$$

Therefore,

$$f'(u) = r - \frac{2r}{K}u.$$

To determine local stability of the equilibrium state $u_e = K$ we check the eigenvalue

$$\lambda = f'(K) = r - \frac{2r}{K}K = -r.$$

Because $\lambda < 0$ the equilibrium $u_e = K$ is stable; small perturbations decay away. The other equilibrium solution is $u_e = 0$. In this case $\lambda = f'(0) = r > 0$, and therefore the zero state is unstable; if an initial small deviation were imposed, it would grow and the system would depart from equilibrium. \square

Stability for PDEs

A similar theory of local stability of equilibrium solutions can be developed for PDEs. In the interval $0 < x < L$ consider the reaction-diffusion equation

$$u_t = Du_{xx} + f(u),$$

with no-flux boundary conditions $u_x(0, t) = u_x(\pi, t) = 0$. Let $u(x, t) = u_e$ be a constant equilibrium solution (so that $f(u_e) = 0$). To fix the idea let $a = f'(u_e) > 0$. Note that the equilibrium solution satisfies the PDE and the boundary conditions. Next, let $U(x, t)$ be a small perturbation from the

equilibrium solution, or $u(x, t) = u_e + U(x, t)$. The *perturbation equation* is determined by substituting this expression into the PDE and the boundary conditions:

$$U_t = DU_{xx} + f(u_e + U), \quad U_x(0, t) = U_x(L, t) = 0.$$

To linearize this equation we expand, as above, the right side in a Taylor series and discard the nonlinear terms:

$$f(u_e + U) = f(u_e) + f'(u_e)U + \cdots = f'(u_e)U + \cdots$$

Then we obtain the **linearized perturbation equation**

$$U_t = DU_{xx} + aU, \quad a = f'(u_e) > 0 \quad (5.25)$$

subject to boundary conditions

$$U_x(0, t) = U_x(L, t) = 0. \quad (5.26)$$

This problem, which is on a bounded interval, can be solved by the separation of variables method (Chapter 4). We assume $U = g(x)h(t)$ and then substitute into the PDE (5.25) and boundary conditions (5.26) to obtain

$$gh' = Dg''h + agh,$$

or

$$\frac{h'}{h} = \frac{Dg''}{g} + a = \lambda.$$

Then $h = Ce^{\lambda t}$ and

$$g'' + \left(\frac{a - \lambda}{D}\right)g = 0, \quad g'(0) = g'(L) = 0.$$

This equation cannot have nontrivial exponential solutions that satisfy the boundary conditions; therefore $a - \lambda \geq 0$. In the case $\lambda = a$ we obtain a constant solution, and in the case $a - \lambda > 0$ we obtain

$$g(x) = A \sin \sqrt{\frac{a - \lambda}{D}}x + B \cos \sqrt{\frac{a - \lambda}{D}}x.$$

Applying $g'(0) = 0$ forces $A = 0$; then $g'(L) = 0$ implies

$$\sin \sqrt{\frac{a - \lambda}{D}}L = 0,$$

or

$$\sqrt{\frac{a - \lambda}{D}}L = n\pi, \quad n = 1, 2, \dots$$

Therefore, incorporating the case $\lambda = a$, we obtain eigenvalues

$$\lambda = \lambda_n = a - \frac{Dn^2\pi^2}{L^2}, \quad n = 0, 1, 2, \dots \quad (5.27)$$

The modal solutions are therefore

$$U_n(x, t) = e^{\lambda_n t} \cos \frac{n\pi}{L} x, \quad n = 0, 1, 2, \dots \quad (5.28)$$

What conclusions can we draw from this calculation? Because the general solution $U(x, t)$ to the boundary value problem (5.25–5.26) is a linear combination of the modal solutions (5.28),

$$U(x, t) = c_0 e^{at} + \sum_{n=1}^{\infty} c_n e^{\lambda_n t} \cos \frac{n\pi}{L} x,$$

it will decay if all of the modes decay, and it will grow if one of the modes grow. The constants c_n are determined by the initial perturbation. The spatial part of the modal solutions, i.e., the cosine, remains bounded. The amplitude factor $e^{\lambda_n t}$, and therefore the eigenvalues λ_n , determine growth or decay. Let us examine the modes. In the case $n = 0$ the eigenvalue is $\lambda_n = a$ and the modal solution is $c_0 e^{at}$, which grows exponentially. In fact, any mode satisfying $a \geq \frac{Dn^2\pi^2}{L^2}$ is unstable. Therefore, instabilities are likely to occur for modes of low frequency (n small), or in systems of large size L or low diffusion properties D . Oppositely, small systems with large diffusion constants are stabilizing, as are the high frequency modes. In the most general case the initial perturbation contains all modes and the steady state is locally unstable.

Cell Aggregation

We apply these ideas to a problem in cell aggregation. A slime mold population is a collection of unicellular amoeboid cells that feed on bacteria in the soil. When the food supply is plentiful, the bacteria are generally uniformly spatially distributed throughout the soil; but as the food supply becomes depleted and starvation begins, the amoeba start to secrete a chemical (cyclic AMP) that acts as an attractant to the other amoeba and aggregation sites form. The rest of the story is even more interesting as the aggregation sites evolve into slugs that ultimately develop into a sporangiophores consisting of a stalk and head containing new spores. The spores are released and the process begins anew. We are interested here in only the first part of this complicated problem, the onset of aggregation. We work in one spatial dimension.

Let $a = a(x, t)$ and $c = c(x, t)$ denote the density and concentration of the cellular amoeba and cyclic AMP, respectively. The fundamental conservation laws are

$$a_t = -\phi_x^{(a)}, \quad c_t = -\phi_x^{(c)} + F,$$

where $\phi^{(a)}$ and $\phi^{(c)}$ are the fluxes of the amoeba and the chemical, respectively. There are no source terms in the amoeba equation because we do not consider birth and death processes on the time scale of the analysis. The source term F in the chemical equation consists of two parts: production by the amoeba and degradation in the soil. We assume the chemical is produced by the amoeba at a rate proportional to the density of the amoeba, and the chemical degrades at a rate proportional to its concentration; i.e.,

$$F = fa - kc.$$

The chemical moves by diffusion only, and we assume Fick's law:

$$\phi^{(c)} = -\delta c_x,$$

where δ is the diffusion constant. The amoeba are also assumed to randomly diffuse, but there is another flux source for the amoeba, namely attraction to the chemical. We assume this attraction is *up the chemical gradient*, toward high concentrations of c . Additionally, it should depend on the amoeba population because that increases the magnitude of the chemical concentration released. This type of flow toward a source, induced by chemical gradients, is called **chemotaxis**. Therefore we assume

$$\begin{aligned}\phi^{(a)} &= \text{random flux} + \text{chemotactic flux} \\ &= -\mu a_x + \nu a c_x,\end{aligned}$$

where μ is the amoeba motility and ν is the strength of the chemotaxis, both assumed to be positive constants. Note that the random flux, having the form of Fick's law, has a negative sign since flow is "down the gradient" (from high to low densities), and the chemotactic flux has a positive sign since that term induces flow "up the chemical gradient" (from low to high concentrations). Putting all these equations all together gives the system

$$a_t = \mu a_{xx} - \nu (ac_x)_x, \quad c_t = \delta c_{xx} + fa - kc. \quad (5.29)$$

Both a and c satisfy no-flux boundary conditions, i.e., $a_x = c_x = 0$ at $x = 0, L$, which means there is no escape from the medium.

Notice that there will be an equilibrium solution $a = \bar{a}$, $c = \bar{c}$ to (5.29) provided

$$f\bar{a} = k\bar{c}.$$

That is, the production of the chemical equals its degradation. This equilibrium state represents the spatially uniform state in the soil before aggregation begins.

To determine the local stability of this state we let

$$a = \bar{a} + A(x, t), \quad c = \bar{c} + C(x, t),$$

where A and C are small perturbations. Substituting these quantities into (5.29) gives, after simplification, the perturbation equations

$$A_t = \mu A_{xx} - \nu \left((\bar{a} + A) C_x \right)_x, \quad C_t = \delta C_{xx} + fA - kC.$$

These equations are nonlinear because of the AC_x term in the amoeba equation. If we discard the nonlinear term on the assumption that the product of small terms is even smaller, then we obtain the linearized perturbation equations

$$A_t = \mu A_{xx} - \nu \bar{a} C_{xx}, \quad C_t = \delta C_{xx} + fA - kC. \quad (5.30)$$

Easily one can see that the perturbations satisfy the no-flux boundary conditions.

Motivated by our knowledge of the form of solutions to linear equations, we assume there are modal solutions of the form

$$A(x, t) = c_1 e^{\sigma t} \cos rx, \quad C(x, t) = c_2 e^{\sigma t} \cos rx, \quad (5.31)$$

where r and σ are to be determined, and c_1 and c_2 are constants. Notice the form of these assumed solutions. The spatial part is bounded and periodic with frequency r and period $2\pi/r$, and the temporal part is exponential with growth factor σ , which may be a real or complex number. If σ is negative or has a negative real part, then the perturbation will decay and the equilibrium state will return (stability); if σ is positive or has positive real part, then the perturbations will grow and the equilibrium will be unstable.

Let us ask why solutions of (5.30) should be of this form (5.31) without going through the entire separation of variables argument. Equations (5.30) are linear with constant coefficients, and both equations contain A and C and their derivatives. If we are to have a solution, then all the terms must match up in one way or another in order to cancel. So both A and C must essentially have the same form. Because there is a first derivative in t , the time factor must be exponential so it will cancel, and the spatial part must be a sine or a cosine because of the appearance second spatial derivative. We anticipate the cosine function because of the no-flux boundary conditions, as in Chapter 4. If we substitute (5.31) into (5.30) we obtain the two equations

$$\left(\sigma + \mu r^2 \right) c_1 - \nu \bar{a} r^2 c_2 = 0, \quad -f c_1 + \left(\sigma + k + \delta r^2 \right) c_2 = 0$$

which relate all the parameters. We may regard these two equations as two linear, homogeneous for the constants c_1 and c_2 . If we want a nontrivial solution for c_1 and c_2 , then from matrix theory the determinant of the coefficient matrix must be zero. That is,

$$\left(\sigma + \mu r^2 \right) \left(\sigma + k + \delta r^2 \right) - f \nu \bar{a} r^2 = 0,$$

which is an equation relating the temporal growth factor σ , the spatial frequency r , and the other constants in the problem. Expanded, this equation is a quadratic in σ ,

$$\sigma^2 + \gamma_1\sigma + \gamma_2 = 0,$$

where

$$\gamma_1 = r^2(\mu + \gamma) + k > 0, \quad \gamma_2 = r^2 \left[\mu(\delta r^2 + k) - f\nu\bar{a} \right].$$

The roots of the quadratic are

$$\sigma = \frac{1}{2} \left(-\gamma_1 \pm \sqrt{\gamma_1^2 - 4\gamma_2} \right).$$

Clearly one of the roots is always negative or has negative real part. The other root can have positive or negative real part, depending upon the value of the discriminant $\gamma_1^2 - 4\gamma_2$. We are interested in determining if there are parameter choices that lead to an instability; so we want σ positive. Hence, γ_2 must be negative, or

$$\mu(\delta r^2 + k) < f\nu\bar{a}.$$

If this inequality holds, there is an unstable mode and perturbations will grow. We analyze this further.

The number r is the spatial frequency of the perturbations. Applying the no-flux boundary conditions forces

$$r = \frac{n\pi}{L}, \quad n = 0, 1, 2, 3, \dots$$

For each value of n we obtain a frequency $r = r_n$ and a corresponding growth factor σ_n . The n th mode will therefore grow and lead to local instability when

$$\mu \left(\delta \frac{n^2\pi^2}{L^2} + k \right) < f\nu\bar{a}. \quad (5.32)$$

We can now ask what factors destabilize the uniform, equilibrium state in the amoeba-cAMP system and therefore promote aggregation. That is, when is (5.32) likely to hold? We can list the factors that may make the left side of the inequality (5.32) smaller than the right side: low motility μ of the bacteria; low degradation rate k or large production rate f of cAMP; large chemotactic strength ν ; large dimensions L of the medium; a small value of n (thus, low frequency, or long wave length, perturbations are less stabilizing than short wave, or high frequency, perturbations); decreasing the diffusion constant of the cAMP. Figure 5.5 shows time snapshots of the amoeba density for the mode $n = 2$ when it is unstable. The intervals where the amplitude is high correspond to higher concentrations of amoeba, i.e., regions of aggregation.

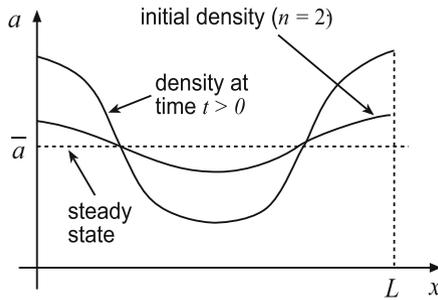


Figure 5.5 Plot showing the growing amoeba density at time t when the uniform state is unstable to local perturbations in the mode $n = 2$

EXERCISES

1. Consider an fish population that grows logistically, and at the same time is harvested at a rate proportional to the population. The model is

$$\frac{du}{dt} = ru \left(1 - \frac{u}{K}\right) - hu$$

where r , K , and h are the growth rate, carrying capacity, and harvesting rate, respectively. Find all the equilibria and analyze their stability. What are the possible long term fish populations?

2. (**Turing system**) Consider the system of reaction diffusion equations on the spatial domain $0 < x < L$ given by

$$u_t = \alpha u_{xx} + f(u, v), \quad v_t = \beta v_{xx} + g(u, v)$$

with no-flux boundary conditions $u_x = v_x = 0$ at $x = 0, L$. Let $u = \bar{u}$, $v = \bar{v}$ be an equilibrium solution and define small perturbations U and V from equilibrium given by

$$u = \bar{u} + U(x, t), \quad v = \bar{v} + V(x, t).$$

- (a) Show that U and V satisfy no-flux boundary conditions and the linearized perturbation equations

$$U_t = \alpha U_{xx} + f_u(\bar{u}, \bar{v})U + f_v(\bar{u}, \bar{v})V, \quad (5.33)$$

$$V_t = \beta V_{xx} + g_u(\bar{u}, \bar{v})U + g_v(\bar{u}, \bar{v})V. \quad (5.34)$$

(b) Introduce matrix notation

$$\vec{W} = \begin{pmatrix} U \\ V \end{pmatrix}, \quad D = \begin{pmatrix} \alpha & 0 \\ 0 & \beta \end{pmatrix}, \quad J = \begin{pmatrix} f_u(\bar{u}, \bar{v}) & f_v(\bar{u}, \bar{v}) \\ g_u(\bar{u}, \bar{v}) & g_v(\bar{u}, \bar{v}) \end{pmatrix},$$

and show that (5.33–5.34) can be written as

$$\vec{W}_t = D\vec{W}_{xx} + J\vec{W}. \quad (5.35)$$

(c) Assume modal solutions to (5.35) of the form

$$\vec{W} = \vec{C} e^{\sigma_n t} \cos \frac{n\pi x}{L}, \quad \vec{C} = \begin{pmatrix} c_{1n} \\ c_{2n} \end{pmatrix}, \quad n = 0, 1, 2, \dots,$$

and show that for a nontrivial solution we must have

$$\det \left(\sigma_n I + \frac{n^2 \pi^2}{L^2} D - J \right) = 0. \quad (5.36)$$

When expanded, this equation is a quadratic equation for the growth factor σ_n of the n th mode. The roots σ_n depend upon the diffusion constants α, β , the equilibrium solution \bar{u}, \bar{v} , the size of the medium L , and the wavelength $2L/n$ of the perturbation. If one can find values of the parameters that make one of the roots positive or have positive real part, then there is an unstable mode.

3. Apply the method of Exercise 2 to examine the stability of the steady state of the Turing system

$$u_t = Du_{xx} + 1 - u + u^2v, \quad v_t = v_{xx} + 2 - u^2v, \quad 0 < x < \pi,$$

under no-flux boundary conditions. Specifically, write the condition (5.36) and determine values of D for which various modes (n) are unstable.

4. Consider Fisher's equation with Dirichlet boundary conditions:

$$\begin{aligned} u_t &= u_{xx} + u(1-u), & -\frac{\pi}{2} < x < \frac{\pi}{2}, \\ u &= 3 \quad \text{at} \quad x = \pm \frac{\pi}{2}. \end{aligned}$$

(a) Show that $u_e(x) = \frac{3}{1+\cos x}$ is a *nonconstant* steady state solution.

(b) Define perturbations $U(x, t)$ by the equation $u = u_e(x) + U(x, t)$ and find the linearized perturbation equation and boundary conditions for $U(x, t)$.

(c) Assume a solution to the linearized equation of the form $U = e^{\sigma t}g(x)$ and show that g must satisfy

$$g'' + \frac{\cos x - 5}{1 + \cos x}g = \sigma g, \quad g = 0 \quad \text{at} \quad x = \pm \frac{\pi}{2}. \quad (5.37)$$

(d) Show that if (5.37) has a nontrivial solution, then $\sigma < 0$, thereby showing local stability of the steady solution. Hint: Consider two cases, when g is positive and when g is negative on the interval and then examine at the signs of g'' and the other terms in (5.37) at a maximum or minimum point.