### CHAPTER 5

# PDEs in The Life Sciences

## 1. Age-Structured Models

### Exercise 1: Write

$$1 = \int_{3}^{8} 4e^{-(r+0.03)a} da = -\frac{4}{r+0.03} \left( e^{-8(r+0.03)} - e^{-3(r+0.03)} \right),$$

and use a software package or calculator to solve for r.

**Exercise 2:** First note that u(a,t) = 0 for  $a > t + \delta$ , since f(a) = 0 for  $a > \delta$ . For (a) observe that the renewal equation (5.9) is

$$B(t) = \int_0^t \beta B(t-a)e^{-\gamma a}da + \int_0^\infty \beta f(a-t)e^{-\gamma t}da.$$

The first integral becomes, upon changing variables to s = t - a,

$$\int_0^t \beta B(t-a)e^{-\gamma a}da = \int_0^t \beta B(s)e^{-\gamma(t-s)}ds.$$

The second integral is

$$\int_0^\infty \beta f(a-t)e^{-\gamma t}da = \int_t^{t+\delta} \beta u_0 e^{-\gamma t}da = \beta u_0 \delta e^{-\gamma t}.$$

For (b), differentiate (using Leibniz rule)

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

to get

$$B'(t) = \int_0^t \beta B(s) e^{-\gamma(t-s)} ds(-\gamma) + \beta B(t) - \gamma \beta u_0 \delta e^{-\gamma t} = (\beta - \gamma) B(t).$$

For (c) note that the last equation is the differential equation for growth-decay and has solution

$$B(t) = B(0)e^{(\beta - \gamma)t}.$$

Therefore the solution from (5.7)–(5.8) is given by

$$u(a,t) = \begin{cases} 0, & a > t + \delta \\ u_0 e^{-\gamma t}, & t < a < t + \delta \\ B(0) e^{(\beta - \gamma)t} e^{-\beta a}, & 0 < a < t. \end{cases}$$

Finally, for part (d) we have, using part (c),

$$N(t) = \int_0^t u(a,t)da + \int_t^{t+\delta} u(a,t)da$$
  
= 
$$\int_0^t B(0)e^{(\beta-\gamma)t}e^{-\beta a}da + \int_t^{t+\delta} u_0e^{-\gamma t}da$$
  
= 
$$\frac{B(0)}{\beta}e^{(\beta-\gamma)t}(1-e^{-\beta t}) + \delta u_0e^{-\gamma t}.$$

**Exercise 3:** Integrate the PDE from a = 0 to  $a = \infty$  to get

$$N(t) = -\int_0^\infty u_a da - m(N)N = B(t) - m(N)N.$$

To get an equation for B we differentiate the B(t) equation to get

$$B'(t) = \int_0^\infty b_0 e^{-\gamma a} u_t da = \int_0^\infty b_0 e^{-\gamma a} (-u_a - m(N)u) da$$
  
=  $-m(N)B(t) - \int_0^\infty b_0 e^{-\gamma a} (u_a) da$   
=  $-m(N)B(t) - \left[ b_0 e^{-\gamma a} u |_0^\infty + \int_0^\infty b_0 \gamma e^{-\gamma a} u da \right]$   
=  $-m(N)B(t) - b_0 B(t) - \gamma B(t).$ 

To obtain the next-to-last line we used integration by parts. In summary we have the dynamical system

$$N' = B - m(N)N,$$
  
 $B' = (b_0 - \gamma - m(N))B.$ 

In the phase plane the paths or integral curves are defined by

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

Observe that  $B = (b_0 - \gamma)N$  is easily shown to be a solution to this equation. It represents a straight line in the NB plane. The line B=0 is a horizontal nullcline where the vector field points to the left. Another horizontal nullcline is the vertical line  $N = N^*$ , where  $N^*$  is the root of  $m(N) = (b_0 - \gamma)$ . The point  $P = (N^*, (b_0 - \gamma)N^*)$  is an equilibrium that lies on the straight line solution curve  $B = (b_0 - \gamma)N$ . The solution cannot oscillate since that it would require it cross the straight line, violating uniqueness. On the straight line solution, the direction is toward the point P.

Exercise 4: In preparation.

**Exercise 5:** Let  $\xi = a - t, \tau = t$ . In these characteristic coordinates the PDE becomes

$$U_{\tau} = -\frac{c}{d-\xi-\tau}U.$$

Separating variable and integrating gives

$$U = (d - \xi - \tau)^c \varphi(\xi)$$

or

$$u(a,t) = (d-a)^c \varphi(a-t),$$

which is the general solution. Now, for the region a > t we use the initial condition to determine  $\varphi$ . We have

$$u(a,0) = (d-a)^c \varphi(a) = f(a),$$

which gives  $\varphi(a) = f(a)(d-a)^c$ . Hence

$$u(a,t) = (d-a)^{c} f(a-t)(d-a-t)^{-c}, \quad a > t.$$

For the region a < t we use the boundary conditon. to determine  $\varphi$ . Thus,

$$u(0,t) = d^c \varphi(-t) = B(t),$$

or

$$\varphi(t) = B(-t)d^{-c}.$$

Whence

$$u(a,t) = (d-a)^{c}B(t-a)d^{-c}, \quad 0 < a < t.$$

Exercise 6: Using Taylor's expansion to write

 $u(a + da, t + dt) = u(a, t) + u_t(a, t)da + u_t(a, t)dt +$  higher order terms.

#### 2. Traveling Wave Fronts

Exercise 1: The traveling wave equation can be written

$$-cU' = DU'' - \frac{1}{2}(U^2)'.$$

Integrating, we get

$$-cU = DU' - \frac{1}{2}U^2 + A.$$

Using the boundary condition at  $z = +\infty$  forces A = 0. Using the boundary condition at  $z = -\infty$  gives the wave speed c = 1/2. Therefore

$$DU' = \frac{1}{2}U(U-1).$$

This DE has equilibria at U = 0, 1; the solution can be found by separating variables or noting it is a Bernoulli equation (see the Appendix on Differential Equations). The graph falls from left to right (decreasing), approaching 0 at plus infinity and 1 at minus infinity.

**Exercise 2:** The traveling wave equation may be written

$$-cU' = U'' - \frac{1}{3}(U^3)'.$$

Integrating, we find that the constant of integration is zero from the  $z = +\infty$  boundary condition. Then

$$-cU = U' - \frac{1}{3}U^3.$$

Applying the condition at  $z = -\infty$  we get

$$-cU_l = -\frac{1}{3}U_l^3,$$

 $\mathbf{or}$ 

$$-cU_l + \frac{1}{3}U_l^3 = -\frac{1}{3}U_l(3c - U_l^2) = 0.$$

Therefore  $U_l = \sqrt{3c}$ .

**Exercise 3:** To have constant states at infinity we must have  $F(0, v_r) = 0 = F(u_l, 0) = 0$ . The traveling wave equations are

$$\begin{array}{rcl} -cU' &=& DU'' - \gamma U' - aF(U,V), \\ -cV' &=& -bF(U,V). \end{array}$$

Clearly we may write a single equation

$$-cU' = DU'' - \gamma U' - \frac{ac}{b}V'.$$

Now we may integrate to get

$$-cU = DU' - \gamma U - \frac{ac}{b}V + A.$$

The right boundary condition forces  $A = acv_r/b$ . The left boundary condition then gives

$$-cu_l = -\gamma u_l + \frac{ac}{b}v_r$$

or

$$(\gamma - c)u_l = \frac{ac}{b}v_r > 0.$$

Therefore  $c < \gamma$ 

Exercise 4: In preparation.

**Exercise 5:** The traveling wave equation is

$$-c\left[(1+b)U - mU^{2}\right]' = U'' - U'.$$

Integrating gives

$$-c[(1+b)U - mU^2] = U' - U + A.$$

; From the boundary condition  $U(+\infty) = 0$  we get A = 0. Since  $U(-\infty) = 1$ , we get

$$c = \frac{1}{1+b-m} > 0$$

The differential equation then simplifies to

$$U' = (1 - c - cb)U + cmU^2,$$

which is a Bernoulli equation. It is also separable.

#### 3. Equilibria and Stability

**Exercise 1:** The equilibria are roots of

$$f(u) = ru(1 - u/K) - hu = u(r - \frac{r}{K}u - h) = 0.$$

So the equilibria are

$$u_1 = 0, \quad u_2 = \frac{r-h}{r}K.$$

To check stability we calculate  $f'(u_1) = r - \frac{2r}{K}u - h$ . Then f'(0) = r > 0, so  $u_1 = 0$  is unstable. Next

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

Therefore  $u_2$  is stable if r > h and unstable if r < h.

Exercise 2: In preparation.

Exercise 3: In preparation.

**Exercise 4:** To obtain (a) just substitute  $u_e(x)$  into the PDE and check the boundary conditions. To get (b) substitute  $u = u_e(x) + U(x,t)$  into the PDE to obtain

$$U_t = u_e'' + U_{xx} + (u_e(x) + U(x,t))(1 - u_e(x) - U(x,t)),$$

 $\mathbf{or}$ 

 $U_t = u''_e + U_{xx} + u_e(x)(1 - u_e(x)) - u_e(x)U + U(1 - u_e(x)) - U^2(x, t).$ 

But  $u''_e + u_e(x)(1 - u_e(x)) = 0$ , and neglecting the nonlinear term gives

 $U_t = U_{xx} + (1 - 2u_e(x))U,$ 

which is the linearized perturbation equation. The boundary conditions are  $U(\pm \pi/2) = 0$ . For part (c) assume that  $U = e^{\sigma t}g(x)$  and substitute to get

$$\sigma g = g'' + (1 - 2u_e(x))g,$$

 $\operatorname{or}$ 

$$g'' + \frac{\cos x - 5}{1 + \cos x}g = \sigma g,$$

with g = 0 at  $x = \pm \pi/2$ . Finally, to prove (d), we proceed as in the hint. If this BVP has a nontrivial solution, then it must be, say, positive somewhere in the interval. (The negative case can be treated similarly). So it must have a positive maximum in the interval. At this maximum, g > 0, g'' < 0. Therefore

$$\frac{\cos x - 5}{1 + \cos x}g < 0.$$

So the left side of the DE is negative, so  $\sigma < 0$ .