13. Biological Waves: Single-Species Models

13.1 Background and the Travelling Waveform

There is a vast number of phenomena in biology in which a key element or precursor to a developmental process seems to be the appearance of a travelling wave of chemical concentration, mechanical deformation, electrical signal and so on. Looking at almost any film of a developing embryo it is hard not to be struck by the number of wavelike events that appear after fertilisation. Mechanical waves are perhaps the most obvious. There are, for example, both chemical and mechanical waves which propagate on the surface of many vertebrate eggs. In the case of the egg of the fish *Medaka* a calcium (Ca^{++}) wave sweeps over the surface; it emanates from the point of sperm entry: we briefly discuss this problem in Section 13.6 below. Chemical concentration waves such as those found with the Belousov–Zhabotinskii reaction are visually dramatic examples (see Chapter 1, Volume II). From the analysis on insect dispersal in Section 11.3 in Chapter 11 we can also expect wave phenomena in that area, and in interacting population models where spatial effects are important. Another example, related to interacting populations, is the progressing wave of an epidemic, of which the rabies epizootic currently spreading across Europe is a dramatic and disturbing example; we study a model for this in some detail in Chapter 13. The movement of microorganisms moving into a food source, chemotactically directed, is another. The slime mould *Dictyostelium discoideum* is a particularly widely studied example of chemotaxis; we discuss this phenomenon later (see the photograph in Figure 1.1, Volume II which shows associated waves).

The book by Winfree (2000) is replete with wave phenomena in biology. The introductory text on mathematical models in molecular and cellular biology edited by Segel (1980) also deals with some aspects of wave motion. Although not so application oriented, there are several books on reaction diffusion equations such as by Fife (1979), Britton (1986) and Grindrod (1996) which are all relevant. Zeeman (1977) considers wave phenomena in development and other biological areas from a catastrophe theory standpoint.

The point to be emphasised is the widespread existence of wave phenomena in the biomedical sciences which necessitates a study of travelling waves in depth and of the modelling and analysis involved. This chapter and Chapter 1, Volume II (with many other examples throughout Volume II) deal with various aspects of wave behaviour where diffusion plays a crucial role. The waves studied here are quite different from those discussed in Chapter 12. The mathematical literature on them is now vast, so the number of topics and the depth of the discussions have to be severely limited. Among other things, we shall cover what is now accepted as part of the basic theory in the field and describe two practical problems, one associated with insect dispersal and control and the other related to calcium waves on amphibian eggs.

In developing living systems there is almost continual interchange of information at both the inter- and intra-cellular level. Such communication is necessary for the sequential development and generation of the required pattern and form in, for example, embryogenesis. Propagating waveforms of varying biochemical concentrations are one means of transmitting such biochemical information. In the developing embryo, diffusion coefficients of biological chemicals can be very small: values of the order of 10^{-9} to $10^{-11}\ \mathrm{cm}^2\ \mathrm{sec}^{-1}$ are fairly common. Such small diffusion coefficients imply that to cover macroscopic distances of the order of several millimetres requires a very long time if diffusion is the principal process involved. Estimation of diffusion coefficients for insect dispersal in interacting populations is now studied with care and sophistication (see, for example, Kareiva 1983 and Tilman and Kareiva 1998): not surprisingly the values are larger and species-dependent.

With a standard diffusion equation in one space dimension, which from Section 11.1 is typically of the form

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2}, \tag{13.1}$$

for a chemical of concentration u, the time to convey information in the form of a changed concentration over a distance L is $O(L^2/D)$. You get this order estimate from the equation using dimensional arguments, similarity solutions or more obviously from the classical solution given by equation (11.10) in Chapter 11. So, if L is of the order of 1 mm, typical times with the above diffusion coefficients are $O(10^7$ to 10^9 sec), which is excessively long for most processes in the early stages of embryonic development. Simple diffusion therefore is unlikely to be the main vehicle for transmitting information over significant distances. A possible exception is the generation of butterfly wing patterns, which takes place during the pupal stage and involves several days (for example, Murray 1981 and Nijhout 1991).

In contrast to simple diffusion we shall show that when reaction kinetics and diffusion are coupled, travelling waves of chemical concentration exist and can effect a biochemical change very much faster than straight diffusional processes governed by equations like (13.1). This coupling gives rise to reaction diffusion equations which (cf. Section 11.1, equation (11.16)) in a simple one-dimensional scalar case can look like

$$\frac{\partial u}{\partial t} = f(u) + D\frac{\partial^2 u}{\partial x^2}, \tag{13.2}$$

where u is the concentration, $f(u)$ represents the kinetics and D is the diffusion coefficient, here taken to be constant.

We must first decide what we mean by a travelling wave. We saw in Chapter 11 that the solutions (11.21) and (11.24) described a kind of wave, where the shape and speed of propagation of the front continually changed. Customarily a travelling wave is taken to be a wave which travels *without change of shape*, and this will be our understanding here. So, if a solution $u(x, t)$ represents a travelling wave, the *shape* of the solution will be the same for all time and the speed of propagation of this shape is a constant, which we denote by c. If we look at this wave in a travelling frame moving at speed c it will appear stationary. A mathematical way of saying this is that if the solution

$$u(x, t) = u(x - ct) = u(z), \quad z = x - ct \tag{13.3}$$

then $u(x, t)$ is a travelling wave, and it moves at constant speed c in the positive x-direction. Clearly if $x - ct$ is constant, so is u. It also means the coordinate system moves with speed c. A wave which moves in the negative x-direction is of the form $u(x + ct)$. The wavespeed c generally has to be determined. The dependent variable z is sometimes called the *wave variable*. When we look for travelling wave solutions of an equation or system of equations in x and t in the form (13.3), we have $\partial u/\partial t = -c du/dz$ and $\partial u/\partial x = du/dz$. So *partial* differential equations in x and t become *ordinary* differential equations in z. To be physically realistic $u(z)$ has to be bounded for all z and nonnegative with the quantities with which we are concerned, such as chemicals, populations, bacteria and cells.

It is part of the classical theory of linear parabolic equations, such as (13.1), that there are no physically realistic travelling wave solutions. Suppose we look for solutions in the form (13.3); then (13.1) becomes

$$D\frac{d^2u}{dz^2} + c\frac{du}{dz} = 0 \quad \Rightarrow \quad u(z) = A + Be^{-cz/D},$$

where A and B are integration constants. Since u has to be bounded for all z, B must be zero since the exponential becomes unbounded as $z \to -\infty$. $u(z) = A$, a constant, is not a wave solution. In marked contrast the parabolic reaction diffusion equation (13.2) can exhibit travelling wave solutions, depending on the form of the reaction/interaction term $f(u)$. This solution behaviour was a major factor in starting the whole mathematical field of reaction diffusion theory.

Although most realistic models of biological interest involve more than one dimension and more than one dependent variable, whether concentration or population, there are several multi-species systems which reasonably reduce to a one-dimensional single-species mechanism which captures key features. This chapter therefore is not simply a pedagogical mathematical exposition of some common techniques and basic theory. We discuss two very practical problems, one in ecology and the other in developmental biology: both belong to important areas where modelling has played a significant role.

13.2 Fisher–Kolmogoroff Equation and Propagating Wave Solutions

The classic simplest case of a nonlinear reaction diffusion equation (13.2) is

$$\frac{\partial u}{\partial t} = ku(1 - u) + D\frac{\partial^2 u}{\partial x^2}, \tag{13.4}$$

where k and D are positive parameters. It was suggested by Fisher (1937) as a deterministic version of a stochastic model for the spatial spread of a favoured gene in a population. It is also the natural extension of the logistic growth population model discussed in Chapter 11 when the population disperses via linear diffusion. This equation and its travelling wave solutions have been widely studied, as has been the more general form with an appropriate class of functions $f(u)$ replacing $ku(1-u)$. The seminal and now classical paper is that by Kolmogoroff et al. (1937). The books by Fife (1979), Britton (1986) and Grindrod (1996) mentioned above give a full discussion of this equation and an extensive bibliography. We discuss this model equation in the following section in some detail, not because in itself it has such wide applicability but because it is the prototype equation which admits travelling wavefront solutions. It is also a convenient equation from which to develop many of the standard techniques for analysing single-species models with diffusive dispersal.

Although (13.4) is now referred to as the Fisher–Kolmogoroff equation, the discovery, investigation and analysis of travelling waves in chemical reactions was first reported by Luther (1906). This rediscovered paper has been translated by Arnold et al. (1987). Luther's paper was first presented at a conference; the discussion at the end of his presentation (and it is included in the Arnold et al. 1988 translation) is very interesting. There, Luther states that the wavespeed is a simple consequence of the differential equations. Showalter and Tyson (1987) put Luther's (1906) remarkable discovery and analysis of chemical waves in a modern context. Luther obtained the wavespeed in terms of parameters associated with the reactions he was studying. The analytical form is the same as that found by Kolmogoroff et al. (1937) and Fisher (1937) for (13.4).

Let us now consider (13.4). It is convenient at the outset to rescale (13.4) by writing

$$t^* = kt, \quad x^* = x\left(\frac{k}{D}\right)^{1/2} \tag{13.5}$$

and, omitting the asterisks for notational simplicity, (13.4) becomes

$$\frac{\partial u}{\partial t} = u(1-u) + \frac{\partial^2 u}{\partial x^2}. \tag{13.6}$$

In the spatially homogeneous situation the steady states are $u = 0$ and $u = 1$, which are respectively unstable and stable. This suggests that we should look for travelling wavefront solutions to (13.6) for which $0 \le u \le 1$; negative u has no physical meaning with what we have in mind for such models.

If a travelling wave solution exists it can be written in the form (13.3), say

$$u(x,t) = U(z), \quad z = x - ct, \tag{13.7}$$

where c is the wavespeed. We use $U(z)$ rather than $u(z)$ to avoid any nomenclature confusion. Since (13.6) is invariant if $x \to -x$, c may be negative or positive. To be specific we assume $c \ge 0$. Substituting this travelling waveform into (13.6), $U(z)$ satisfies

$$U'' + cU' + U(1-U) = 0, \tag{13.8}$$

where primes denote differentiation with respect to z. A typical wave*front* solution is where U at one end, say, as $z \to -\infty$, is at one steady state and as $z \to \infty$ it is at the other. So here we have an eigenvalue problem to determine the value, or values, of c such that a nonnegative solution U of (13.8) exists which satisfies

$$\lim_{z\to\infty} U(z) = 0, \qquad \lim_{z\to-\infty} U(z) = 1. \tag{13.9}$$

At this stage we do not address the problem of how such a travelling wave solution might evolve from the partial differential equation (13.6) with given initial conditions $u(x,0)$; we come back to this point later.

We study (13.8) for U in the (U, V) phase plane where

$$U' = V, \quad V' = -cV - U(1-U), \tag{13.10}$$

which gives the phase plane trajectories as solutions of

$$\frac{dV}{dU} = \frac{-cV - U(1-U)}{V}. \tag{13.11}$$

This has two singular points for (U, V), namely, $(0,0)$ and $(1,0)$: these are the steady states of course. A linear stability analysis (see Appendix A) shows that the eigenvalues λ for the singular points are

$$\begin{aligned} (0,0):\quad \lambda_\pm &= \frac{1}{2}\left[-c \pm (c^2-4)^{1/2}\right] \Rightarrow \begin{cases}\text{stable node} & \text{if } c^2 > 4\\ \text{stable spiral} & \text{if } c^2 < 4\end{cases}\\ (1,0):\quad \lambda_\pm &= \frac{1}{2}\left[-c \pm (c^2+4)^{1/2}\right] \Rightarrow \text{saddle point}. \end{aligned} \tag{13.12}$$

Figure 13.1(a) illustrates the phase plane trajectories.

If $c \geq c_{\min} = 2$ we see from (13.12) that the origin is a stable node, the case when $c = c_{\min}$ giving a degenerate node. If $c^2 < 4$ it is a stable spiral; that is, in the vicinity

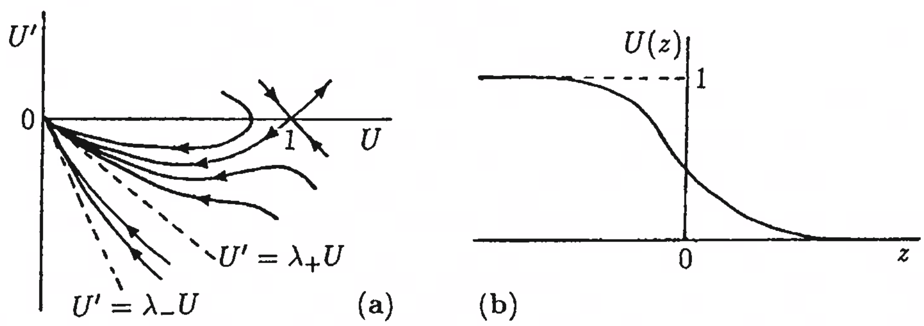

Figure 13.1. **(a)** Phase plane trajectories for equation (13.8) for the travelling wavefront solution: here $c^2 > 4$. **(b)** Travelling wavefront solution for the Fisher–Kolmogoroff equation (13.6): the wave velocity $c \geq 2$.

of the origin U oscillates. By continuity arguments, or simply by heuristic reasoning from the phase plane sketch of the trajectories in Figure 13.1(a), there is a trajectory from $(1, 0)$ to $(0, 0)$ lying entirely in the quadrant $U \geq 0$, $U' \leq 0$ with $0 \leq U \leq 1$ for *all* wavespeeds $c \geq c_{\min} = 2$. In terms of the original dimensional equation (13.4), the range of wavespeeds satisfies

$$c \geq c_{\min} = 2(kD)^{1/2}. \tag{13.13}$$

Figure 13.1(b) is a sketch of a typical travelling wave solution. There are travelling wave solutions for $c < 2$ but they are physically unrealistic since $U < 0$, for some z, because in this case U spirals around the origin. In these, $U \to 0$ at the leading edge with decreasing oscillations about $U = 0$.

A key question at this stage is what kind of initial conditions $u(x, 0)$ for the original Fisher–Kolmogoroff equation (13.6) will evolve to a travelling wave solution and, if such a solution exists, what is its wavespeed c. This problem and its generalisations have been widely studied analytically; see the references in the books cited above in Section 13.1. Kolmogoroff et al. (1937) proved that if $u(x, 0)$ has compact support, that is,

$$u(x, 0) = u_0(x) \geq 0, \quad u_0(x) = \begin{cases} 1 & \text{if } x \leq x_1 \\ 0 & \text{if } x \geq x_2 \end{cases}, \tag{13.14}$$

where $x_1 < x_2$ and $u_0(x)$ is continuous in $x_1 < x < x_2$, then the solution $u(x, t)$ of (13.6) evolves to a travelling wavefront solution $U(z)$ with $z = x - 2t$. That is, it evolves to the wave solution with *minimum* speed $c_{\min} = 2$. For initial data other than (13.14) the solution depends critically on the behaviour of $u(x, 0)$ as $x \to \pm\infty$.

The dependence of the wavespeed c on the initial conditions at infinity can be seen easily from the following simple analysis suggested by Mollison (1977). Consider first the leading edge of the evolving wave where, since u is small, we can neglect u^2 in comparison with u. Equation (13.6) is linearised to

$$\frac{\partial u}{\partial t} = u + \frac{\partial^2 u}{\partial x^2}. \tag{13.15}$$

Consider now

$$u(x, 0) \sim Ae^{-ax} \quad \text{as} \quad x \to \infty, \tag{13.16}$$

where $a > 0$ and $A > 0$ is arbitrary, and look for travelling wave solutions of (13.15) in the form

$$u(x, t) = Ae^{-a(x-ct)}. \tag{13.17}$$

We think of (13.17) as the leading edge form of the wavefront solution of the nonlinear equation. Substitution of the last expression into the linear equation (13.15) gives the *dispersion relation*, that is, a relationship between c and a,

$$ca = 1 + a^2 \quad \Rightarrow \quad c = a + \frac{1}{a}. \tag{13.18}$$

If we now plot this dispersion relation for c as a function of a, we see that $c_{\min} = 2$ the value at $a = 1$. For all other values of $a(> 0)$ the wavespeed $c > 2$.

Now consider $\min[e^{-ax}, e^{-x}]$ for x large and positive (since we are only dealing with the range where $u^2 \ll u$). If

$$a < 1 \quad \Rightarrow \quad e^{-ax} > e^{-x},$$

and so the velocity of propagation with asymptotic initial condition behaviour like (13.16) will depend on the *leading edge* of the wave, and the wavespeed c is given by (13.18). On the other hand, if $a > 1$ then e^{-ax} is bounded above by e^{-x} and the front with wavespeed $c = 2$. We are thus saying that if the initial conditions satisfy (13.16), then the asymptotic wavespeed of the travelling wave solution of (13.6) is

$$c = a + \frac{1}{a}, \quad 0 < a \leq 1, \qquad c = 2, \quad a \geq 1. \tag{13.19}$$

The first of these has been proved by McKean (1975), the second by Larson (1978) and both verified numerically by Manoranjan and Mitchell (1983).

The Fisher–Kolmogoroff equation is invariant under a change of sign of x, as mentioned before, so there is a wave solution of the form $u(x, t) = U(x + ct)$, $c > 0$, where now $U(-\infty) = 0$, $U(\infty) = 1$. So if we start with (13.6) for $-\infty < x < \infty$ and an initial condition $u(x, 0)$ which is zero outside a finite domain, such as illustrated in Figure 13.2, the solution $u(x, t)$ will evolve into two travelling wavefronts, one moving left and the other to the right, both with speed $c = 2$. Note that if $u(x, 0) < 1$ the $u(1 - u)$ term causes the solution to grow until $u = 1$. Clearly $u(x, t) \to 1$ as $t \to \infty$ for all x.

The axisymmetric form of the Fisher–Kolmogoroff equation, namely,

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial r^2} + \frac{1}{r}\frac{\partial u}{\partial r} + u(1 - u) \tag{13.20}$$

does not possess travelling wavefront solutions in which a wave spreads out with constant speed, because of the $1/r$ term; the equation does not become an ordinary differential equation in the variable $z = r - ct$. Intuitively we can see what happens given

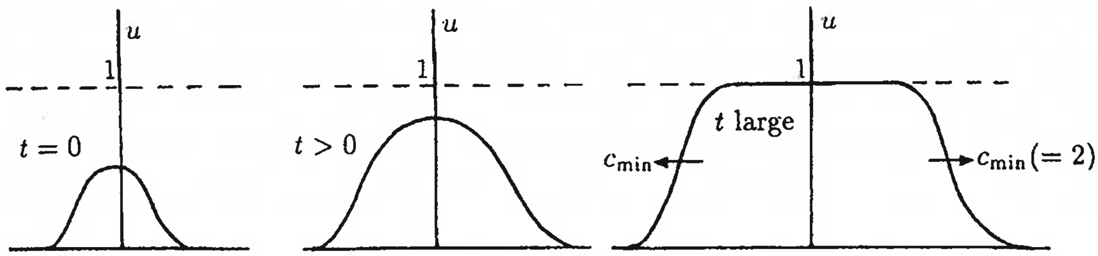

Figure 13.2. Schematic time development of a wavefront solution of the Fisher–Kolmogoroff equation on the infinite line.

$u(r, 0)$ qualitatively like the u in the first figure of Figure 13.2. The u will grow because of the $u(1-u)$ term since $u < 1$. At the same time diffusion will cause a wavelike dispersal outwards. On the 'wave' $\partial u/\partial r < 0$ so it effectively reduces the value of the right-hand side in (13.20). This is equivalent to reducing the diffusion by an apparent convection or alternatively to reducing the source term $u(1-u)$. The effect is to reduce the velocity of the outgoing wave. For large r the $(1/r)\partial u/\partial r$ term becomes negligible so the solution will tend asymptotically to a travelling wavefront solution with speed $c = 2$ as in the one-dimensional case. So, we can think of the axisymmetric wavelike solutions as having a 'wavespeed' $c(r)$, a function of r, where, for r bounded away from $r = 0$, it increases monotonically with $c(r) \sim 2$ for r large.

Equation (13.4) has been the basis for a variety of models for spatial spread. Aoki (1987), for example, discussed gene-culture waves of advance. Ammerman and Cavali-Sforza (1971, 1983), in an interesting direct application of the model, applied it to the spread of early farming in Europe.

13.3 Asymptotic Solution and Stability of Wavefront Solutions of the Fisher–Kolmogoroff Equation

Travelling wavefront solutions $U(z)$ for equation (13.6) satisfy (13.8); namely,

$$U'' + cU' + U(1-U) = 0, \tag{13.21}$$

and monotonic solutions exist, with $U(-\infty) = 1$ and $U(\infty) = 0$, for all wavespeeds $c > 2$. The phase plane trajectories are solutions of (13.11); that is,

$$\frac{dV}{dU} = \frac{-cV - U(1-U)}{V}. \tag{13.22}$$

No analytical solutions of these equations for general c have been found although there is an exact solution for a particular $c(> 2)$, as we show below in Section 13.4. There is, however, a small parameter in the equations, namely, $\varepsilon = 1/c^2 \leq 0.25$, which suggests we look for asymptotic solutions for $0 < \varepsilon \ll 1$ (see, for example, the book by Murray 1984 for a simple description of these asymptotic techniques and that by Kevorkian and Cole 1996 for a more comprehensive study of such techniques). Canosa (1973) obtained such asymptotic solutions to (13.21).

Since the wave solutions are invariant to any shift in the origin of the coordinate system (the equation is unchanged if $z \to z + \text{constant}$) let us take $z = 0$ to be the point where $U = 1/2$. We now use a standard singular perturbation technique. The procedure is to introduce a change of variable in the vicinity of the front, which here is at $z = 0$, in such a way that we can find the solution as a Taylor expansion in the small parameter ε. We can do this with the transformation

$$U(z) = g(\xi), \quad \xi = \frac{z}{c} = \varepsilon^{1/2} z. \tag{13.23}$$

The actual transformation in many cases is found by trial and error until the resulting transformed equation gives a consistent perturbation solution satisfying the boundary fact that the waves are stable to finite domain perturbations makes it clear why typical numerical simulations of the Fisher–Kolmogoroff equation result in stable wavefront solutions with speed $c = 2$.

13.4 Density-Dependent Diffusion-Reaction Diffusion Models and Some Exact Solutions

We saw in Section 11.3 in Chapter 11 that in certain insect dispersal models the diffusion coefficient D depended on the population u. There we did not include any growth dynamics. If we wish to consider longer timescales then we should include such growth terms in the model. A natural extension to incorporate density-dependent diffusion is thus, in the one-dimensional situation, to consider equations of the form

$$\frac{\partial u}{\partial t} = f(u) + \frac{\partial}{\partial x}\left[D(u)\frac{\partial u}{\partial x}\right], \tag{13.39}$$

where typically $D(u) = D_0 u^m$, with D_0 and m positive constants. Here we consider functions $f(u)$ which have two zeros, one at $u = 0$ and the other at $u = 1$. Equations in which $f \equiv 0$ have been studied much more widely than those with nonzero f; see, for example, Chapter 11. To be even more specific we consider $f(u) = ku^p(1 - u^q)$, where p and q are positive constants. By a suitable rescaling of t and x we can absorb the parameters k and D_0 and the equations we thus consider in this section are then of the general form

$$\frac{\partial u}{\partial t} = u^p(1 - u^q) + \frac{\partial}{\partial x}\left[u^m\frac{\partial u}{\partial x}\right], \tag{13.40}$$

where p, q and m are positive parameters. If we write out the diffusion term in full we get

$$\frac{\partial u}{\partial t} = u^p(1 - u^q) + mu^{m-1}\left(\frac{\partial u}{\partial x}\right)^2 + u^m\frac{\partial^2 u}{\partial x^2}$$

which shows that the nonlinear diffusion can be thought of as contributing an equivalent *convection* with 'velocity' $-mu^{m-1}\partial u/\partial x$.

It might be argued that the forms in (13.40) are rather special. However with the considerable latitude to choose p, q and m such forms can qualitatively mimic more complicated forms for which only numerical solutions are possible. The usefulness of analytical solutions, of course, is the ease with which we can see how solutions depend analytically on the parameters. In this way we can then infer the qualitative behaviour of the solutions of more complicated but more realistic model equations. There are, however, often hidden serious pitfalls, one of which is important and which we point out below.

To relate the exact solutions, which we derive, to the above results for the Fisher–Kolmogoroff equation we consider first $m = 0$ and $p = 1$ and (13.40) becomes

$$\frac{\partial u}{\partial t} = u(1-u^q) + \frac{\partial^2 u}{\partial x^2}, \quad q > 0. \tag{13.41}$$

Since $u = 0$ and $u = 1$ are the uniform steady states, we look for travelling wave solutions in the form

$$u(x,t) = U(z), \quad z = x - ct, \quad U(-\infty) = 1, \quad U(\infty) = 0, \tag{13.42}$$

where $c > 0$ is the wavespeed we must determine. The ordinary differential equation for $u(z)$ is

$$L(U) = U'' + cU' + U(1-U^q) = 0, \tag{13.43}$$

which defines the operator L. This equation can of course be studied in the (U', U) phase plane. With the form of the first term in the asymptotic wavefront solution to the Fisher–Kolmogoroff equation given by (13.29) let us optimistically look for solutions of (13.43) in the form

$$U(z) = \frac{1}{(1+ae^{bz})^s}, \tag{13.44}$$

where a, b and s are positive constants which have to be found. This form automatically satisfies the boundary conditions at $z = \pm\infty$ in (13.42). Because of the translational invariance of the equation we can say at this stage that a is arbitrary: it can be incorporated into the exponential as a translation $b^{-1}\ln a$ in z. It is, however, useful to leave it in as a way of keeping track of the algebraic manipulation. Another reason for keeping it in is that if b and s can be found so that (13.44) is an exact solution of (13.43) then they cannot depend on a.

Substitution of (13.44) into (13.43) gives, after some trivial but tedious algebra,

$$\begin{aligned} L(U) = \frac{1}{(1+ae^{bz})^{s+2}} &\Big\{\Big[s(s+1)b^2 - sb(b+c) + 1\Big]a^2e^{2bz} \\ &+ [2 - sb(b+c)]ae^{bz} + 1 - \Big[1+ae^{bz}\Big]^{2-sq}\Big\}, \end{aligned} \tag{13.45}$$

so that $L(U) = 0$ for all z; the coefficients of e^0, e^{bz} and e^{2bz} within the curly brackets must all be identically zero. This implies that

$$2 - sq = 0, 1 \text{ or } 2 \quad \Rightarrow \quad s = \frac{2}{q}, \frac{1}{q} \quad \text{or} \quad sq = 0.$$

Clearly $sq = 0$ is not possible since s and q are positive constants. Consider the other two possibilities.

With $s = 1/q$ the coefficients of the exponentials from (13.45) give

$$\left.\begin{array}{ll} e^{bz}: & 2 - sb(b+c)^{-1} = 0 \quad \Rightarrow \quad sb(b+c) = 1 \\ e^{2bz}: & s(s+1)b^2 - sb(b+c) + 1 = 0 \end{array}\right\} \quad \Rightarrow \quad s(s+1)b^2 = 0$$
$$\Rightarrow \quad b = 0$$

since $s > 0$. This case is therefore also not a possibility since necessarily $b > 0$.

Finally if $s = 2/q$ the coefficients of e^{bz} and e^{2bz} are

$$e^{bz}: \; sb(b+c) = 2; \quad e^{2bz}: \; s(s+1)b^2 - sb(b+c) + 1 \quad \Rightarrow \quad s(s+1)b^2 = 1$$

which together give b and c as

$$s = \frac{2}{q}, \quad b = \frac{1}{[s(s+1)]^{1/2}}, \quad c = \frac{2}{sb} - b$$

which then determine s, b and a *unique* wavespeed c in terms of q as

$$s = \frac{2}{q}, \quad b = \frac{q}{[2(q+2)]^{1/2}}, \quad c = \frac{q+4}{[2(q+2)]^{1/2}}. \tag{13.46}$$

From these we see that the wavespeed c increases with $q(> 0)$. A measure of the steepness, S, given by the magnitude of the gradient at the point of inflexion, is easily found from (13.44). The point of inflexion, z_i, is given by $z_i = -b^{-1}\ln(as)$ and hence the gradient at z_i gives the steepness, S, as

$$S = \frac{b}{(1 + \frac{1}{s})^{s+1}} = \frac{\frac{1}{2}q}{(1 + \frac{q}{2})^{3/2+2/q}}.$$

So, with increasing q the wavespeed c increases and the steepness decreases, as was the case with the Fisher–Kolmogoroff wavefront solutions.

When $q = 1$, equation (13.41) becomes the Fisher–Kolmogoroff equation (13.6) and from (13.46)

$$s = 2, \quad b = \frac{1}{\sqrt{6}}, \quad c = \frac{5}{\sqrt{6}}.$$

We then get an exact analytical travelling wave solution from (13.44). The arbitrary constant a can be chosen so that $z = 0$ corresponds to $U = 1/2$, in which case $a = \sqrt{2} - 1$ and the solution is

$$U(z) = \frac{1}{\left[1 + (\sqrt{2} - 1)e^{z/\sqrt{6}}\right]^2}. \tag{13.47}$$

This solution has a wavespeed $c = 5/\sqrt{6}$ and on comparison with the asymptotic solution (13.29) to $O(1)$ it is much steeper.

This example highlights one of the serious problems with such exact solutions which we alluded to above: namely, they often do not determine all possible solutions and indeed, may not even give the most relevant one, as is the case here. This is not because the wavespeed is not 2, in fact $c = 5/\sqrt{6} \approx 2.04$, but rather that the quantitative waveform is so different. To analyse this general form (13.43) properly, a careful phase plane analysis has to be carried out.

Another class of exact solutions can be found for (13.40) with $m = 0$, $p = q + 1$ with $q > 0$, which gives the equation as

$$\frac{\partial u}{\partial t} = u^{q+1}(1 - u^q) + \frac{\partial^2 u}{\partial x^2}. \tag{13.48}$$

Substituting $U(z)$ from (13.44) into the travelling waveform of the last equation and proceeding exactly as before we find a travelling wavefront solution exists, with a unique wavespeed, given by

$$U(z) = \frac{1}{(1 + ae^{bz})^s}, \quad s = \frac{1}{q}, \quad b = \frac{q}{(q+1)^{1/2}}, \quad c = \frac{1}{(q+1)^{1/2}}. \tag{13.49}$$

A more interesting and useful exact solution has been found for the case $p = q = 1$, $m = 1$ with which (13.40) becomes

$$\frac{\partial u}{\partial t} = u(1 - u) + \frac{\partial}{\partial x}\left[u\frac{\partial u}{\partial x}\right], \tag{13.50}$$

a nontrivial example of density-dependent diffusion with logistic population growth. Physically this model implies that the population disperses to regions of lower density more rapidly as the population gets more crowded. The solution, derived below, was found independently by Aronson (1980) and Newman (1980). Newman (1983) studied more general forms and carried the work further.

Let us look for the usual travelling wave solutions of (13.50) with $u(x, t) = U(z)$, $z = x - ct$, and so we consider

$$(UU')' + cU' + U(1 - U) = 0,$$

for which the phase plane system is

$$U' = V, \quad UV' = -cV - V^2 - U(1 - U). \tag{13.51}$$

We are interested in wavefront solutions for which $U(-\infty) = 1$ and $U(\infty) = 0$: we anticipate $U' < 0$. There is a singularity at $U = 0$ in the second equation. We remove this singularity by defining a new variable ζ as

$$U\frac{d}{dz} = \frac{d}{d\zeta} \quad \Rightarrow \quad \frac{dU}{d\zeta} = UV, \quad \frac{dV}{d\zeta} = -cV - V^2 - U(1 - U), \tag{13.52}$$

which is not singular. The critical points in the (U, V) phase plane are

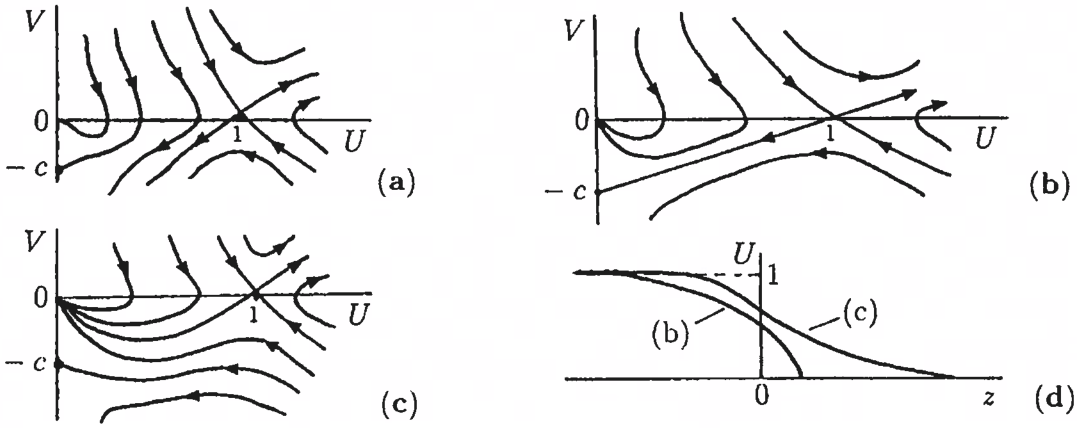

Figure 13.4. Qualitative phase plane trajectories for the travelling wave equations (13.52) for various c. (After Aronson 1980) In **(a)** no trajectory is possible from (1, 0) to $U = 0$ at a finite V. In **(b)** and **(c)** travelling wave solutions from $U = 1$ to $U = 0$ are possible but with different characteristics: the travelling wave solutions in **(d)** illustrate these differences. Importantly the solution corresponding to **(b)** has a discontinuous derivative at the leading edge.

$$(U, V) = (0, 0), \quad (1, 0), \quad (0, -c).$$

A linear analysis about $(1, 0)$ and $(0, -c)$ shows them to be saddle points while $(0, 0)$ is like a stable nonlinear node—nonlinear because of the UV in the U-equation in (13.52). Figure 13.4 illustrates the phase trajectories for (13.52) for various c. From Section 11.2 we can expect the possibility of a wave with a discontinuous tangent at a specific point z_c, the one where $U \equiv 0$ for $z \geq z_c$. This corresponds to a phase trajectory which goes from $(1, 0)$ to a point on the $U = 0$ axis at some finite nonzero negative V. Referring now to Figure 13.4(a), if $0 < c < c_{\min}$ there is no trajectory possible from $(1, 0)$ to $U = 0$ except unrealistically for infinite V. As c increases there is a bifurcation value $c_{\min}$ for which there is a unique trajectory from $(1, 0)$ to $(0, -c_{\min})$ as shown in Figure 13.4(b). This means that at the wavefront z_c, where $U = 0$, there is a discontinuity in the derivative from $V = U' = -c_{\min}$ to $U' = 0$ and $U = 0$ for all $z > z_c$; see Figure 13.4(d). As c increases beyond $c_{\min}$ a trajectory always exists from $(1, 0)$ to $(0, 0)$ but now the wave solution has $U \to 0$ and $U' \to 0$ as $z \to \infty$; this type of wave is also illustrated in Figure 13.4(d).

As regards the exact solution, the trajectory connecting $(1, 0)$ to $(0, -c)$ in Figure 13.4(b) is in fact a straight line $V = -c_{\min}(1 - U)$ if $c_{\min}$ is appropriately chosen. In other words this is a solution of the phase plane equation which, from (13.51), is

$$\frac{dV}{dU} = \frac{-cV - V^2 - U(1 - U)}{UV}.$$

Substitution of $V = -c_{\min}(1 - U)$ in this equation, with $c = c_{\min}$, shows that $c_{\min} = 1/\sqrt{2}$. If we now return to the first of the phase equations in (13.51), namely, $U' = V$ and use the phase trajectory solution $V = -(1 - U)/\sqrt{2}$ we get

$$U' = -\frac{1 - U}{\sqrt{2}},$$

which, on using $U(-\infty) = 1$, gives

$$U(z) = 1 - \exp\left[\frac{z - z_c}{\sqrt{2}}\right] \quad z < z_c$$
$$= 0 \quad z > z_c, \tag{13.53}$$

where z_c is the front of the wave: it can be arbitrarily chosen in the same way as the a in the solutions (13.44). This is the solution sketched in Figure 13.4(d).

This analysis, showing the existence of the travelling waves, can be extended to more general cases in which the diffusion coefficient is u^m, for $m \neq 1$, or even more general $D(u)$ in (13.40) if it satisfies certain criteria.

It is perhaps appropriate to state briefly here the travelling wave results we have derived for the Fisher–Kolmogoroff equation and its generalisations to a general $f(u)$ normalised such that $f(0) = 0 = f(1)$, $f'(0) > 0$ and $f'(1) < 0$. In dimensionless terms we have shown that there is a travelling wavefront solution with $0 < u < 1$ which can evolve, with appropriate initial conditions, from (13.31). Importantly these solutions have speeds $c \geq c_{\text{min}} = 2[f'(0)]^{1/2}$ with the usual computed form having speed c_{min}. For the Fisher–Kolmogoroff equation (13.4) this dimensional wavespeed, c^* say, using the nondimensionalisation (13.5), is $c^* = 2[kD]^{1/2}$; here k is a measure of the linear growth rate or of the linear kinetics. If we consider not untypical biological values for D of 10^{-9}–$10^{-11}\,\text{cm}^2\,\text{sec}^{-1}$ and k is $O(1\,\text{sec}^{-1})$ say, the speed of propagation is then $O(2 \times 10^{-4.5}$–$10^{-5.5}\,\text{cm sec}^{-1})$. With this, the time it takes to cover a distance of the order of 1 mm is $O(5 \times 10^{2.5}$–$10^{3.5}\,\text{sec})$ which is *very* much shorter than the pure diffusional time of $O(10^7$–$10^9\,\text{sec})$. It is the combination of reaction and diffusion which greatly enhances the efficiency of information transferral via travelling waves of concentration changes. This reaction diffusion interaction, as we shall see in Volume II, totally changes our concept of the role of diffusion in a large number of important biological situations.

Before leaving this section let us go back to something we mentioned earlier in the section when we noted that nonlinear diffusion could be thought of as equivalent to a nonlinear convection effect: the equation following (13.40) demonstrates this. If the convection arises as a natural extension of a conservation law we get, instead, equations such as

$$\frac{\partial u}{\partial t} + \frac{\partial h(u)}{\partial x} = f(u) + \frac{\partial^2 u}{\partial x^2}, \tag{13.54}$$

where $h(u)$ is a given function of u. Here the left-hand side is in standard 'conservation' form: that is, it is in the form of a divergence, namely, $(\partial/\partial t, \partial/\partial x).\,(u, h(u))$, the convective 'velocity' is $h'(u)$. Such equations arise in a variety of contexts, for example, in ion-exchange columns and chromatography; see Goldstein and Murray (1959). They have also been studied by Murray (1968, 1970a,b, 1973), where other practical applications of such equations are given, together with analytical techniques for solving them. The book by Kevorkian (2000) is an excellent very practical book on partial differential equations.

The effect of nonlinear convection in reaction diffusion equations can have dramatic consequences for the solutions. This is to be expected since we have another major transport process, namely, convection, which depends nonlinearly on u. This process may or may not enhance the diffusional transport. If the diffusion process is negligible compared with the convection effects the solutions can exhibit shock-like solutions (see Murray 1968, 1970a,b, 1973).

Although the analysis is harder than for the Fisher–Kolmogoroff equation, we can determine conditions for the existence of wavefront solutions. For example, consider the simple, but nontrivial, case where $h'(u) = ku$ with k a positive or negative constant and $f(u)$ logistic. Equation (13.54) is then

$$\frac{\partial u}{\partial t} + ku\frac{\partial u}{\partial x} = u(1-u) + \frac{\partial^2 u}{\partial x^2}. \tag{13.55}$$

With $k = 0$ this reduces to equation (13.6) the wavefront solutions of which we just discussed in detail.

Suppose $k \neq 0$ and we look for travelling wave solutions to (13.55) in the form (13.7); namely,

$$u(x,t) = U(z), \quad z = x - ct, \tag{13.56}$$

where, as usual, the wavespeed c has to be found. Substituting into (13.55) gives

$$U'' + (c - kU)U' + U(1-U) = 0 \tag{13.57}$$

for which appropriate boundary conditions are given by (13.9); namely,

$$\lim_{z\to\infty} U(z) = 0, \quad \lim_{z\to-\infty} U(z) = 1. \tag{13.58}$$

Equations (13.57) and (13.58) define the eigenvalue problem for the wavespeed $c(k)$.

From (13.57), with $V = U'$, the phase plane trajectories are solutions of

$$\frac{dV}{dU} = \frac{-(c-kU)V - U(1-U)}{V}. \tag{13.59}$$

Singular points of the last equation are $(0,0)$ and $(1,0)$. We require conditions on $c = c(k)$ such that a monotonic solution exists in which $0 \leq U \leq 1$ and $U'(z) \leq 0$; that is, we require a phase trajectory lying in the quadrant $U \geq 0$, $V \leq 0$ which joins the singular points. A standard linear phase plane analysis about the singular points shows that $c \geq 2$, which guarantees that $(0,0)$ is a stable node and $(1,0)$ a saddle point. The specific equation (13.55) and the travelling waveform (13.59) were studied analytically and numerically by the author and R.J. Gibbs (see Murray 1977). It can be shown (see below) that a travelling wave solution exists for all $c \geq c(k)$ where

$$c(k) = \begin{cases} 2 \\ \dfrac{k}{2} + \dfrac{2}{k} \end{cases} \quad \text{if} \quad \begin{cases} 2 > k > -\infty \\ 2 \leq k < \infty \end{cases}. \tag{13.60}$$

We thus see that here $c = 2$ is a lower bound for only a limited range of k, a more accurate bound being given by the last equation. We present the main elements of the analysis below.

The expression $c = c(k)$ in the last equation gives the wavespeed in terms of a key parameter, k, in the model. It is another example of a *dispersion relation*, here associated with wave phenomena. The general concept of dispersion relations are of considerable importance and real practical use and is a subject we shall be very much involved with later in Volume II, particularly in Chapters 2 to 6, 8 and 12.

Brief Derivation of the Wavespeed Dispersion Relation

Linearising (13.59) about (0, 0) gives

$$\frac{dV}{dU} = \frac{-cV - U}{V}$$

with eigenvalues

$$e_{\pm} = \frac{-c \pm (c^2 - 4)^{1/2}}{2}. \tag{13.61}$$

Since we require $U \geq 0$ these must be real and so we must have $c \geq 2$. Thus $0 > e_+ > e_-$ and so (0, 0) is a stable node and, for large z,

$$\begin{pmatrix} V \\ U \end{pmatrix} \quad \to \quad a \begin{pmatrix} e_+ \\ 1 \end{pmatrix} \exp[e_+ z] + b \begin{pmatrix} e_- \\ 1 \end{pmatrix} \exp[e_- z],$$

where a and b are constants. This implies that

$$\frac{dV}{dU} \quad \to \quad \begin{cases} e_+ \\ e_- \end{cases} \quad \text{as} \quad z \to \infty \quad \text{if} \quad \begin{cases} a \neq 0 \\ a = 0 \end{cases}. \tag{13.62}$$

An exact solution of (13.59) is

$$V = -\frac{k}{2}U(1 - U) \quad \text{if} \quad c = \frac{k}{2} + \frac{2}{k}. \tag{13.63}$$

With this expression for c,

$$(c^2 - 4)^{1/2} = \begin{cases} \dfrac{k}{2} - \dfrac{2}{k} \\ \dfrac{2}{k} - \dfrac{k}{2} \end{cases} \quad \text{if} \quad \begin{cases} k \geq 2 \\ k < 2 \end{cases}$$

and so from (13.61)

$$e_+ = \begin{cases} -\dfrac{2}{k} \\ -\dfrac{k}{2} \end{cases} \quad \text{if} \quad \begin{cases} k \geq 2 \\ k < 2 \end{cases}, \quad e_- = \begin{cases} -\dfrac{k}{2} \\ -\dfrac{2}{k} \end{cases} \quad \text{if} \quad \begin{cases} k \geq 2 \\ k < 2 \end{cases}.$$