Chapter 6

Reaction-diffusion equations

6.1 Introduction

It happens rarely that the changes in time of some quantity are due to just one mechanism: as a rule several mechanisms are involved. In a finite time interval the contributions of the various mechanisms are entangled. The great success of differential equations as a modelling tool derives to a large extent from the fact that in infinitesimal time intervals (by which we just mean that we let the length of the considered time interval go to zero) the contributions to the *rate* of change become independent and can simply be added. So in the modelling phase we can concentrate on one mechanism at a time and derive the corresponding term for the ultimate differential equation. The *solutions* of the differential equation then take into account the joint, intertwined influence of all mechanisms.

In the present chapter we consider the system of equations

$$\frac{\partial u}{\partial t} = d\Delta u + f(u) \tag{6.1.1}$$

where

$$u = \begin{pmatrix} u_1 \\ u_2 \\ \vdots \\ u_k \end{pmatrix} \tag{6.1.2}$$

is a vector of, say, the concentrations of k different chemical substances that are subject to both diffusion and reaction. The function $f : \mathbb{R}^k \to \mathbb{R}^k$ describes the velocities and the stoichiometry of the various reactions. The Laplacian acts componentwise and d is a diagonal matrix with elements $d_1, \ldots, d_k$, so $d\Delta u$ is the vector

$$\begin{pmatrix} d_1\Delta u_1 \\ d_2\Delta u_2 \\ \vdots \\ d_k\Delta u_k \end{pmatrix} \tag{6.1.3}$$

If the space variable

$$x = \begin{pmatrix} x_1 \\ x_2 \\ \vdots \\ x_m \end{pmatrix}$$

has m components, then

$$\Delta u_i = \frac{\partial^2 u_i}{\partial x_1^2} + \frac{\partial^2 u_i}{\partial x_2^2} + \cdots + \frac{\partial^2 u_i}{\partial x_m^2} \tag{6.1.4}$$

In Chapters 2 and 3 we concentrated on the reaction part and ignored spatial dependence. In Chapter 4 we concentrated on the diffusion part and ignored reactions. At the level of *formulation* we do not need to invest further work: (6.1.1) is obtained by adding the contributions to the rate of change of u. But at the level of model *analysis*, things are not at all clear. What new phenomena can we expect? And are the values of k and m important in this respect? And what about boundary conditions?

Concerning the last point, we shall give most attention to two cases in which the boundary conditions per se do not have any "forcing" influence:

- a bounded domain Ω with no-flux boundary conditions at $\partial\Omega$
- $\Omega = \mathbb{R}^m$ (with very mild boundedness conditions which are usually not even mentioned)

(But for $k = 1$, $m = 1$, $\Omega =$ interval, we shall also study the case of zero Dirichlet boundary conditions, to get at least a feel for the difference between no-flux and zero Dirichlet boundary conditions.)

The new phenomena that we shall encounter are:

- pattern formation
- growth (or decay) by way of travelling waves, i.e., growth by way of spatial expansion

But for mathematicians a very important point is also that we need to enlarge our toolbox, as we enter into the realm of *infinite* dimensional dynamical systems (the infinity aspect of a partial differential equation stems from the fact that $x \in \mathbb{R}$, so for each fixed x we in fact have a differential equation, coupled to all the others; another way of looking at it is that, for fixed time t, solutions to partial differential equations are *functions* $u(t, \cdot)$, which depend on infinitely many $x \in \mathbb{R}$). Due to the smoothing effect of diffusion, not that much changes though. If we consider, for instance, linearised stability, then, in a sense, the main difference is that we have to analyse countably many matrices rather than just one.

6.2 Stability criteria for uniform steady states

A solution of (6.1.1) that is independent of time is called a *steady state*. If that solution is also independent of spatial position, we speak about a *uniform steady state*. If we denote both such a solution and the value it takes in $\mathbb{R}^k$ by $\bar{u}$, then we should have

$$f(\bar{u}) = 0 \tag{6.2.1}$$

For $k = 1$, we can find solutions of (6.2.1) by a graphical analysis and, in one go, also determine their stability with respect to the reaction dynamics with spatial dependence ignored. See Figure 6.1. The analytical criterion is

$$Df(\bar{u}) < 0 \implies \bar{u} \text{ is stable}$$
$$Df(\bar{u}) > 0 \implies \bar{u} \text{ is unstable}$$

For $k > 1$, (6.2.1) is short hand for k equations in as many unknowns and in the absence of space dependence the stability can be determined from the eigenvalues of the Jacobian matrix $Df(\bar{u})$:

- if $\Re\lambda < 0$ for *all* eigenvalues λ of $Df(\bar{u})$, then $\bar{u}$ is (locally asymptotically; in fact exponentially) stable

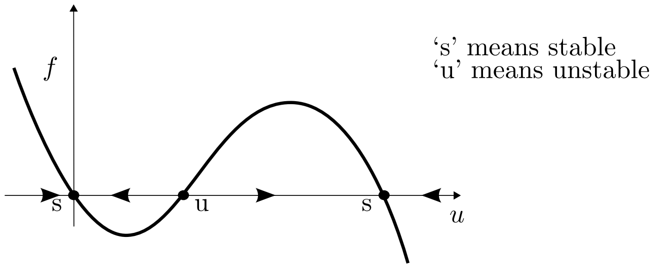

FIGURE 6.1.

- if $\Re\lambda > 0$ for *some* eigenvalue λ of $Df(\bar{u})$, then $\bar{u}$ is unstable

The proof is based on linearisation, i.e., on an analysis of the linearised equation

$$\frac{dv}{dt} = Df(\bar{u})v \tag{6.2.2}$$

combined with estimates for higher order terms (note that the proof of stability is much easier than the proof of instability, since in general an unstable steady state is a saddle point and there are solutions that actually do approach the steady state for $t \to \infty$). The connection between (6.2.2) and the eigenvalue problem

$$Df(\bar{u})\bar{v} = \lambda\bar{v} \tag{6.2.3}$$

is separation of variables (with variables t and the index indicating the component): if we substitute

$$v(t) = \psi(t)\bar{v} \tag{6.2.4}$$

with $\psi(t) \in \mathbb{R}$ and $\bar{v} \in \mathbb{R}^k$ into (6.2.2) we find that

$$\frac{\psi'}{\psi}\bar{v} = Df(\bar{u})\bar{v}$$

which can hold only if ψ'/ψ is a constant (i.e., independent of t), say λ. Hence $\psi(t) = \psi(0)e^{\lambda t}$, and (6.2.3) must hold.

Now, let us include the diffusion term and investigate its impact. If we supply (6.1.1) with no-flux boundary conditions

$$\left.\frac{\partial u}{\partial n}\right|_{\partial\Omega} = 0 \tag{6.2.5}$$

then solutions of (6.2.1) yield uniform steady states. The linearised equation now reads

$$\frac{\partial v}{\partial t} = d\Delta v + Df(\bar{u})v \tag{6.2.6}$$

$$\left.\frac{\partial v}{\partial n}\right|_{\partial\Omega} = 0 \tag{6.2.7}$$

We apply, as before, separation of variables, but this time there are *three* variables: t, x, and the index that indicates the component. So we substitute

$$v(t,x) = \psi(t)\phi(x)\bar{v} \tag{6.2.8}$$

with $\psi(t)$, $\phi(x) \in \mathbb{R}$, and $\bar{v} \in \mathbb{R}^k$. After division by $\psi(t)\phi(x)$ we obtain

$$\frac{\psi'(t)}{\psi(t)}\bar{v} = \frac{\Delta\phi(x)}{\phi(x)}d\bar{v} + Df(\bar{u})\bar{v} \tag{6.2.9}$$

which requires that ψ'/ψ and $\Delta\phi/\phi$ are constant. Hence, as before, $\psi(t) = \psi(0)e^{\lambda t}$. With foresight (inspired by Section 5.2) we call the constant value that $\Delta\phi/\phi$ takes

$-\mu^2$, so require that

$$\Delta\phi = -\mu^2\phi \tag{6.2.10}$$

$$\left.\frac{\partial\phi}{\partial n}\right|_{\partial\Omega} = 0 \tag{6.2.11}$$

and, in addition,

$$[Df(\bar{u}) - \mu^2 d]\bar{v} = \lambda\bar{v} \tag{6.2.12}$$

Note the order: we can determine the relevant values of μ first by studying (6.2.10), and only after that determine, for each relevant μ, the values of λ that satisfy

$$\det\left(Df(\bar{u}) - \mu^2 d - \lambda I\right) = 0 \tag{6.2.13}$$

with I the $k \times k$ identity matrix. Equation (6.2.13) is often called a *dispersion relation*, as it links a characteristic of the time dependence, λ, to a characteristic of the space dependence, μ.

We now first concentrate on (6.2.10)–(6.2.11) for bounded Ω. In Section 5.2 we dealt with the case $m = 1$, $d = 1$, $\Omega = [0, L]$, and found that μ should be of the form

$$\mu = \frac{k\pi}{L}, \quad k = 0, 1, 2, \ldots \tag{6.2.14}$$

This generalises in the sense that for

$$\mu_0 = 0 \tag{6.2.15}$$

we have a solution ϕ = constant and that there exist μ_1, μ_2, ..., with $\mu_{i+1} > \mu_i$ for $i = 0, 1, 2, \ldots$, with corresponding λ_i determined by the dispersion relation (6.2.13), for which (6.2.10)–(6.2.11) has a nontrivial solution while there is no such solution for any other value of μ. The mathematical background of this result has various facets (see e.g., (Renardy and Rogers, 1993)):

- elliptic differential equations
- self-adjoint operators with compact resolvent
- positivity

Unless Ω is symmetric, for instance a rectangle in $\mathbb{R}^2$, it is not feasible to determine the μ_i for $i \geq 1$ explicitly. But the fact that we know that $\mu_0 = 0$ is the smallest of all μ_i is often very helpful!

In the special case $k = 1$, i.e., a *scalar* equation, (6.2.13) reads

$$\lambda = Df(\bar{u}) - d\mu^2$$

and it follows that

- for every μ there is exactly one λ, which is real
- the λ's are *ordered* exactly as the $-\mu^2$
- $\lambda = Df(\bar{u})$ is the largest

The so-called *Principle of Linearised Stability*, see the “Theorem” below, now implies that $\bar{u}$ is exponentially stable if $Df(\bar{u}) < 0$ and unstable if $Df(\bar{u}) > 0$ (we often formulate this as: $\bar{u}$ is linearly stable iff $Df(\bar{u}) < 0$).

“THEOREM” (Principle of Linearised Stability)
(i) if for every *eigenvalue* $-\mu^2$ *of the diffusion problem with no-flux boundary conditions,* every *eigenvalue* λ *of* $Df(\bar{u}) - \mu^2 d$ *has negative real part, then* $\bar{u}$ *is a (locally exponentially)* stable *steady state.*
(ii) if for some *eigenvalue* $-\mu^2$ *of the diffusion problem with no-flux boundary conditions,* some *eigenvalue* λ *of* $Df(\bar{u}) - \mu^2 d$ *has positive real part, then* $\bar{u}$ *is an* unstable *steady state.*

Several questions now come to mind:

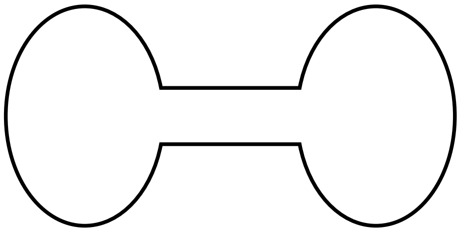

Figure 6.2.

- if $k > 1$ and all eigenvalues of $Df(\bar{u})$ have negative real part, does it follow that $\Re\lambda < 0$ for all λ that satisfy (6.2.13) for some $\mu = \mu_k$? The, perhaps surprising, answer is: NO. It was Alan Turing's great idea that diffusion driven instability is possible in the case of *systems* of equations provided the diffusion constants of the various components are sufficiently different. In Section 6.6 you shall demonstrate this in detail. The bottom line is that *pattern formation* takes place when reaction-stable uniform steady states turn unstable due to differences in the diffusion constants of the various components
- for $k = 1$ and no-flux boundary conditions, is it possible to have a *stable non-uniform* steady state? The short answer is: no, unless you force it by combining bistable dynamics with a special domain shape involving almost disconnected components. In more detail:
  (i) if $m = 1$, $\Omega = [0, L]$, then no, see Section 6.3
  (ii) if $m > 1$, and Ω is convex, then no, see (Kishimoto and Weinberger, 1985)
  (iii) if $m = 2$ and Ω is a "halter" domain (see Figure 6.2) and f has at least two stable steady states, then yes, provided the connecting pipe line is thin enough (the non-uniform steady state is close to different reaction-stable steady state values in the two ball-like parts of the domain; see (Matano, 1979))

6.3 Scalar Reaction-Diffusion equations: global bifurcation theory based on phase plane analysis and symmetry arguments

One reason to focus on steady states and their stability is that the corresponding analysis is relatively easy. But for scalar equations there is a better reason: solutions do converge to steady states. To demonstrate this, we introduce the Lyapunov function

$$V(\phi) = \frac{1}{2}\int_0^L (\phi'(x))^2\,dx - \int_0^L F(\phi(x))dx \tag{6.3.1}$$

where

$$F(w) := \int_0^w f(\sigma)d\sigma \tag{6.3.2}$$

Let $u = u(t,x)$ be a solution of

$$\frac{\partial u}{\partial t} = \frac{\partial^2 u}{\partial x^2} + f(u) \tag{6.3.3}$$

$$\frac{\partial u}{\partial x}(t,0) = 0 = \frac{\partial u}{\partial x}(t,L) \tag{6.3.4}$$

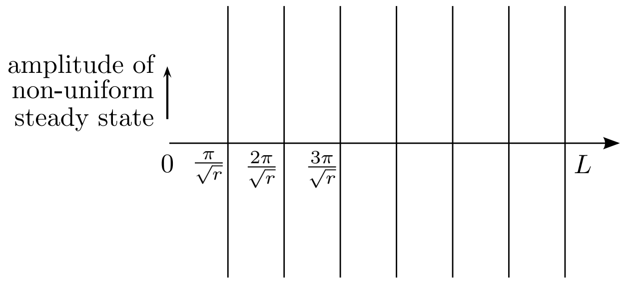

FIGURE 6.3.

(Note that we scaled the spatial variable such that the diffusion constant d equals 1.) Then, performing a partial integration, and using the boundary conditions,

$$\begin{aligned}\frac{d}{dt}V(u(t,\cdot)) &= \int_0^L \left\{\frac{\partial u}{\partial x}(t,x)\frac{\partial^2 u}{\partial t\partial x}(t,x) - f(u(t,x))\frac{\partial u}{\partial t}(t,x)\right\} dx \\ &= -\int_0^L \left(\frac{\partial^2 u}{\partial x^2}(t,x) + f(u(t,x))\right)\frac{\partial u}{\partial t}(t,x)dx \\ &= -\int_0^L \left(\frac{\partial u}{\partial t}(t,x)\right)^2 dx \\ &\leq 0\end{aligned}$$

This rules out the possibility of time-periodic solutions or any other kind of persistent behaviour for which $\frac{\partial u}{\partial t}$ is not identically zero. So only steady states are potentially attractors. Note that local minima of V are *stable* steady states. It appears that non-constant steady states are saddle points of V.

The function V is also a Lyapunov function when we impose Dirichlet rather than no-flux boundary conditions. Moreover, using one of Green's formulas, the proof is easily extended to the case of higher space dimension, i.e., $m > 1$.

We now know that non-uniform steady states cannot be stable when $k = 1$, $m = 1$, $\Omega = [0, L]$ and we impose no-flux boundary conditions. But do they exist?

In Section 5.2 we found that in the *linear* case the diagram in Figure 6.3 summarizes the situation: if we consider the growth rate r as fixed and the length of the domain L as a parameter, then a non-uniform steady state only exists if

$$L = L_k = \frac{k\pi}{\sqrt{r}}, \quad k = 1, 2, \ldots$$

and it is then, modulo a multiplicative constant, given by

$$\bar{u}(x) = \bar{u}_k(x) = \cos\left(\frac{k\pi}{L}x\right)$$

The physicists jargon is that $\bar{u}_k$ is the k-th *spatial mode* and that this mode turns unstable if L is increased beyond L_k.

In this section we replace the linear function $u \mapsto ru$ by the nonlinear function $u \mapsto f(u)$ and next investigate how Figure 6.3 deforms as a result of the nonlinearity. We shall find Figure 6.4, which we call a *bifurcation* diagram (cf. Appendix) with bifurcation parameter L. The choice of L as the key parameter is somewhat arbitrary: it is easy to translate Figure 6.4 into a bifurcation diagram with parameter either the diffusion constant d or the derivative $f'(0)$. Indeed, by scaling we can transform the equation

$$u_t = u_{xx} + f(u) \quad x \in [0, L],$$

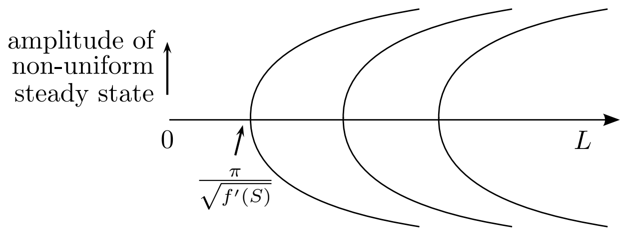

Figure 6.4.

into

$$u_t = \frac{1}{L^2} u_{\xi\xi} + f(u) \quad (\text{taking } \xi = x/L,\ \xi \in [0,1])$$

and next into

$$u_\tau = u_{\xi\xi} + L^2 f(u) \quad (\text{taking } \tau = t/L^2,\ \xi \in [0,1])$$

To investigate the steady state problem, we first rewrite the second order equation, $u_{xx} + f(u) = 0$ as a first-order system of ODEs:

$$u_x = v \tag{6.3.5}$$

$$v_x = -f(u) \tag{6.3.6}$$

The point is that we can analyse this first order system by phase plane methods (so we are going to look at (6.3.5)–(6.3.6) from a dynamical systems point of view, but note that this is just an auxiliary tool and that it has *nothing* to do with the infinite dimensional dynamical system generated by the diffusion equation (6.1.1) with appropriate boundary conditions!)

With, as defined in (6.3.2),

$$F(u) := \int_0^u f(\sigma) d\sigma$$

we find that this first order system has a conserved quantity,

$$H(u,v) := \frac{1}{2} v^2 + F(u), \tag{6.3.7}$$

also called a Hamiltonian. Since $v^2 = (-v)^2$, the phase portrait is symmetric with respect to reflection in the u-axis. Orbits are mapped by $(u,v) \mapsto (u,-v)$ to orbits, which, however, are traversed in the opposite direction. If f happens to be antisymmetric in u (i.e., $f(-u) = -f(u)$), then $F(-u) = F(u)$, and we also have symmetry of the phase plane with respect to reflection in the v-axis. Orbits are now also mapped by $(u,v) \mapsto (-u,v)$ to orbits.

We now first show that there are no bifurcations from a *stable* (with respect to well-stirred dynamics) uniform steady state. Assume that $f(0) = 0$, and $f'(0) < 0$. Then F has a maximum in $u = 0$, and consequently the origin in phase space is a saddle point (Figure 6.5) in the sense of dynamical systems (and also a saddle point as a critical point of the function H).

Therefore, there are locally near the origin neither connections from the v-axis to the v-axis nor connections from the u-axis to the u-axis. So for both the boundary value problem with no-flux conditions and for the zero Dirichlet boundary value problem we can conclude that bifurcations from such a steady state are impossible.

Exercise 6.3.1. Use the principle of linearised stability, to show that the stable uniform state 0 remains stable if we add diffusion and add either no-flux BCs or

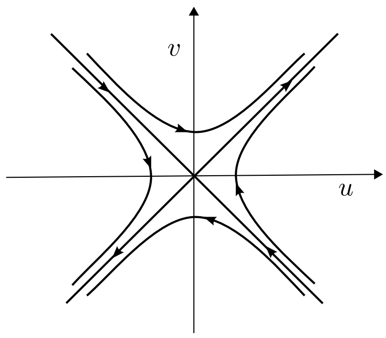

FIGURE 6.5.

compatible (i.e., zero in this case) Dirichlet BCs. In particular, show that the eigenvalues are just the eigenvalues of the Laplacian shifted over $f'(0)$, so in the negative direction, making the new solution even more stable.

Our next aim is to use phase plane analysis to derive the bifurcation diagram depicted in Figure 6.4 for the no-flux nonlinear boundary value problem

$$u_{xx} + f(u) = 0$$
$$u_x(0) = 0 = u_x(L)$$

with bifurcation parameter L. We assume that the graphs of f and F (recall (6.3.2)) have the form shown in Figure 6.6.

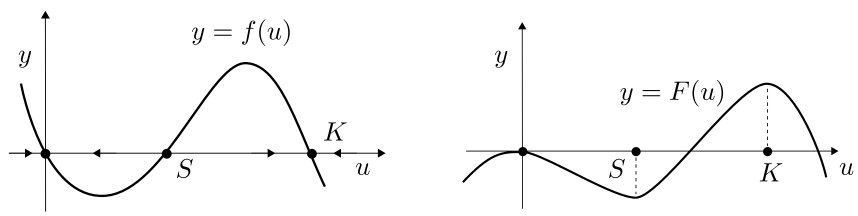

FIGURE 6.6.

Note that $u = 0$ and $u = K$ are stable as steady states for the dynamical systems generated by the ODE $\dot{u} = f(u)$, while the unstable steady state $u = S$ separates their domains of attraction. Also note that we assumed that $F(K) > 0$ (in other words, that the area below the u-axis and above the graph of f is less than the area above the u-axis and below that graph of f, if we consider the interval $[0, K]$). The consequence is that the phase portrait is as depicted in Figure 6.7.

In particular: the family of closed orbits surrounding $(S, 0)$ "ends" in a homoclinic loop issuing from the saddle $(0, 0)$. In an ecological context, u represents the density of a population subject to an Allee effect (meaning that it is bound to go extinct for low densities but that, due to positive density dependence, it grows to the carrying capacity K if abundant enough; the underlying mechanism may be sexual reproduction, so the difficulty of finding a mate when the species is rare in the considered area).

We parameterise the family of closed orbits by the minimum value that u takes and we shall denote this minimum value by p. Note that the corresponding value of H equals $F(p)$. We denote

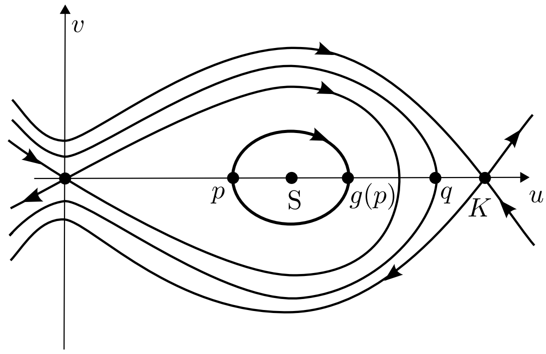

Figure 6.7.

- the corresponding maximum value of u by $g(p)$
- the corresponding period by $T(p)$

Note that

$$T(p) = 2\int_p^{g(p)} \frac{du}{\sqrt{2(F(p)-F(u))}} \tag{6.3.8}$$

Exercise 6.3.2. (i) Derive this identity
(ii) Show that $\lim_{p\downarrow 0} T(p) = \infty$
(iii) Show that $\lim_{p\uparrow S} T(p) = \frac{2\pi}{\sqrt{f'(S)}}$

The question whether or not T is a monotone function of p is, in general, not easy to answer (see e.g. (Chicone, 1987)). But in any case, we know that the range of T includes the interval $(\frac{2\pi}{\sqrt{f'(S)}}, \infty)$.

Now suppose that $2L$ belongs to the range of T. Because of the symmetry of the phase portrait with respect to reflection in the u-axis, we know that it takes "as long" for u to increase from p to $g(p)$ as it takes u to decrease subsequently again from $g(p)$ to p. So if $T(p) = 2L$, each of these changes happens during a stretch L of the independent variable. The corresponding solutions are indicated by N_1 and they are sketched in Figure 6.8. The index specifies the number for intervals on which the solution is monotone. If we denote one solution by u_+ and the other by u_-, then

$$u_+(x) = u_-(L-x)$$

or, in other words, one solution is obtained from the other by a reflection in the midpoint of the interval.

The solutions indicated by N_2 correspond to p such that $T(p) = L$, so they correspond to a full turn. The midpoint of the x-interval is reached after half a turn, so these solutions are themselves symmetric with respect to reflection in the midpoint. Both solutions have exactly one interval of increase and one of decrease, but if we first decrease and then increase the maximum is at the boundary and the minimum in the interior, while with the other order it is the other way around (see Figure 6.8).

The solutions indicated by N_3 correspond to p such that $\frac{3}{2}T(p) = L$, so to $1\frac{1}{2}$ turns. In general we consider p such that $\frac{k}{2}T(p) = L$ and solutions that make $\frac{k}{2}$ turns.[1] For k even these are symmetric, while for k odd the two solutions are related to each other by a symmetry.

[1] Above we used k to denote the number of components of a system of equations. Below we shall use the symbol k to specify a mode number, i.e., to indicate the number of minima and maxima of a steady state solution. The aim of this warning is to avoid that you get confused.

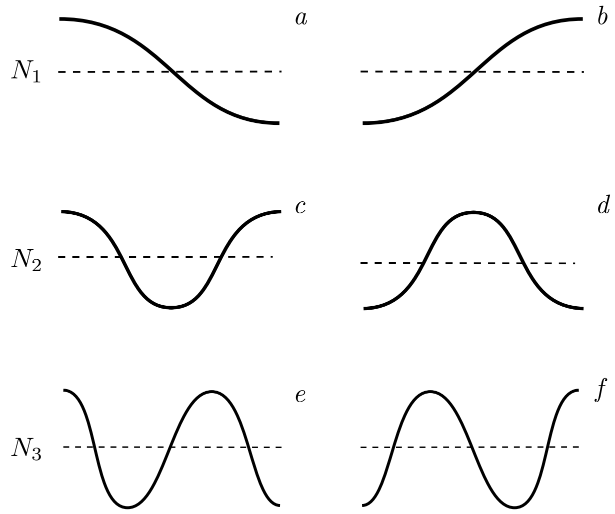

FIGURE 6.8.

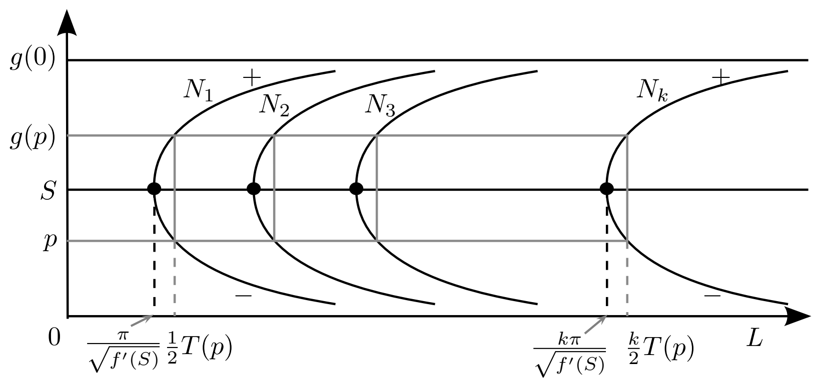

FIGURE 6.9.

Assuming that $p \mapsto T(p)$ is monotone we can now draw a more detailed version of Figure 6.4, shown in Figure 6.9.

If T is *not* monotone, there are wiggles in these branches.

How should we interpret this diagram in the context of the infinite-dimensional dynamical system generated by (6.3.3)–(6.3.4)? The constant steady state $u \equiv S$ is now a *saddle point* (recall (6.3.1) and note that the term involving F has the opposite sign as the term involving F in the formula (6.3.7) for the Hamiltonian H). For small L it has a one-dimensional unstable manifold, but as L increases the dimension of this manifold increases (or, in more physical jargon, more and more modes turn unstable). Presumably, the domains of attraction of the stable constant (i.e., spatially uniform) steady states $u \equiv 0$ and $u \equiv K$ are separated by the union of the stable manifolds of $u \equiv S$ and all the existing non-constant steady states "around" it. So the bifurcations change the structure of the flow within this separatrix.

Consider once more the zero-flux nonlinear boundary value problem

$$u_{xx} + f(u) = 0, \tag{6.3.9}$$

$$u_x(0) = 0 = u_x(L), \tag{6.3.10}$$

with parameter L. We now want to derive relations between solutions by using extension and symmetry arguments instead of phase plane analysis. (The key advantage of such arguments is that they also work for systems.)

Exercise 6.3.3. Show that if u is a solution of (6.3.9)–(6.3.10), so is w, defined by $w(x) = u(L-x)$. We call u *symmetric* if $w = u$. What symmetry does this amount to?

Exercise 6.3.4. Assume $f(0) = 0$, $f'(0) > 0$. Show that then bifurcations occur if $L = \frac{k\pi}{\sqrt{f'(0)}}$. Consider $k = 1$. Give arguments in favour of the claim that the bifurcating solutions are *not* symmetric. Show that, consequently, the bifurcation must be a pitchfork.

Exercise 6.3.5. Whenever u is a solution, extend it to a $2L$-periodic function by

$$\begin{aligned} u(-x) &:= u(x), \qquad 0 \le x \le L, \\ u(x+2L) &:= u(x). \end{aligned}$$

Show that the extension is a solution for parameter value kL, $k = 1, 2, 3, \ldots$. Conclude that the branch bifurcating for $k = 1$ repeats itself for every higher value of k.

Exercise 6.3.6. Show that u is symmetric if and only if the extension has period L. Show that all branches corresponding to even k consist of symmetric solutions. How are in that case the two solutions (one for each subbranch) related to each other?

Exercise 6.3.7. Show that *some* branches for the problem with *Dirichlet* boundary conditions $u(0) = S = u(L)$ can be obtained from extended solutions of the zero flux boundary value problem.

Next, let us look at the situation where there is a big monster at the boundary, so where we replace the no-flux boundary conditions by the zero-Dirichlet conditions

$$u(0) = 0 = u(L) \tag{6.3.11}$$

In terms of the phase portrait Figure 6.7 this means that, in search for steady states, we look for pieces of orbits that start and end at the v-axis.

A glance at Figure 6.7 shows that we can parameterise candidate orbits by the maximum q of u, with

$$g(0) < q < K$$

and that the corresponding steady state solutions of the boundary value problem are symmetric with respect to reflection in the midpoint $x = \frac{L}{2}$ where the maximum q is assumed. Let us denote by $\tilde{T}(q)$ the "time" it takes to arrive at the negative v-axis when starting at the positive v-axis. Then

$$\tilde{T}(q) = 2\int_0^q \frac{du}{\sqrt{2(F(q) - F(u))}}$$

and, as movement slows down near saddle points, necessarily

$$\lim_{q \downarrow g(0)} \tilde{T}(q) = \infty$$

$$\lim_{q \uparrow K} \tilde{T}(q) = \infty$$

So $\tilde{T}$ assumes a minimum and the equation $\tilde{T}(q) = L$ has for

$$\begin{aligned} &L < \min \tilde{T} \quad \text{no solution} \\ &L > \min \tilde{T} \quad \text{at least two solutions} \end{aligned}$$

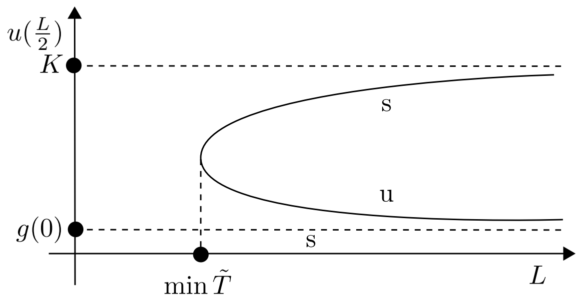

FIGURE 6.10.

If there are *exactly* two solutions of $\tilde{T}(q) = L$ for L larger than the minimum of $\tilde{T}$, then the bifurcation diagram has the form shown in Figure 6.10.

So there is a saddle-node bifurcation for $L = \min \tilde{T}$ at which a stable steady state and an unstable (saddle) steady state are born. Presumably the stability character of these two steady states does not change when L is further increased. The stable manifold of the saddle steady state serves again as a separatrix (note that $u \equiv 0$ is a stable steady state for all L). By using Maximum Principle arguments, cf. (Aronson and Weinberger, 1975, 1978; Ludwig et al., 1979), or more precisely, by constructing sub- and supersolutions, one can get some partial information about the initial conditions for (6.3.3) and (6.3.11) that yield solutions converging to either $u \equiv 0$ or to the stable non-uniform steady state. Note that for very large L the values that the latter takes are very close to K on most of the interval.

Our main conclusion is that the population can persist, despite the big monster at the boundary, *provided* the domain is large enough.

6.4 The non-existence of patterns for scalar equations

We will now show that non-trivial equilibrium solutions ('patterns') to scalar reaction-diffusion equations subject to Neumann boundary conditions can never be stable. This is often loosely summarised with the phrase in the title of this section.

Consider

$$\begin{cases} u_t = u_{xx} + f(u) \quad \text{on } [0, L] \\ u_x(t, 0) = u_x(t, L) = 0 \end{cases} \tag{6.4.1}$$

Let $U(x)$ be a non-trivial equilibrium solution, i.e., $U(x) \not\equiv U_0$. The eigenvalue problem for V, which describes the linear stability of U, is given by

$$\begin{cases} V_{xx} + [\frac{\partial f}{\partial u}(U(x)) - \lambda]V = 0 \quad \text{on } [0, L] \\ V_x(0) = V_x(L) = 0 \end{cases} \tag{6.4.2}$$

This is a standard Sturm-Liouville problem. The eigenvalues, denoted with λ_i^N to signify that they belong to the Neumann problem, are again all real and simple, $-\infty < \ldots < \lambda_2^N < \lambda_1^N < \lambda_0^N$, and the eigenfunction corresponding with λ_i has i zeroes. We need to show that $\lambda_0^N > 0$, thus showing that $U(x)$ is unstable. Note that a similar ordering of eigenvalues exists for the Dirichlet problem. Also now the i-th Dirichlet eigenvalue, λ_i^D has an eigenfunction with i zeroes.

Now observe that, by differentiating the steady state equation for U with respect to x, we know that $W = U_x$ solves

$$\begin{cases} W_{xx} + \frac{\partial f}{\partial u}(U(x))W = 0 \quad \text{on } [0, L], \\ W(0) = W(L) = 0. \end{cases}$$

Therefore, problem (6.4.2) with homogeneous Dirichlet boundary conditions instead of homogeneous Neumann boundary conditions has $\lambda = 0$ as eigenvalue. Denoting the eigenvalues of the Dirichlet problem by λ_i^D, $i = 0, 1, \ldots$, we thus know that $\lambda_i^D = 0$ for a certain i.

We can now use the following Lemma, stating that we can order the eigenvalues of two solutions, if we can order the solutions in some manner.

Lemma 6.4.1*:* Let $g(x)$ be given. Let Φ and Ψ satisfy

$$V_{xx} + (g(x) - \lambda)\, V = 0$$

with eigenvalues λ and μ respectively. Assume $\Phi(0) = \Phi(L) = 0$, and $\Phi(x) > 0$ on $(0, L)$, and $\Psi(x) > 0$ on $[0, L]$. Then $\lambda < \mu$.

Proof. Multiplying the eigenvalue equation for Φ by Ψ and vice versa, and subtracting these two, we find

$$\Phi\Psi'' - \Phi''\Psi + (\mu - \lambda)\Phi\Psi = 0.$$

Hence, integrating over $[0, L]$, and using partial integration yields

$$\Psi\Phi'\Big|_0^L - \Phi\Psi'\Big|_0^L + (\mu - \lambda)\int_0^L \Phi\Psi = 0.$$

The last integral is strictly positive by the assumptions on Φ and Ψ. Since Φ is a Dirichlet solution, the second term vanishes. The first term is a priori only non-positive, which would yield $\lambda \leq \mu$. Note, however, that if $\Phi'(0) = 0$ or $\Phi'(L) = 0$, then $\Phi \equiv 0$, and hence by uniqueness of the boundary value problem we find $\Phi'(0) > 0$ and $\Phi'(L) < 0$. Therefore $\lambda < \mu$. □

Recall that the smallest eigenvalue λ_0^N, which is the one we are actually interested in, corresponds to an eigenfunction without zeroes. Therefore, this function solves (6.4.2) and has the properties of Ψ in the lemma. So from the lemma we conclude that $\lambda_0^N > \lambda_0^D \geq \lambda_i^D = 0$, and that indeed $U(x)$ is unstable.

This argument also works in higher space dimensions, provided that the domain Ω is convex. As we discussed in Section 6.2, stable non-uniform steady states do exist if we choose a bistable function f on a halter-shaped domain (recall Figure 6.2).

Now we turn to the scalar Dirichlet problem

$$\begin{cases} u_t = u_{xx} + f(u) & \text{on } [0, L] \\ u(0) = u(L) = 0 \end{cases} \tag{6.4.3}$$

Let again $U(x)$ be an equilibrium solution and assume that $U(x)$ changes sign on $(0, L)$. Then $U(x)$ is again unstable!

To see this, we again study $W = U_x$. Since U changes sign, there exist $0 < x_1 < x_2 < L$ such that $W(x_1) = W(x_2) = 0$. So W solves

$$\begin{cases} w_{xx} + f'(U)w = 0 & \text{on } [0, L], \\ w(x_1) = w(x_2) = 0. \end{cases}$$

Applying Lemma 6.4.1 again to $\Phi = \pm W$ (choose the sign so that $\Phi > 0$), with $\lambda = 0$, and $\Psi = \Phi_0^D$ with $\mu = \lambda_0^D$, restricted to $[x_1, x_2]$, we conclude $\mu = \lambda_0^D > \lambda = 0$, and that U is unstable.

6.5 Travelling waves for mono- and bistable scalar Reaction-Diffusion

Diffusion, as a mechanism to generate signals used in for instance development, is a very slow process, and doesn't work efficiently over large distances. As we already saw in Section 5.3, augmenting diffusion with some kind of reaction, be it multiplication of a species or the interaction between different species or chemicals, can lead to patterns that travel much faster viz. with constant speed. It may therefore come as no surprise that reaction-diffusion is a mechanism that abounds in all kinds of biological areas. In this section we are going to study the existence of travelling wave profiles for nonlinear scalar reaction-diffusion equations, determine at what speeds these can travel, and in what direction.

Two prototype equations will be studied: the monostable and the bistable case. The first is also known as the Fisher-Kolmogorov equation, and is given by

$$u_t = du_{xx} + ku(1-u), \quad x \in \mathbb{R} \tag{6.5.1}$$

which, using the rescaled variables $t^* = kt$ and $x^* = x\sqrt{k/d}$ becomes

$$u_t = u_{xx} + u(1-u). \tag{6.5.2}$$

Here the stars have immediately been dropped. It is a model equation which was originally devised by Fisher to model the spread of a favourable gene in a population (Fisher, 1937). It was simultaneously (and presumably independently) studied by, as Aronson (1985) put it, the famous troika of Kolmogorov, Petrovskii and Piscunov (Kolmogorov et al., 1937). The bistable equation in non-dimensional form is given by

$$u_t = u_{xx} + u(u-a)(1-u), \quad x \in \mathbb{R} \tag{6.5.3}$$

where $0 < a < 1$. As we will see, both these equations admit travelling wave profiles, but the range of speeds with which such waves progress is quite different.

Let us first consider the monostable case. If we ignore space for the moment, the equation reduces to

$$u' = u(1-u).$$

This is the standard model for logistic growth, having $u = 0$ and $u = 1$ as steady states, the first of which is unstable, and the second stable. This suggests it might be possible to find travelling wave profiles $w(z) = u(x - ct)$ that connect 0 and 1 and which travel at speed c. Let us try to find these. Substituting the travelling wave Ansatz, taking also into consideration the choice of behaviour at $\pm\infty$, we obtain

$$-cw' = w'' + w(1-w) \tag{6.5.4}$$

$$\lim_{z\to-\infty} w(z) = 1, \quad \lim_{z\to\infty} w(z) = 0 \tag{6.5.5}$$

Writing (6.5.4) in phase plane form,

$$w' = v \tag{6.5.6}$$

$$v' = -cv - w(1-w) \tag{6.5.7}$$

we again find two equilibria, $(w, v) = (0, 0)$ and $(1, 0)$. The Jacobian of this system is

$$\begin{pmatrix} 0 & 1 \\ -1+2w & -c \end{pmatrix} \tag{6.5.8}$$

and hence we find the following eigenvalues for the two steady states. For $(0, 0)$,

$$\lambda_\pm = -\frac{c}{2} \pm \frac{1}{2}\sqrt{c^2-4}$$

whereas for $(1, 0)$,

$$\lambda_\pm = -\frac{c}{2} \pm \frac{1}{2}\sqrt{c^2+4}$$

Hence, if $c^2 > 4$, the origin is a stable node, and if $c^2 < 4$, it is a stable spiral, giving rise to physically unrealistic solutions since the solutions then become negative. The other steady state, $(1, 0)$, is always a saddle. The phase plane for (6.5.6) for the case $c^2 > 4$, see Figure 6.11, now strongly suggests that the relevant part of

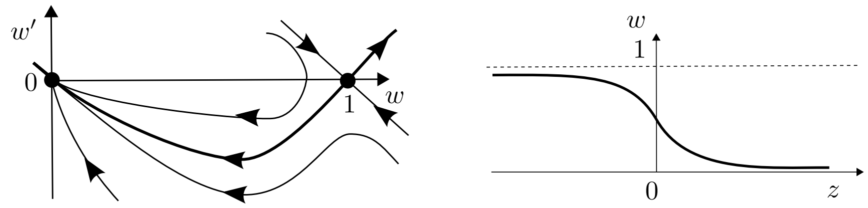

Figure 6.11.

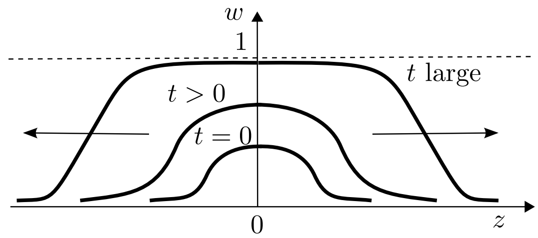

Figure 6.12.

the unstable manifold $(1, 0)$ always has to connect to the stable origin, and thus form a heteroclinic orbit connecting $w = 1$ and $w = 0$. Since we can perform this construction for any $c^2 > 4$, we find a continuum of possible wave speeds for travelling waves of the Fisher-Kolmogorov equation (Kolmogorov et al., 1937; Hadeler and Rothe, 1975).

Having argued that travelling waves do exist for a continuum of wave speeds, we may wonder for which initial conditions the solution in time tends to a travelling wave (or a combination of two travelling waves, one moving to the left, and one to the right)? Kolmogorov, Petrovskii and Piscunov (Kolmogorov et al., 1937) already showed in 1937 that initial conditions of the form

$$\begin{cases} w \equiv 1 \text{ for } x < p \\ w \equiv 0 \text{ for } x > p \end{cases}$$

for some $p \in \mathbb{R}$ do indeed tend to travelling wave profiles which travel with minimum speed $c = 2$. But also a localized initial condition, relevant for instance in models of introduced species, grows out to form an expanding block with two fronts, one travelling to the left and the other to the right (see Figure 6.12).

Let us now turn to the bistable equation and repeat the linear stability analysis. For a general scalar reaction diffusion equation

$$u_t = u_{xx} + f(u)$$

the equation for the travelling wave profile $w(z) = u(x - ct)$ is

$$w'' + cw' + f(w) = 0.$$

Writing this as a two-dimensional system

$$w' = v \tag{6.5.9}$$

$$v' = -cv - f(w) \tag{6.5.10}$$

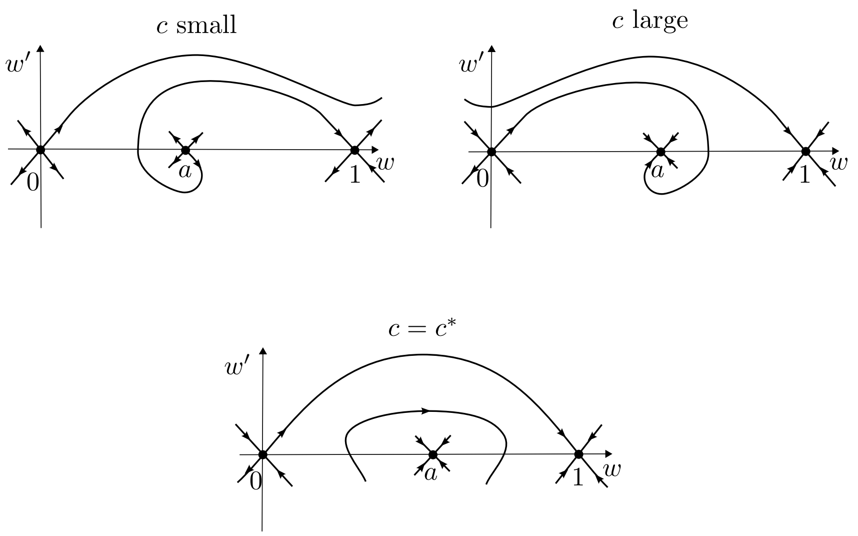

FIGURE 6.13.

we have the Jacobian

$$\begin{pmatrix} 0 & 1 \\ -f'(w) & -c \end{pmatrix} \tag{6.5.11}$$

with eigenvalues

$$\lambda_{\pm} = \frac{c}{2} \pm \frac{1}{2}\sqrt{c^2 - 4f'(w)}.$$

For our particular problem, $f(u) = u(u-a)(1-u)$, so there are three equilibria, which for the 2D system are written as $(w, v) = (0, 0)$, $(a, 0)$, or $(1, 0)$. Computing the eigenvalues at each of these steady states, we find that $(0, 0)$ and $(1, 0)$ are always saddle points, and $(a, 0)$ is a stable node if $c^2 > 4f'(a)$ and a stable spiral if $c^2 < 4f'(a)$. Finding travelling wave solutions w with speed c connecting a stable and unstable equilibrium, such as from $w = 0$ to $w = a$ or from $w = a$ to $w = 1$ is possible for many choices of c, essentially by the reasoning outlined above for the monostable case. Can we also find heteroclinic orbits connecting the unstable manifold of $w = 0$ to the stable manifold of $w = 1$? It is not likely that this is going to be possible: for most speeds c the solution coming from the unstable manifold will converge to the stable node or spiral $(a, 0)$, or will overshoot (the unstable direction at $(1, 0)$ then converges to $(a, 0)$) . However, the phase planes for small and for large c (see Figure 6.13, top row), together with continuity arguments, do suggest that for some exceptional intermediate c^* a heteroclinic from 1 to 0 exists (see Figure 6.13, bottom). This can indeed be made rigorous.

There is a more general rule: if a reaction term $f(u)$ has a number of roots, they generically come alternatingly as saddle points and stable nodes or spirals. Most (in terms of c) heteroclinic orbits connect stable and saddle steady states, and only a few connect two saddle equilibria.

Let us now turn to the question of the *direction* of the wave. After all, within biological contexts it may be all important to know if a wave of some disease or introduced species retreats or advances. A simple argument gives the direction of the speed, i.e., the sign of c. Recall that travelling wave profiles $w(z)$ solve

$$w'' + cw' + f(w) = 0. \tag{6.5.12}$$

Equation (6.5.12) is invariant under $z \mapsto -z$, $c \mapsto -c$, so we need to choose the behaviour of solutions for $z \to \pm\infty$ to be able to determine the true direction

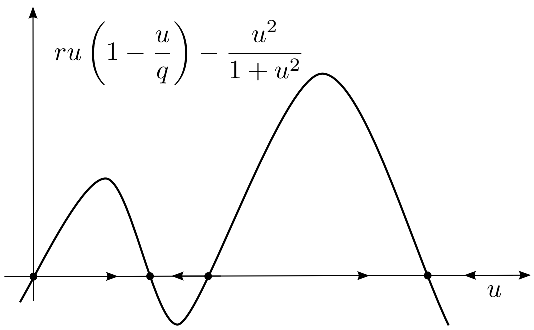

FIGURE 6.14.

of travelling wave solutions. We focus on solutions w which tend to 1 for $z \to -\infty$ and to 0 for $z \to \infty$. In particular, then also $w'(z) \to 0$ for $z \to \pm\infty$. Multiplying (6.5.12) by w' and integrating over $\mathbb{R}$, we find

$$0 = \int_{-\infty}^{\infty} [w'' + cw' + f(w)]w'dz \tag{6.5.13}$$

$$= 0 + c\int_{-\infty}^{\infty} w'^2\,dz + \int_{-\infty}^{\infty} f(w)w'dz \tag{6.5.14}$$

$$= c\int_{-\infty}^{\infty} w'^2\,dz + \int_{1}^{0} f(w)dw \tag{6.5.15}$$

where we have used partial integration and the above limits. We thus conclude that the sign of c is given by $\int_0^1 f(w)dw$, since

$$c = \frac{\int_0^1 f(w)dw}{\int_{-\infty}^{\infty} w'^2\,dz}$$

In the monostable case, $\int_0^1 u(1-u)du = 1/6$, so the wave is always describing an increase of u (for x fixed, $u(x-ct)$ increases from 0 to 1). In the bistable case, $\int_0^1 u(u-a)(1-u)du = \frac{1}{12}(1-2a)$. So for $0 < a < \frac{1}{2}$, the unique wave speed c^* is positive, for $a = \frac{1}{2}$ we find a standing wave ($c^* = 0$), while for $\frac{1}{2} < a < 1$, the wave speed is negative.

Let us consider a well-known example from scalar reaction-diffusion equations, the spread of the spruce budworm, which is a pest in North American forests. The equation, in nondimensional form, reads

$$u_t = u_{xx} + ru\left(1-\frac{u}{q}\right) - \frac{u^2}{1+u^2}$$

The reaction term is sketched in Figure 6.14. Depending on parameter values, there are up to four equilibria, and if we ignore space dependence two of these are stable, and two unstable. As before, including space again and looking for travelling wave profiles, the time-stable steady states become saddle points, and the time-unstable steady states become stable nodes or spirals. There exist travelling wave profiles connecting the two saddles, which have a certain unique speed. By adjusting the (scaled) carrying capacity q (for instance, by limiting the amount of food available to the budworms), the direction of the wave may be controlled, and thus the outbreak of these pests may be contained. See (Murray, 2002) for a detailed discussion of this much-studied problem.

6.6 Pattern formation: The Turing instability

A key aim of developmental biology is to understand morphogenesis: how can, starting from a uniform state, spatial structure, i.e., pattern, develop? Localised differentiation of cells is certainly an essential component. But how do cells know which differentiation pathway to follow? If this hinges on positional information, then how do these cells know "where" they are? Genetic information needs physico-chemical mechanisms to be expressed, to be translated into form.

Earlier we observed that for a *scalar quantity* that diffuses and reacts, spatial structure disappears (rather than originates), unless we force it upon the system by the boundary conditions or the shape of the domain (recall the halter from Figure 6.2). What if there are *several* quantities that interact and diffuse?

Here we focus on the system of reaction-diffusion equations 6.4.1 for $k = 2$ (two components) and $m = 1$ (one-dimensional spatial domain) and establish conditions such that a uniform steady state, that is stable as a steady state of the purely kinetic system, turns unstable if we allow both components to diffuse, but with rather different diffusion constants. So differences in the time scale of spatial transport of the various components can interfere with the interaction and localised instability can manifest itself as spontaneous pattern formation (to show this in mathematical detail one needs to go beyond linearised instability and apply bifurcation methods to construct non-uniform steady states).

It is most efficient to first consider

$$\frac{\partial u_1}{\partial t} = d_1 \frac{\partial^2 u_1}{\partial x^2} + f_1(u_1, u_2) \tag{6.6.1}$$

$$\frac{\partial u_2}{\partial t} = d_2 \frac{\partial^2 u_2}{\partial x^2} + f_2(u_1, u_2) \tag{6.6.2}$$

for $x \in \mathbb{R}$ and only later consider the effect of no-flux boundary conditions on a bounded domain.

Let

$$\bar{u} = \begin{pmatrix} \bar{u}_1 \\ \bar{u}_2 \end{pmatrix}$$

be such that $f(\bar{u}) = 0$, and assume that all eigenvalues of the Jacobian matrix

$$M = Df(\bar{u}) = \begin{pmatrix} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{pmatrix}_{u=\bar{u}}$$

with entries m_{ij} have negative real part.

EXERCISE 6.6.1. Repeat the steps leading to equation (6.2.13) and show that, written out in detail, this equation reads

$$\lambda^2 + \lambda(-m_{22} - m_{11} + d_2\mu^2 + d_1\mu^2) + \{(m_{11} - d_1\mu^2)(m_{22} - d_2\mu^2) - m_{12}m_{21}\} = 0 \tag{6.6.3}$$

EXERCISE 6.6.2. By assumption the inequalities

$$m_{11} + m_{22} < 0, \tag{6.6.4}$$

$$m_{11}m_{22} - m_{12}m_{21} > 0$$

hold (why?). Verify that if we write (6.6.3) as

$$\lambda^2 + \theta_1\lambda + \theta_2 = 0 \tag{6.6.5}$$

then $\theta_1 > 0$. Explain why we may conclude from this that destabilization is never by way of Hopf bifurcation.

Exercise 6.6.3. A transcritical bifurcation occurs when $\lambda = 0$ is a root of (6.6.5) (or, more precisely, if a real root of (6.6.5) changes sign when parameters are varied). Evidently, this requires

$$0 = \theta_2 := d_1 d_2 (\mu^2)^2 - (d_1 m_{22} + d_2 m_{11})\mu^2 + m_{11} m_{22} - m_{12} m_{21} \tag{6.6.6}$$

Check that, as a function of μ^2, θ_2 describes a parabola with a minimum at

$$\mu^2 = \frac{1}{2}\left(\frac{m_{11}}{d_1} + \frac{m_{22}}{d_2}\right) \tag{6.6.7}$$

Compute that the minimum value equals

$$\theta_2^{\min} = m_{11} m_{22} - m_{12} m_{21} - \frac{1}{4}\frac{(d_1 m_{22} + d_2 m_{11})^2}{d_1 d_2} \tag{6.6.8}$$

Show that $\theta_2^{\min} < 0$ iff

$$m_{11} d_2 + m_{22} d_1 > 2\sqrt{d_1 d_2 (m_{11} m_{22} - m_{12} m_{21})} > 0 \tag{6.6.9}$$

Check that the right hand side of (6.6.7) is positive if (6.6.9) holds (why is this important?). Show that under our assumptions, (6.6.9) cannot hold if $d_1 = d_2$. Show that (6.6.9) requires (under our assumptions) that m_{11} and m_{22} have opposite signs. Show that then also m_{12} and m_{21} should have opposite signs.

Exercise 6.6.4. If the sign structure of M is

$$\begin{pmatrix} + & - \\ + & - \end{pmatrix}$$

we call species/substance 1 an *activator* and species/substance 2 an *inhibitor*. Explain the rationale of this terminology.

Exercise 6.6.5. Without loss of generality we may assume that the sign structure is as assumed in the preceding exercise. Substantiate this claim.

Hint: the other possibilities are

$$\begin{pmatrix} + & + \\ - & - \end{pmatrix}, \quad \begin{pmatrix} - & + \\ - & + \end{pmatrix}, \quad \text{and} \quad \begin{pmatrix} - & - \\ + & + \end{pmatrix}$$

It is, of course, rather arbitrary how we number the species. In addition one might do the bookkeeping in terms of $-u_2$ rather than u_2 (but note carefully that often the interpretation requires quantities to be *positive*; yet *deviations* from a strictly positive steady state value may assume both signs. The message is that "without loss of generality" is a subtle notion when the interpretation leads to constraints on mathematical transformations).

Exercise 6.6.6. One often encounters statements like "Diffusive instability requires long range inhibition and short range activation". With the sign structure of M as in Exercise 6.6.4 we can rewrite (6.6.9), with the middle part omitted, as

$$\tau_1 d_1 < \tau_2 d_2 \tag{6.6.10}$$

with $\tau_1 := m_{11}^{-1}$ and $\tau_2 = |m_{22}|^{-1}$. Explain the relation between this inequality and the statement between the quotation marks.

Exercise 6.6.7. Assume that $M - \mu^2 d$ has eigenvalue zero and that M has activator-inhibitor sign structure, cf. Exercise 6.6.4. Let $\bar{v}$ be the eigenvector corresponding to this eigenvalue zero. Show that $\operatorname{sign} \bar{v}_1 = \operatorname{sign} \bar{v}_2$. Explain in a hand-waiving manner that accordingly the two components of a bifurcating non-uniform steady state are in-phase, meaning that one increases as a function of x if and only the other does too. What changes if the sign pattern of M is $\begin{pmatrix} + & + \\ - & - \end{pmatrix}$?

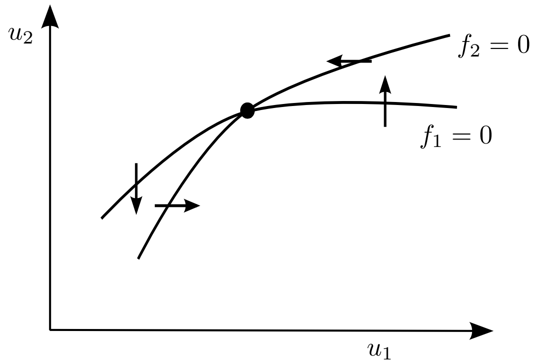

FIGURE 6.15. Local phase portrait of the kinetic system in Exercise 6.6.8.

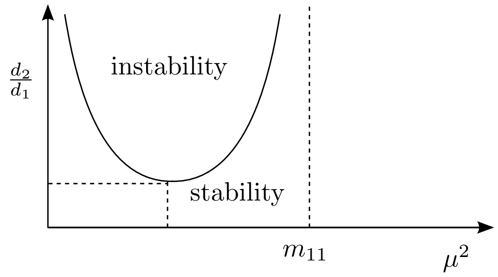

FIGURE 6.16. The graph of the right hand side of (6.6.12) as a function of μ^2 in Exercise 6.6.9.

EXERCISE 6.6.8. Assume that M has activator-inhibitor sign structure and that M has a positive determinant. Show that the local phase portrait of the kinetic system is as shown in Figure 6.15. Hint: solve $f_i = 0$ for u_2 as a function u_1 by way of the Implicit Function Theorem. How does the phase portrait look if $\begin{pmatrix} + & + \\ - & - \end{pmatrix}$?

EXERCISE 6.6.9. Show that by *scaling* of the spatial variable we may arrive at a *ratio* of diffusion coefficients and that this, for a particular choice of scaling, amounts to replacing μ^2 by μ^2/D_1 so that (6.6.6) transforms into

$$0 = \theta_2 = \frac{d_2}{d_1}(\mu^2)^2 - \left(\frac{d_2}{d_1}m_{11} + m_{22}\right)\mu^2 + m_{11}m_{22} - m_{12}m_{21} \tag{6.6.11}$$

or, if we solve for d_2/d_1 as a function of μ^2,

$$\frac{d_2}{d_1} = \frac{m_{22}\mu^2 - m_{11}m_{22} + m_{12}m_{21}}{\mu^2(\mu^2 - m_{11})} \tag{6.6.12}$$

Show that under the conditions (6.6.4) and (6.6.9) the graph of the right hand side, as a function of μ^2, is as depicted in Figure 6.16.

Thus we have determined the stability boundary in the two parameter plane formed by the ratio d_2/d_1 of the diffusion constants and the mode parameter μ^2 (which is a continuous quantity when the spatial domain is the line $-\infty < x < \infty$). This graph is an essential ingredient for the stability analysis for finite intervals with no-flux boundary conditions, as we shall see in the next exercise.

EXERCISE 6.6.10. Now restrict the spatial domain to

$$0 \leq x \leq L$$

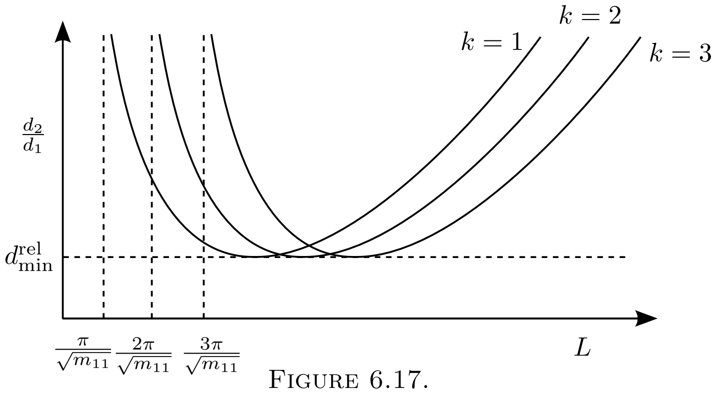

FIGURE 6.17.

and impose the no-flux boundary conditions

$$u_x(0) = 0 = u_x(L)$$

Derive that necessarily

$$\mu \in \left\{ \frac{k\pi}{L} \ : \ k = 1, 2, \dots \right\}$$

By considering L as a parameter we regain continuity (i.e., we eliminate to a certain extent the imposed discreteness), but we obtain denumerably many curves, one for each mode (see Figure 6.17). Describe the instability domain in $(\frac{d_2}{d_1}, L)$-space and its boundary. Describe what happens when we consider L as a free parameter for d_2/d_1 fixed at a value just slightly above $d_{\text{min}}^{\text{rel}}$ (you may find it useful to think in terms of "resonance" between the "natural" wave length associated with the instability on the one hand, and the size of the domain on the other).

EXERCISE 6.6.11. If we cross the curve corresponding to a particular k, the nonlinear system undergoes a pitchfork bifurcation. How can we be so sure about "pitchfork" without doing any calculations? Also, formulate that there is a certain arbitrariness in the pattern that arises in a real experiment.

EXERCISE 6.6.12. (builds on the Appendix on Bifurcation Methods) Derive a formula for the direction of the pitchfork bifurcation, i.e., determine whether it is is subcritical or supercritical. Formulate the Principle of Exchange of Stability for this particular case.

EXERCISE 6.6.13. Reflect on the patterns that one expects to see on a two-dimensional rectangular spatial domain, depending on the ratio of the two lengths (so when we enlarge the domain but keep this ratio fixed). Next, go to the zoo and look for spotted bodies and striped tails!

We now consider a concrete example which is rather debatable from a modelling point of view (in particular because of the H in the denominator) but which has the great advantage that the calculations are not too cumbersome. It is often called the Gierer-Meinhardt model, see (Meinhardt, 1982).

The system of reaction diffusion equations

$$\frac{\partial A}{\partial t} = 1 + R\frac{A^2}{H} - A + \frac{\partial^2 A}{\partial x^2}, \tag{6.6.13}$$

$$\frac{\partial H}{\partial t} = Q(A^2 - H) + P\frac{\partial^2 H}{\partial x^2} \tag{6.6.14}$$

provided with no-flux boundary conditions

$$\frac{\partial A}{\partial x}(t,0) = 0 = \frac{\partial A}{\partial x}(t,L), \tag{6.6.15}$$

$$\frac{\partial H}{\partial x}(t,0) = 0 = \frac{\partial H}{\partial x}(t,L) \tag{6.6.16}$$

describes the interaction between an autocatalytic activator A and an inhibitor H in a one-dimensional spatial domain, the x-interval $[0,L]$. The system (6.6.14) is already in a scaled form and only three parameters, R, Q, and P remain. In particular, the spatial variable x has been scaled to make the diffusion constant of A equal to 1. In the term RA^2/H, the denominator H is an approximation to (constant + H) and accordingly, predictions based on (6.6.14) should not be trusted when they involve small values of H. The greatest advantage of this approximation is that it makes the calculations below far simpler, which is why it is made.

EXERCISE 6.6.14.

(i) Find the uniform (in x) steady (in t) state.
(ii) Compute the Jacobian matrix of the reaction part.
(iii) Show that the constant steady state is *stable* with respect to homogeneous (i.e., x-independent) perturbations, provided the parameter inequality

$$\frac{R-1}{R+1} < Q \tag{6.6.17}$$

holds.

EXERCISE 6.6.15.

(i) Show that the k-th mode, characterised by dependence on x of the form $\cos\left(\frac{k\pi x}{L}\right)$, is stable when

$$P\left(\frac{k\pi}{L}\right)^4 + \left(Q - P\frac{R-1}{R+1}\right)\left(\frac{k\pi}{L}\right)^2 + Q > 0 \tag{6.6.18}$$

but unstable when the reverse inequality holds.
(ii) Deduce from (6.6.18) that a necessary condition for instability is

$$Q < P\frac{R-1}{R+1} \tag{6.6.19}$$

(iii) Deduce, by comparing (6.6.17) and (6.6.19), that a necessary condition for pattern forming instability is

$$P > 1$$

and interpret this condition.

EXERCISE 6.6.16. Show that the quadratic polynomial in α,

$$P\alpha^2 + \left(Q - P\frac{R-1}{R+1}\right)\alpha + Q$$

has minimum value

$$-\frac{1}{4}P\left(\frac{R-1}{R+1} - \frac{Q}{P}\right)^2 + Q$$

and check that it is attained for a *positive* value of α when (6.6.19) holds.

EXERCISE 6.6.17. (Re)formulate the results in biological terms and draw conclusions.

6.7 Discrete-space version of spectral decoupling as in Turing

Let X be a $k \times n$ matrix with components x_{ij}, to be interpreted as the density of the i-th species in the j-th patch. So for $j = 1, \dots, n$, the column k-vector $x_{ij} = (x_{1j}, \dots, x_{kj})^T$ describes the desities of the various species in the j-th patch, while for $i = 1, \dots, k$, the row n-vector $(x_{i1}, \dots, x_{in})$ describes the densities of species i in the various patches.

Let now $f : \mathbb{R}^k \to \mathbb{R}^k$ describe given (nonlinear) local interactions; $C : \mathbb{R}^n \to \mathbb{R}^n$ a linear map describing redistribution, so that c_{ij} describes movement from i to j; and $M : \mathbb{R}^k \to \mathbb{R}^k$ a linear and diagonal map describing the tendency to migrate with components m_i, $i = 1, \dots, k$.

We now lift all three of these maps to $\mathbb{R}^{k\times n}$ by the definitions

$$\begin{aligned} f(X) &= \Big(f(x_{\cdot 1}, \dots, x_{\cdot n})\Big) && \text{local interaction} \\ XC &= \Big(x_{1\cdot}C, \dots, x_{k\cdot}C)\Big)^T && \text{species independent redistribution} \\ MX &= (Mx_{\cdot 1}, \dots, Mx_{\cdot n}) && \text{patch independent migration tendency} \end{aligned}$$

The problems to be investigated are

$$\dot{X} = f(X) + MXC \quad \text{continuous time,} \tag{6.7.1}$$

and

$$X' = f(X) + Mf(X)C \quad \text{discrete time.} \tag{6.7.2}$$

Compared with the continuous-space problem

$$\frac{\partial u}{\partial t} = D\Delta u + f(u),$$

matrix M has the role of D, and C the role of the Laplacian Δ.

If $a \in \mathbb{R}^k$ and $b \in \mathbb{R}^n$ we shall write $X = ab$ as a shorthand for $X_{ij} = a_i b_j$. Let $\mathbb{1}_n = (1, \dots, 1)$, and *assume* that $\mathbb{1}_n C = 0$. Let y be a $\mathbb{R}^k$-valued function of time such that

$$\dot{y} = f(y) \quad \text{or} \quad y' = f(y)$$

so that y is a solution of the 1-patch problem. Then $X = y\mathbb{1}_n$ is a solution of the n-patch problem (note that $f(X) = f(y)\mathbb{1}_n$ when verifying the discrete time case). Conversely, if $X = y\mathbb{1}_n$ is a solution of the n-patch problem, then necessarily y is a solution of the 1-patch problem. We call these the *flat* solutions.

Let $X = y\mathbb{1}_n$ be a flat solution. The Jacobi $k\times k$-matrix $Df(y)$ is lifted to $\mathbb{R}^{k\times n}$ exactly as M. Then the linearised problems of (6.7.1) and (6.7.2) are respectively

$$\begin{aligned} \dot{\xi} &= Df(y)\xi + M\xi C, \\ \xi' &= Df(y)\xi + MDf(y)\xi C. \end{aligned}$$

Next *assume* that C has n linearly independent eigenvectors ψ^i, $i = 1, \dots, n$, corresponding to eigenvalues λ_i, i.e.,

$$\psi^i C = \lambda_i \psi^i, \quad i = 1, \dots, n.$$

The result, that any n-vector can be written as a linear combination of the ψ^i, can be lifted to $\mathbb{R}^{k\times n}$:

$$\xi = \sum_{i=1}^{n} a^i \psi^i \quad \text{for some } a_i \in \mathbb{R}^k, i = 1, \dots, n.$$

With this respresentation for ξ we have

$$Df(y)\xi = \sum_{i=1}^{n} Df(y)a^i\psi^i$$

(where the right hand side $Df(y)$ is again the $k \times k$ matrix), and

$$M\xi C = \sum_{i=1}^{n} Ma^i\psi^i C = \sum_{i=1}^{n} \lambda_i Ma^i\psi^i.$$

The independence of the ψ^i then implies that the $k \times n$-dimensional problems decouple into n problems of dimension k,

$$\dot{a}^i = Df(y)a^i + \lambda Ma^i,$$

or

$$(a^i)' = Df(y)a^i + \lambda MDf(y)a^i.$$

And each of these can be analysed by spectral methods, i.e., the decay or growth of the solutions is completely determined by the eigenvalues of

$$Df(y) + \lambda_i M \quad \text{position relative to imaginary axis,}$$

or

$$Df(y) + \lambda_i MDf(y) \quad \text{position relative to unit circle.}$$

The analysis above is *completely the same* as the standard Turing instability analysis of

$$\frac{\partial u}{\partial t} = D\Delta u + f(u).$$

To conclude, we make some remarks about C and, in particular, the interpretation of the assumption $\mathbb{1}_n C = 0$.

The matrix C_n is positive-off-diagonal (i.e., only diagonal elements can be negative). If migrants cannot die in the process, we should have the conservation relation

$$\sum_{j=1}^{n} c_{ij} = 0.$$

If redistribution is only governed by relative distances, we should have the symmetry

$$c_{ji} = c_{ij},$$

and consequently

$$\sum_{i=1}^{n} c_{ij} = 0.$$

The latter relation expresses, when written in the form

$$\sum_{i=1,\ i\neq j}^{n} c_{ij} = -c_{jj},$$

that immigration into a patch is matched by emigration from a patch at the per capita level. This could be called a "no accumulation" condition. As a consequence of the conservation relation, the column n-vector $\mathbb{1}_n^T$ is a right eigenvector of C_n corresponding to eigenvalue zero. Under the no-accumulation condition $\mathbb{1}_n$ is a left eigenvector corresponding to eigenvalue zero.

It helps to think of λ in

$$Df(y) + \lambda M$$

as a continuous variable (taking only negative values).