Lecture 15: Biological Waves

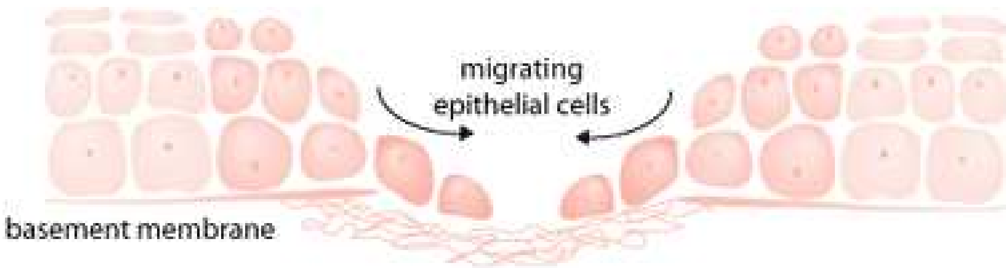
Jonathan A. Sherratt

Contents

1 Wave Fronts I: Modelling Epidermal Wound Healing

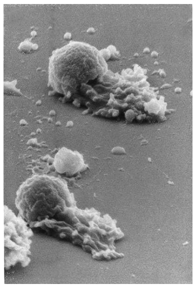
1.1 Epidermal Wound Healing

Epidermal wounds are very shallow (no bleeding), e.g. blisters

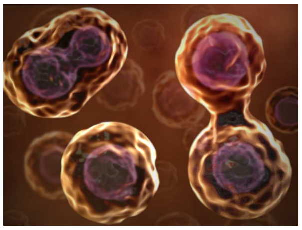


Healing is due to

- cell movement



- increased cell division near the wound edge



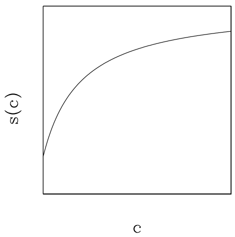
Cell division is upregulated by chemicals produced by the cells

1.2 A Mathematical Model

Cell division is upregulated by chemicals produced by the cells
Model variables: $n(\underline{x}, t)$ and $c(\underline{x}, t)$.

Model equations:

$$\begin{aligned} \partial n/\partial t &= \overbrace{D\nabla^2 n}^{\text{cell movement}} + \overbrace{s(c)(N-n)n}^{\text{cell division}} - \overbrace{\delta n}^{\text{cell death}} \\ \partial c/\partial t &= \underbrace{D_c\nabla^2 c}_{\text{chemical diffusion}} + \underbrace{An/(1+\alpha n^2)}_{\text{production by cells}} - \underbrace{\lambda c}_{\text{decay}} \end{aligned}$$



1.3 Reduction to One Equation

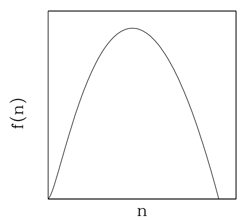
$$\begin{aligned}\partial n/\partial t &= D\nabla^2 n + s(c)(N-n)n - \delta n\\ \partial c/\partial t &= D_c\nabla^2 c + An/(1+\alpha n^2) - \lambda c\,.\end{aligned}$$

The chemical kinetics are very fast $\Rightarrow A$, λ large.
So to a good approximation $c = (A/\lambda)\cdot n/(1+\alpha n^2)$.

$$\Rightarrow \partial n/\partial t = D\nabla^2 n + f(n)$$

where

$$f(n) = s\left(\frac{An}{\lambda(1+\alpha n^2)}\right)(N-n)n - \delta n\,.$$



2 Wave Fronts II: The Speed of Epidermal Repair

2.1 Travelling Wave Solutions

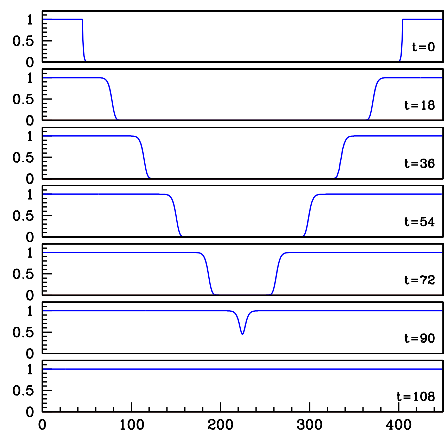


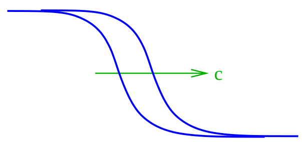
Figure 1: This figure shows a typical model solution

During most of the healing, the solution moves with constant speed and shape. This is a "travelling wave solution"

$$n(x,t) = N(x - at)$$

where a is the wave speed. We will write $z = x - at$. Then $\partial n/\partial x = dN/dz$ and $\partial n/\partial t = -a\, dN/dz$

$$\Rightarrow D\frac{d^2N}{dz^2} + a\frac{dN}{dz} + f(N) = 0$$



2.1.1 The Speed of Travelling Waves

We know that $N \to 0$ as $z \to \infty$. Recall that

$$D\frac{d^2N}{dz^2} + a\frac{dN}{dz} + f(N) = 0\,.$$

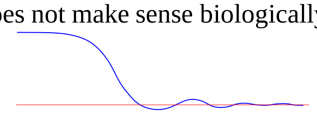
Therefore when N is small

$$D\frac{d^2N}{dz^2} + a\frac{dN}{dz} + f'(0)N = 0$$

to leading order. This has solutions $N(z) = N_0 e^{\lambda z}$ with

$$\lambda^2 + a\lambda + 1 = 0 \Rightarrow \lambda = \tfrac{1}{2}\left(-a \pm \sqrt{a^2 - 4Df'(0)}\right).$$

If $a < 2\sqrt{Df'(0)}$ then λ is complex $\Rightarrow$ the solutions oscillate about $N = 0$, which does not make sense biologically.



So we require $a \geq 2\sqrt{Df'(0)}$. Mathematical theory implies that in applications, waves will move at the minimum possible speed, $2\sqrt{Df'(0)}$.

For the wound healing model

$$f'(0) = Ns(0) - \delta$$

$$\Rightarrow \text{wave speed } a = 2\sqrt{D(Ns(0) - \delta)}\,.$$

2.2 General Results on Wave Speed

Consider the equation $\partial u/\partial t = D\,\partial^2 u/\partial x^2 + f(u)$ with $f(0) = f(1) = 0$, $f(u) > 0$ on $0 < u < 1$, $f'(0) > 0$ and $f'(u) < f'(0)$ on $0 < u \leq 1$.

For this equation, two important theorems were proved by Kolmogorov, Petrovskii and Piskunov; a similar but slightly less general study was done at the same time by Fisher.

Theorem 1. There is a positive travelling wave solution for all wave speeds $\geq 2\sqrt{Df'(0)}$, and no positive travelling waves for speeds less than this critical value.

A proof of theorem 1 is in the supplementary material.

Theorem 2. Suppose that $u(x, t = 0) = 1$ for x sufficiently large and negative, and $u(x, t = 0) = 0$ for x sufficiently large and positive. Then the solution $u(x, t)$ approaches the travelling wave solution with the critical speed $2\sqrt{Df'(0)}$ as $t \to \infty$.

The form of the approach to the travelling wave is discussed in depth by Bramson (1983). *The proof of theorem 2 is extremely difficult.*

References:

Bramson, M.D. 1983 Convergence of solutions of the Kolmogorov equation to travelling waves. *Mem. AMS* 44 no. 285.

Fisher, R.A. 1937 The wave of advance of advantageous genes. *Ann. Eug.* 7, 355-369.

Kolmogorov, A., Petrovskii, I., Piskunov, N. 1937 Etude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique. *Moscow Univ. Bull. Math.* 1, 1-25.

2.2.1 Therapeutic Addition of Chemical

Now return to the wound healing model and consider adding extra chemical to the wound as a therapy.

The equation for the chemical changes to

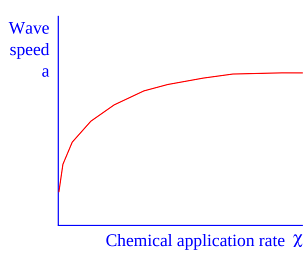
$$\partial c/\partial t = An/(1 + \alpha n^2) - \lambda c + \gamma$$

$\Rightarrow$ $f(n)$ changes to

$$s\left(\frac{\gamma}{\lambda} + \frac{An}{\lambda(1 + \alpha n^2)}\right)(N - n)n - \delta n$$

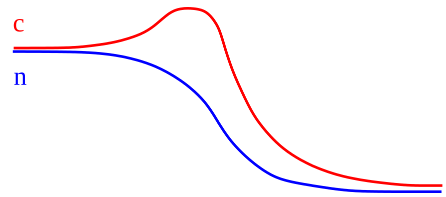
$\Rightarrow$ $f'(0)$ changes to $Ns(\gamma/\lambda) - \delta$

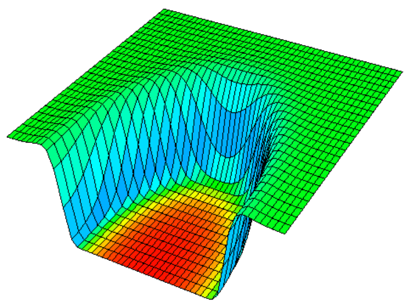
$\Rightarrow$ observed (min poss) wave speed $a = 2\sqrt{D(Ns(\gamma/\lambda) - \delta)}$



2.2.2 Deducing the Chemical Profile

Since we know c as a function of n, there is also a travelling wave of chemical, whose form we can deduce. The chemical profile has a peak in the wave front.





However, there are no theorems on the speed of wave fronts in systems of reaction-diffusion equations, except in a few special cases (which do not include this model).

3 Wave Fronts III: Bistable Kinetics (Spruce Budworm)

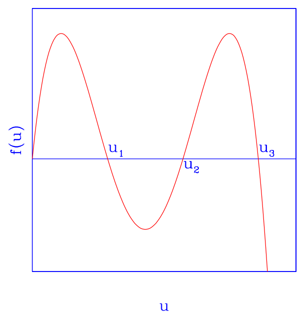
3.1 Spruce Budworm Dynamics

The spruce budworm is an important forestry pest in North America.

3.1.1 Travelling Waves in the Spruce Budworm Model

A simple model is

$$\begin{aligned} \partial u/\partial t &= D\,\partial^2 u/\partial x^2 + f(u) \\ \text{where} & \\ f(u) &= \underbrace{k_1 u(1-u/k_2)}_{\substack{\text{logistic}\\ \text{growth}}} + \underbrace{u^2/(1+u^2)}_{\substack{\text{predation}\\ \text{by birds}}} \end{aligned}$$



In applications, waves travelling between $u = u_1$ ("refuge state") and $u = u_3$ ("outbreak state") are important. Both of these steady states are locally stable. Therefore the direction of wave propagation is not obvious.

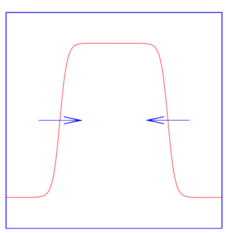
3.2 Direction of Wave Propagation

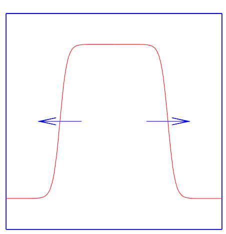
Travelling wave solutions $U(z)$ $(z = x - ct)$ satisfy

$$\begin{aligned} DU'' + cU' + f(U) &= 0 \\ \Rightarrow \left[\tfrac{1}{2}DU'^2\right]_{-\infty}^{+\infty} + c\int_{-\infty}^{+\infty} U'^2 dz + \int_{-\infty}^{+\infty} f(U)U'dz &= 0 \end{aligned}$$

We know that $U'(\pm\infty) = 0$. Therefore for a wave front with $U(-\infty) = u_1$ and $U(+\infty) = u_3$, c has the same sign as $-\int_{u_1}^{u_3} f(U)dU$.

For the spruce budworm model, this can be used to predict whether a local outbreak will die out or spread.


Outbreak dies out


Outbreak spreads

3.3 Existence of Travelling Waves

Theorem [Fife & McLeod, 1977]. Consider the equation $\partial u/\partial t = D\,\partial^2 u/\partial x^2 + f(u)$ with $f(u_1) = f(u_2) = f(u_3) = 0$, $f'(u_1) < 0$, $f'(u_2) > 0$, $f'(u_3) < 0$. This equation has a travelling wave solution $u(x,t) = U(x-ct)$ with $U(-\infty) = u_1$ and $U(+\infty) = u_3$ for exactly one value of the wave speed c.

A proof of this theorem is in the supplementary material.

Reference:

Fife, P.C. & McLeod, J.B. 1977 The approach of solutions of nonlinear diffusion equations to travelling front solutions. *Arch. Rat. Mech. Anal.* 65, 335-361.

There is no general result on the *value* of the unique wave speed for a reaction-diffusion equation with bistable kinetics.

4 Periodic Travelling Waves

4.1 A Model for Predator-Prey Interactions

$$\boxed{\text{predators}}$$

$$\partial p/\partial t = \underbrace{D_p \nabla^2 p}_{\text{dispersal}} + \underbrace{akph/(1+kh)}_{\text{benefit from predation}} - \underbrace{bp}_{\text{death}}$$

$$\boxed{\text{prey}}$$

$$\partial h/\partial t = \underbrace{D_h \nabla^2 h}_{\text{dispersal}} + \underbrace{rh(1-h/h_0)}_{\text{intrinsic birth \& death}} - \underbrace{ckph/(1+kh)}_{\text{predation}}$$

4.1.1 Predator-Prey Kinetics

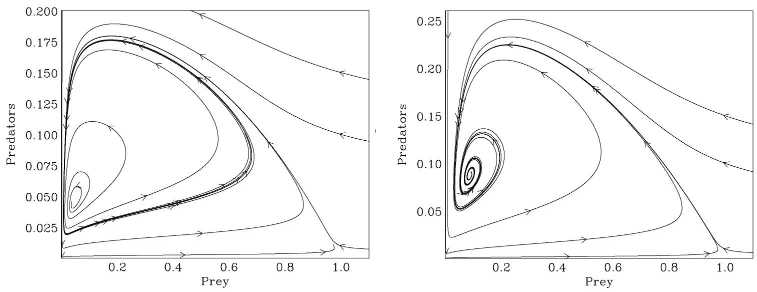
For some parameters, the kinetic ODEs have a stable coexistence steady state (left-hand phase plane). For other parameters, the coexistence steady state is unstable, and there is a stable limit cycle (right-hand phase plane).

$$\boxed{\text{predators}}$$

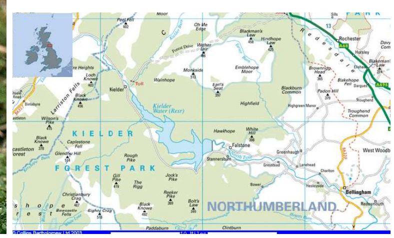
$$\partial p/\partial t = akph/(1+kh) - bp$$

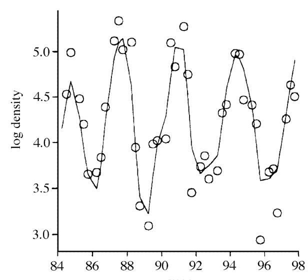
$$\boxed{\text{prey}}$$

$$\partial h/\partial t = rh(1-h/h_0) - ckph/(1+kh)$$



4.1.2 Example of a Cyclic Population

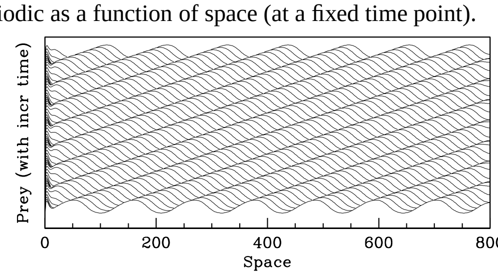




Field voles in Kielder Forest are cyclic (period 4 years). Spatiotemporal field data shows that the cycles are spatially organised into a periodic travelling wave

4.2 What is a Periodic Travelling Wave?

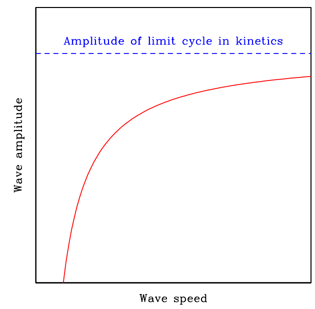
A periodic travelling wave is an oscillatory solution moving with constant shape and speed. It is periodic as a function of space (at a fixed time point).



Speed = space period/time period

4.2.1 The Periodic Travelling Wave Family

Theorem [Kopell & Howard, 1973]. Any oscillatory reaction-diffusion system has a one-parameter family of periodic travelling waves.



Reference: Kopell, N. & Howard, L.N. 1973 Plane wave solutions to reaction-diffusion equations. *Stud. Appl. Math.* 52, 291-328.

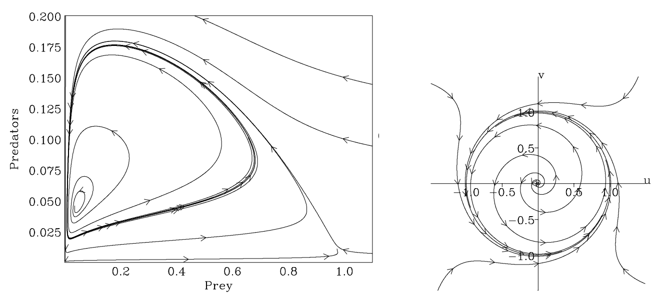
4.3 λ–ω Equations

Mathematical analysis is not possible for the predator-prey equations. Instead we consider a simpler example known as the λ–ω equations:

$$\begin{aligned} u_t &= u_{xx} + \lambda(r)u - \omega(r)v \\ v_t &= v_{xx} + \omega(r)u + \lambda(r)v \end{aligned}$$

$$\text{where} \quad \begin{aligned} \lambda(r) &= 1 - r^2 \\ \omega(r) &= \omega_0 + \omega_1 r^2. \end{aligned}$$

Typical phase planes of the predator-prey and λ–ω kinetics are:



The periodic travelling wave family is

$$\begin{aligned} u &= R\ \cos\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right] \\ v &= R\ \sin\left[\omega(R)t \pm \sqrt{\lambda(R)}x\right] \end{aligned}$$

4.3.1 λ–ω Equations in Polar Coordinates

λ–ω equations are simplified by working with $r = \sqrt{u^2+v^2}$ and $\theta = \tan^{-1}(v/u)$, giving

$$\begin{aligned} r_t &= r_{xx} - r\theta_x^2 + r(1-r^2) \\ \theta_t &= \theta_{xx} + 2r_x\theta_x/r + \omega_0 - \omega_1 r^2 . \end{aligned}$$

The periodic travelling waves are

$$r = R \qquad \theta = \pm\sqrt{\lambda(R)}x + \omega(R)t$$

which have

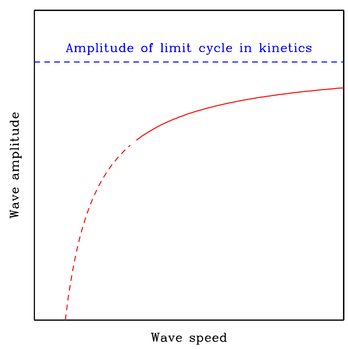
$$\text{wavelength} = \frac{2\pi}{\sqrt{\lambda(R)}} \quad \text{time period} = \frac{2\pi}{|\omega(R)|} \quad \text{speed} = \frac{|\omega(R)|}{\sqrt{\lambda(R)}} .$$

4.4 Stability in the Periodic Travelling Wave Family

Some members of the periodic travelling wave family are stable as solutions of the partial differential equations, while others are unstable.

For the λ–ω system, the stability condition is

$$4\lambda(R)\left[1+\omega'(R)^2/\lambda'(R)^2\right] + R\lambda'(R) \le 0 .$$



This condition is hard to derive in general (see Kopell & Howard, 1973). For the special case of $\omega(.)$ constant, the derivation is given in the supplementary material.

4.5 Extensions: Wave Generation and Spiral Waves

4.5.1 Generation of Periodic Travelling Waves

One way in which periodic travelling waves develop in the λ–ω equations is via the local perturbation of the unstable equilibrium $u = v = 0$. This process selects a particular wave amplitude, that can be calculated explicitly. Details of this are given in the supplementary material.

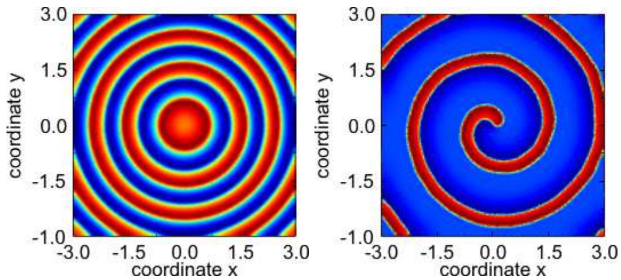
For the predator-prey model, a corresponding process is the generation of periodic travelling waves by the invasion of a prey population by predators. For details of this, see

Sherratt, J.A., Lewis, M.A. & Fowler, A.C. 1995 Ecological chaos in the wake of invasion. *Proc. Natl. Acad. Sci. USA* 92, 2524-2528.

(This paper can be downloaded from `www.ma.hw.ac.uk/~jas/publications.html`)

4.5.2 Extension to Two Space Dimensions: Spiral Waves

Periodic travelling waves are important in their own right, and also as the one-dimensional equivalents of target patterns and spiral waves.



A brief introduction to spiral waves in the λ–ω equations is given in the supplementary material.