- Derivation of the logistic equation with time delay

So far we have assumed that $\frac{dN}{dt}$, the rate of change of population size depends on the instantaneous population size $N(t)$. However we come across in which $\frac{dN}{dt}$ also depends on popⁿ size at earlier instance of time ie on $N(t-s)$, $s \geq 0$.

The effect of $N(t-s)$ on $\frac{dN}{dt}$ depends on s, the time elapsed and is measured by a positive weight function $K(s)$.

Now the weighted average of all earlier popⁿ size on $\frac{dN}{dt}$ is given by

$$\frac{\int_0^\infty N(t-s)\,K(s)\,ds}{\int_0^\infty K(s)\,ds} \quad \text{---} (1)$$

We shall always normalise the weight function $K(s)$ so that

$$\int_0^\infty K(s)\,ds = 1 \quad \text{---} (2)$$

Such that the influence of all earlier popⁿ sizes on $N(t)$ depends on $\int_0^\infty N(t-s)\,K(s)\,ds$

$$= \int_{-\infty}^{t} K(t-s)\,N(s)\,ds \quad \text{---} (3)$$

Thus the logistic equation with time delay effect become

This is an integro-differential equation for determining $N(t)$. In general, if $N(t)$ is specified for $-\infty < t < 0$ then the relation (4) enables us to obtain $N(t)$ for $t > 0$.

If $K(s) = \delta(s)$, the Dirac Delta function, then (4) becomes

$$\frac{dN}{dt} = aN - (b+c)N^2(t) \quad —(6)$$

If $K(s) = \delta(t-\tau)$, then (4) becomes

$$\frac{dN}{dt} = aN - bN^2 - cN(t)N(t-\tau) \quad —(7)$$

This is called the delay-differential equation for solving $N(t)$. If $N(t)$ is specified for time $[0, \tau]$, then one can use (7) to find $N(t)$ for $t > \tau$. This equation arises due to discrete time lag τ whereas ~~as~~ the equation (4) or (5) is due to the continuous time lag.

§ Biological mechanism responsible for time delay:

One possible biological mechanism which accounts for time lag is age-structure. The response to growth may be delayed by

(i) maturation period, for example, the period required for Larvae to become adult.

(ii) gestation period, the ~~pe~~ time required ~~to~~ by the predators to digest prey (food).

(iii) regeneration period, the time taken by plants

Another possible biological mechanism results from self poisoning of environment by living organism caused by emission of metabolic waste products of the system. The pollutants continue to accumulate over a period of time.

§ The solution of the logistic equation in special case:

In general, the equation (4) or (5) cannot be solved analytically. However, we deal with the case when any physical phenomenon starts with $=0$ and and $K(s)=$ constant. Then equation (5) gives

$$\frac{dN}{dt} = aN - bN^2 - CN\int_0^t N(s)\,ds \quad —(8) \qquad \left[\begin{array}{l} K(t-s) = \text{constant} \\ \int_{-\infty}^{0} N(s)\,ds = 0 \\ C = cK(t-s) = \text{c.c} \end{array}\right.$$

Taking $M(t) = \int_0^t N(s)\,ds$ —(9),

we have from (8),

$$\frac{d^2M}{dt^2} = a\frac{dM}{dt} - b\left(\frac{dM}{dt}\right)^2 - CM\frac{dM}{dt}. \quad —(10)$$

Multiplying both sides of (10) by e^{bM}, we get

$$e^{bM}\frac{d^2M}{dt^2} + be^{bM}\left(\frac{dM}{dt}\right)^2 = e^{bM}\left[a\frac{dM}{dt} - CM\frac{dM}{dt}\right]$$

$$\text{or}\quad \frac{d}{dt}\left(e^{bM}\frac{dM}{dt}\right) = \frac{d}{dt}\left\{e^{bM}\left(\frac{a}{b}+\frac{C}{b^2}-\frac{C}{b}M\right)\right\} \quad —(11)$$

Integrating between 0 and t, we have

$$e^{bM}\frac{dM}{dt} - e^{bM(0)}\left.\frac{dM}{dt}\right|_{t=0} = e^{bM}\left(\frac{a}{b}+\frac{C}{b^2}-\frac{C}{b}M\right) - e^{bM(0)}$$

Since $M(0)=0$, $\left.\frac{dM}{dt}\right|_{t=0} = N(0) = N_0$, we have

$$e^{bM}\frac{dM}{dt} \ldots e^{bM}\left(\frac{a}{b}+\frac{C}{b^2}-\frac{C}{b}M\right) - \left(\frac{a}{b}+\frac{C}{b^2}\right)$$

$$N(t) = \frac{dM}{dt} = \left(\frac{a}{b} + \frac{c}{b^2} - \frac{c}{b}M\right) - \left\{\left(\frac{a}{b} + \frac{c}{b^2}\right) - N_0\right\} e^{-bM} \quad \text{—— (14)}$$

a. $$\frac{dM}{dt} = F(M) \text{ (say)}$$

$$t = \int_0^M \frac{dM}{F(M)} \quad \text{—— (15)}$$

The relation (14) and (15) gives N and t as function of M so that, together they represent a parametric solution of the equation (8), the parameter being M.

Since $F(0) = N(0) > 0$ and $F(\infty) < 0$, $F(M)$ vanishes for some 've' finite M and for this value of M from (8) and (14) both $N(t)$ and $\frac{dN}{dt}$ vanish so that the population becomes extinct as $t \to \infty$.

From (14), $$\frac{dN}{dt} = F'(M)\frac{dM}{dt}$$

$$= \left\{\left(N_0 - \frac{a}{b} - \frac{c}{b^2}\right)\left(-be^{-bM}\right) - \frac{c}{b}\right\} N(t)$$

$$= \left\{\left(N_0 - \frac{a}{b}\right)\left(-be^{-bM}\right) - \frac{c}{b}\left(1 - e^{-bM}\right)\right\} N(t) \quad \text{—— (16)}$$

Now if $N(0) \geq a/b$, $\frac{dN}{dt} < 0$ and the pop^n steadily decreases to zero. If $N(0) < a/b$ then

$$\left(\frac{dN}{dt}\right)_{t=0} = \left(\frac{dN}{dt}\right)_{M=0} = -b\left(N(0) - \frac{a}{b}\right) > 0 \quad \text{—— (17)}$$

so that the population initially increases and reaches a maximum when

$$M_{max} = \frac{1}{b} \ln \left| \frac{c + ab - b^2 N_0}{c} \right| \quad \text{—— (18)} \quad \left[\begin{array}{l}\text{obtained from (16)} \\ \text{putting } \frac{dN}{dt} = 0\end{array}\right]$$

Then the

Thus the maximum pop^n is

$$N_{max} = \left(\frac{a}{b} + \frac{c}{b^2} - \frac{c}{b} M_{max}\right) - \left\{\frac{a}{b} + \frac{c}{b^2} - N_0\right\} e^{-bM_{max}} \quad \left[\text{From (14)}\right.$$

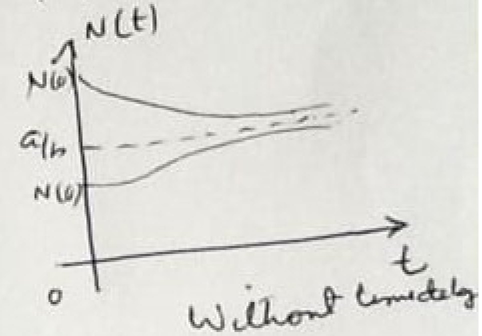
$$= \frac{a}{b} + \frac{c}{b^2} - \frac{c}{b} M_{max} - \left\{\frac{ab + c - N_0 b^2}{b^2}\right\}\left(\frac{c}{ab + c - N_0 b^2}\right)$$

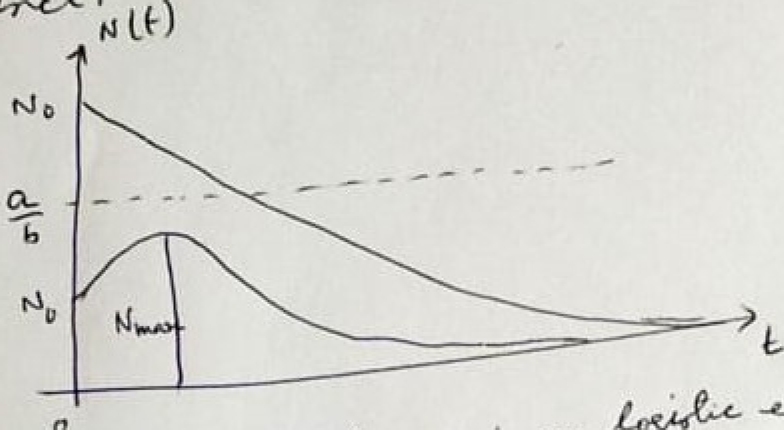
$$= \frac{a}{b} + \frac{c}{b^2} - \frac{c}{b} M_{max} - \frac{c}{b^2}$$

$$N_{max} = \frac{a}{b} - \frac{c}{b} \cdot \frac{1}{b} \ln\left|\frac{c + ab - N_0 b^2}{c}\right| < \frac{a}{b} \quad \text{—(19)}$$

After this the pop^n declines and tends to zero.

In either case ($N_0 \geq \frac{a}{b}$ or $N_0 < \frac{a}{b}$) the population tends to extinct.





The effect of time delay in a logistic equation.

[S]tability of equilibrium position for a logistic model [w]ith general delay function

[W]e consider the delay equation in the last article i.e

$$\left.\begin{aligned} \frac{dN}{dt} &= aN - bN^2 - cN\int_0^\infty N(t-s)K(s)\,ds \\ \text{or } \frac{dN}{dt} &= aN - bN^2 - cN\int_{-\infty}^{t} K(t-s)\,N(s)\,ds \end{aligned}\right\} \quad \text{—(1)}$$

[I]n general, we can not solve analytically the equation for [a] general delay in $K(s)$. So we try to find the equilibrium solution of the equation (1).

If $N(t) = N_*$ be such solution, then

$$0 = aN_* - bN_*^2 - cN_*\int_0^\infty N_* K(s)\,ds$$

$$0 = N_*(a - bN_* - cN_*) \quad \text{—(2)}$$

Here $N_* = 0$ is trivial solution and it is unstable.

The nontrivial solution is $N_* = \dfrac{a}{b+c} = d$ (say) —(3)

To discuss the local stability of the equilibrium state N_* we substitute

$$N(t) = N_* + x(t) \quad \text{—(4)}$$

into equation(1) and we get

$$\frac{dx}{dt} = a(N_* + x) - b(N_* + x)^2 - c(N_*+x)\int_0^\infty (N_* + x(t-s))\,K(s)\,ds \quad \text{—(5)}$$

$$ax - 2bN_*x - cN_*x$$

$$\text{or } \frac{dx}{dt} = ax - \cancel{2bx} - c\int_0^\infty x\int_0^\infty x(t-s)$$
$$- cN_*\int_0^\infty K(s)\,x(t-s)\,ds + aN_* - bN_*^2 - cN_*^2 + O(2) \quad \text{—(6)}$$

ie $$\frac{dx}{dt} = ax - 2bN_* x - cN_* x - cN_* \int_0^\infty K(s)\, x(t-s)\, ds \quad -(6)$$

Let us suppose that the solution be of the type $x(t) = Ae^{\lambda t}$

Then (6) gives

~~$D(\lambda) = \lambda + b$~~

$$\lambda = \underbrace{a - bN_* - cN_*}_{=0} - bN_* - cN_* K^*(\lambda), \quad K^*(\lambda) = \int_0^\infty e^{-\lambda s} K(s)\, ds$$

a Laplace Transform of $K(s)$

$$D(\lambda) \equiv \lambda + bN_* + cN_* K^*(\lambda) = 0 \quad — \quad (7)$$

If we assume that $b > c$, then since $|K^*(\lambda)| \leq 1$ for $\mathrm{Re}\,\lambda \geq 0$

we find that

$$|\lambda + bN_*| \geq bN_* > |cN_* K^*(\lambda)| \text{ for } \mathrm{Re}\,\lambda \geq 0.$$

Then $D(\lambda)$ cannot vanish for $\mathrm{Re}\,\lambda \geq 0$.

$\therefore D(\lambda) = 0$ can have roots with negative real parts of λ.

Hence if $b > c$, the equilibrium point N_* is asymptotically stable. If there is no delay, then the equilibrium pt. is asymptotically stable.

If $b < c$, then we can not say anything about the stability unless we know more about the ~~$K^*(\lambda)$~~ $K^*(\lambda)$.

§ Stability of logistic model with discrete time delay:

Let the discrete time lag be τ, then the logistic model takes the following form:

$$\frac{dN}{dt} = aN - bN^2 - cN\,N(t-\tau) \quad \text{——} \quad (1)$$

The equilibrium position is still as earlier positions i.e

$N_* = 0, \quad N_* = \frac{a}{b+c}$.

Proceeding as before, we get the characteristic equation as

$$\lambda + N_*(b + c e^{-\lambda\tau}) = 0$$

i.e $$\lambda + \frac{a}{b+c}(b + c e^{-\lambda\tau}) = 0 \quad \text{——} \quad (2)$$

This can also be obtained from the fact that, in this case, the delay f^n $K(s) = \delta(s-\tau)$ whose Laplace transform is $e^{-\lambda\tau}$.

Equation (2), can be written as

$$\lambda + k_1 + k_2 e^{-\lambda} = 0 \quad \text{——} \quad (3)$$

where $k_1 = \frac{ab}{b+c}$, $k_2 = \frac{ac}{b+c}$ and $\tau = 1$ is considered for simpli the sake of simplicity.

(3) can also be written as

$$z + ke^{-z} = 0 \quad \text{——} \quad (4)$$

where $z = \lambda + k_1$, $k = k_2 e^{k_1}$

If $z = \mu + i\nu$ is the root of (4), then

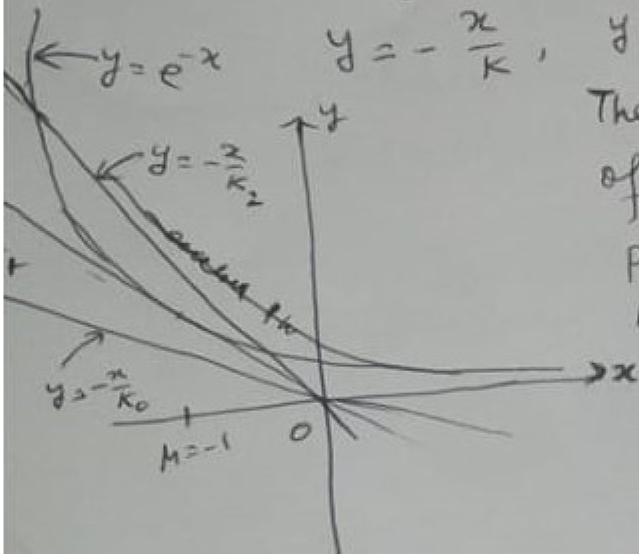
$$\mu + i\nu + Ke^{-(\mu+i\nu)} = 0$$

ie $\mu + Ke^{-\mu}\cos\nu = 0, \quad \nu - Ke^{-\mu}\sin\nu = 0$ —(5)

om (5), we see that if $\mu+i\nu$ satisfies (4), $\mu-i\nu$ so satisfies (4), So that the complex roots of (4) ccur in conjugate pair.

We shall now investigate the existence of real roots for which $\nu=0$ and $\mu + Ke^{-\mu} = 0$ — (6)

The roots are obtained as the abscissae of the pt. of intersection of the curves $y = -\frac{x}{K}$, $y = e^{-x}$ — (7) [from (6)]



The two curves will have two point of intersection if $K=K_2$, two coincident point of intersection if $K=K_1$ and no point of intersection at $K=K_0$.

For coincident point, we must have a double root of the eq (6).

ie $\mu + Ke^{-\mu} = 0$

and $1 - Ke^{-\mu} = 0 \Rightarrow e^{-\mu} = \frac{1}{K}$

So, $\mu = -1$. So that $K = \frac{1}{e}$ —(8)

Thus if $K > \frac{1}{e}$, (6) has two negative real roots,
if $K < \frac{1}{e}$, (6) has no negative real roots,
if $K = \frac{1}{e}$, (6) has one negative real root.

(Here $K_0 < K_1 < K_2$).

Now we examine the existence of complex roots with $\nu \neq 0$. From eqs (5), we have

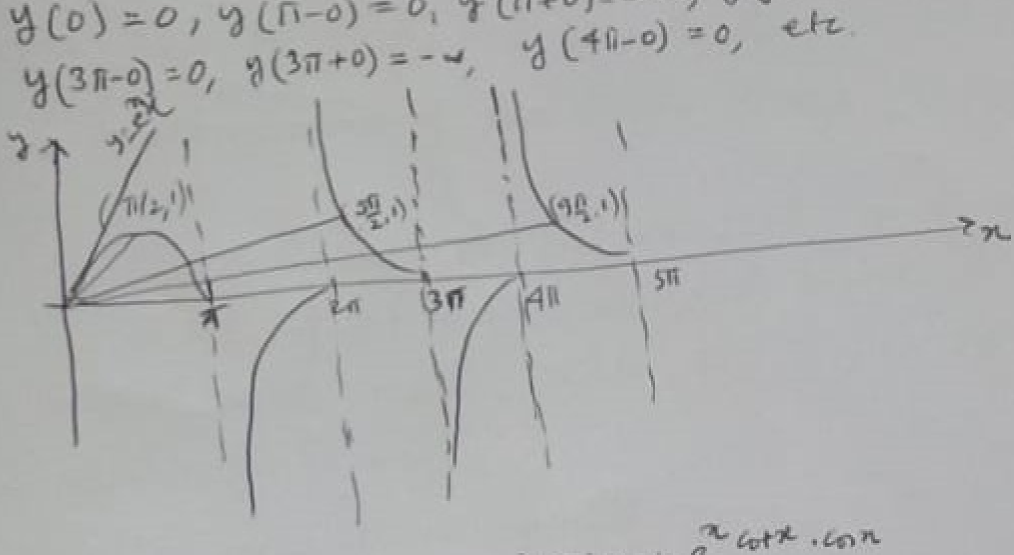
$$\left.\begin{aligned} \mu &= -\nu \cot\nu \\ \frac{\nu}{K} &= e^{\nu\cot\nu} \cdot \sin\nu \end{aligned}\right\} \quad \text{——} (9)$$

To find the roots of the 2nd equation of (9), we first find the abscissae of the points of intersection of the curve

$$y = \frac{x}{K}, \quad y = e^{x\cot x} \cdot \sin x \quad \text{—}(10)$$

Since x satisfies both the equation in (10), $-x$ also satisfies them, and hence we need to find only the +ve values of x. The graph of the 2nd curve is obtained by noting that

$$\left.\begin{aligned} &y(0)=0,\ y(\pi-0)=0,\ y(\pi+0)=-\infty,\ y(2\pi-0)=0,\ y(2\pi+0)=-\infty \\ &y(3\pi-0)=0,\ y(3\pi+0)=-\infty,\ y(4\pi-0)=0, \text{ etc.} \end{aligned}\right\} (11)$$



$$\frac{dy}{dx} = e^{x\cot x} \cdot (\cot x - x\,\mathrm{cosec}^2 x)\sin x + e^{x\cot x} \cdot \cos x$$

$$\left.\frac{dy}{dx}\right|_{(0,0)} = e$$

The tangent to the curve at the origin is $y = ex$.
From the above figure the following deduction can be made:

From the figure, the following deductions can be made:

i) If $\frac{1}{k} > e$ or $k < \frac{1}{e}$, the straight line $y = \frac{x}{k}$ cuts the 2nd curve of (10) at pts for which x lies in the intervals $(2\pi, \frac{5\pi}{2})$, $(4\pi, \frac{9\pi}{2})$, ...
for all of which $-x\cot x < 0$.

ii) If $\frac{1}{k} < e$ but $\frac{1}{k} > \frac{2}{\pi}$ ie if $\frac{1}{e} < k < \frac{\pi}{2}$ then one additional pt lies in the interval $(0, \pi/2)$ for which $-x \cot x$ still negative.

iii) If $\pi/2 < k < \frac{5\pi}{2}$, then the 1st point of intersection lies between $(\pi/2, \pi)$ for which $-x\cot x$ is '+ve' and $\forall$ other pts of intersection it is '-ve'.

(iv) If $\frac{5\pi}{2} < k < \frac{9\pi}{2}$, then for ~~pt~~ the 1st two pts of intersection $-x\cot x > 0$ and for remaining pts., $-x\cot x < 0$ and so on.

Now from (9), when $-x\cot x > 0$ for the pts of intersection the real parts of the roots of eqs (2)/(3)/(4) is '+ve'.

From this discussion it follows that as long as ~~$\frac{1}{e}$~~ $k < \frac{\pi}{2}$, all the roots of (3) are real and ~~no~~ '-ve' or complex with '-ve' real parts. When $k > \frac{\pi}{2}$, it has roots with '+ve' real parts only.

We now consider some special cases:

(1) Let $b = 0$ in eq (1). Then the logistic model with discrete delay reduces to

$$\frac{dN}{dt} = aN(t) - cN(t)N(t-\tau) \quad \text{--- (12)}$$

then equation (3) reduces to $\quad [\tau = 1$

$$\lambda + ae^{-\lambda} = 0 \quad \text{--- (13)}$$

The equilibrium position is $N_* = \frac{a}{c}$ which is unstable if $a > \pi/2$ and locally asymptotically stable if $a < \pi/2$

2) If $b \neq 0$ in (1) so that the basic equation is

$$\frac{dN}{dt} = aN(t) - bN(t)^2 - cN(t)N(t-1), \quad \text{—— (14)}$$

The characteristic eq^n is:

$$z + Ke^{-z} = 0$$

with $z = \lambda + K_1$, $K = K_2 e^{K_1}$, $K_1 = \frac{ab}{b+c}$, $K_2 = \frac{ac}{b+c}$, —(15)

If $K < \pi/2$, all the values of z have '-ve' real parts and therefore all values of λ also have '-ve' real parts.
Hence equilibrium position $N_* = \frac{a}{b+c}$ is asymptotically stable if $K < \frac{\pi}{2}$ ie if

$$\left(\frac{ac}{b+c}\right) e^{\frac{ab}{b+c}} < \frac{\pi}{2} \quad \text{— (16)}$$

However, from (15) it follows that when z has '+ve' real part, λ may have '+ve' or '-ve' real part. In fact,

$$Re\,\lambda = -x\cot x - K_1 \quad \text{—— (17)}$$

where x corresponds to a pt. of intersection of the st. line and the curve as shown in the above figure.
The marginal case of that separate the stable & unstable states arises when

$$-x\cot x - K_1 = 0 \quad \text{———— (18)}$$

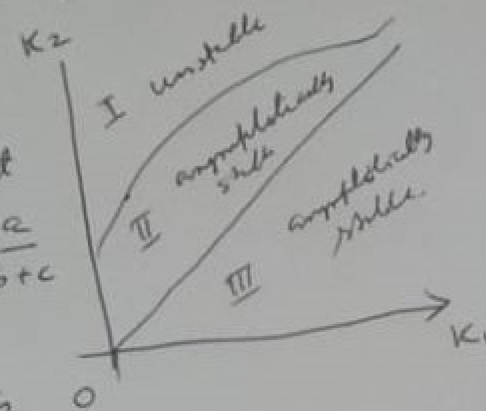
Again from (9),

$$\begin{aligned} x &= Ke^{x\cot x} \cdot \sin x \\ &= Ke^{-K_1} \cdot \sin x \\ &= K_2 e^{K_1} \cdot e^{-K_1} \sin x \quad \text{———— (19)} \\ &= K_2 \sin x \end{aligned}$$

~~when~~ so that $K_1 = -x\cot x, \quad K_2 = \dfrac{x}{\sin x} \qquad (\pi/2 < x < \pi)$ —(20)

The eq (26) can be regarded as the parametric equations of a curve in K_1K_2-plane that separates the region of stable and unstable equilibrium.

As $x \to \pi$, $K_1 \to \infty$, $K_2 \to \infty$ so that $K_1/K_2 = 1$ so the curves ultimately parallel to the straight line $K_1 = K_2$.



Finally, one can conclude that the equilibrium position $N^* = \frac{a}{b+c}$ is asymptotically stable if $K_1 > K_2$ i.e. if $b > c$ and this corresponds to the region III.

Reaction - Diffusion Equations

Partial differential equations (PDE) arises in biological systems for modelling the change of quantity continuously with respect to time as well as spacial location. Movement of cells, animals, and living organisms are in the study of the biological systems. The assumption of random diffusion with pop^n growth leads to 2nd order PDE's known as reaction-diffusion equations. The minimum spatial region needed for population survival is an another important classical problem in spatial ecology. The minimum region is sometimes referred to as the critical patch size. Pattern formation is another important problem in biologic application arises in the Reaction-diffusion equation due to the spatial variation.

Derivation of diffusion equation:

Let $N(x;t)$ represent the density of pop^n at time $t \in [0,$ and $x \in \Omega$. The domain Ω may be finite or infinite subset of $\mathbb{R}, \mathbb{R}^2, \mathbb{R}^3$. A simple 1-D diffusion equation has the form

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} \quad \text{——} \quad (1)$$

If $f(N)$ be the pop^n growth rate, then the respective reaction-diffusion equation is:

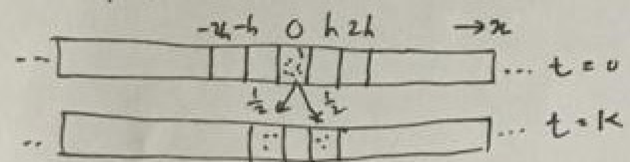
$$\frac{\partial N}{\partial t} = f(N) + D\frac{\partial^2 N}{\partial x^2} \quad \text{——} \quad (2)$$

We describe the derivation of diffusion eq^n (1).

The substance which are the population here spread due to the diffusion according Fick's law moving from areas of high concentration to low concentrat

Brownian motion is the motion of particles of pollen in water named after British Botanist Robert Brown. The several pollen particle concentrated in a region of the liquid collide with water molecule due the hits which comes at random intervals and from all direction. This causes the spread out of the particles which is diffusion.

To derive the diffusion eq(1), we assume that at time $t = t + K$ each particle moves left or right with equal (unbiased) probability $P/2$, or stays in the same place with probability $1 - p$.



The expected concentration at $t = t + K$ is given by:

$$N(x, t+K) = \frac{p}{2} N(x-h, t) + \frac{p}{2} N(x+h, t) + (1-p) N(x,t) \quad -(3)$$

Subtracting $N(x,t)$ from both sides we have

$$N(x, t+K) - N(x,t) = \frac{p}{2} N(x-h, t) + \frac{p}{2} N(x+h,t) + (1-p) N(x,t) - N(x,t)$$

$$\text{or.}\quad K.\ \frac{N(x, t+K) - N(x,t)}{K} = \frac{p}{2} h^2 \left[\{ N(x-h,t) - 2N(x,t) + N(x+h,t) \} \right.$$

Now the left hand side is the discretization of $K \frac{\partial N}{\partial t}$ and the RHS is that of $\frac{ph^2}{2} \frac{\partial^2 N}{\partial x^2}$. when both h & K tend to 0

Now in the above figure $p = 1$ is considered. Then expres (4) reduces to

$$K \frac{\partial N}{\partial t} = \frac{h^2}{2} \frac{\partial^2 N}{\partial x^2}$$

$$\text{or} \quad \frac{\partial N}{\partial t} = D \frac{\partial^2 N}{\partial x^2} \quad -(5)$$

where D is $\frac{h^2}{2K}$, a constant known as diffusion coeff.

The diffusion equation in 2D and 3D have the following form:

$$\left.\begin{aligned}\frac{\partial N}{\partial t} &= D\left(\frac{\partial^2 N}{\partial x^2}+\frac{\partial^2 N}{\partial y^2}\right)\\ \text{and}\quad \frac{\partial N}{\partial t} &= D\left(\frac{\partial^2 N}{\partial x^2}+\frac{\partial^2 N}{\partial y^2}+\frac{\partial^2 N}{\partial z^2}\right)\end{aligned}\right\} \quad -(6)$$

where N is function of x, y, t and x, y, z, t respectively.

In addition to the diff. eq. above we need their behaviour at the boundary or at when $x \to \pm\infty$ and initial condition to solve them. Boundary condition may be Cauchy or Neumann type. The eqn can be solve using Fourier transform and then the solution of (5) is given by

$$N(x,t) = \frac{N_0}{2\sqrt{D\pi t}} \exp\left(-\frac{(x-x_0)^2}{4Dt}\right) \quad -(7)$$

where $N(x,0) = N_0 = N_0\,\delta(x-x_0)$, δ is the Dirac Delta f^n and $N(x,t) \to 0$ as $x \to \pm\infty$.

Consider the eqn with exponential growth of the pop^n and random diffusion over a finite spatial domain $(0, L)$

i.e.

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + f(N), \quad x \in (0,L),\ t \in (0,\infty) \quad -(8)$$

$$N(x,0) = N_0(x), \quad x \in [0,L]$$
$$N(0,t) = 0 = N(L,t), \quad t \in (0,\infty)$$

If $f(N) = rN$ then the change of variable gives rise to an equation

$$\frac{\partial P}{\partial t} = D\frac{\partial^2 P}{\partial x^2} \quad \text{where } P(x,t) = N(x,t)e^{-rt} \quad -(9)$$

I.C. $P(x,0) = N_0(x)$,

$$P(0,t) = 0 = P(L,t)$$

Then the solution is

$$N(x,t) = \sum_{n=1}^{\infty} B_n \sin\left(\frac{n\pi x}{L}\right)\exp\left(rt - D\left(\frac{n\pi}{L}\right)^2 t\right) \quad -($$

$$2\int^{L} N_0(x)\sin\left(\frac{n\pi x}{L}\right)dx, \quad n=1,2,\dots$$

The equations (5) & (8) are linear PDE whose explicit sol^n are found above.

For nonlinear PDE on more complicated domains, explicit solution cannot be found. So, the method will be different to study the solution behaviour.

§ Sufficient condition for unique bounded solution:

We now state some sufficient conditions on the initial condition $N_0(x)$ and growth rate function $f(N)$ that guarantee a unique bounded solution exists to the reaction-diffusion equation of the form (2) or (8).

Suppose that $N_0(x)$ is continuous for $x \in \bar{\Omega}$ or $x \in \mathbb{R}$.

In addition suppose there exists constants a and b such that $a \le N_0(x) \le b$, for $x \in \bar{\Omega}$, $f(a) \ge 0$, $f(b) \le 0$ and that f is uniformly Lipschitz continuous, that is, there exist a constant c such that

$$|f(u)-f(v)| \le c|u-v|$$

for all values of $u, v \in [a,b]$. Then ~~for~~ for Cauchy problem the IBVP with homogeneous Dirichlet or Neumann boundary conditions there exists a unique ~~boundary condition~~ bounded solution $N(x,t)$ ~~$\in [a,b]$~~ for $x \in \Omega$ or $x \in \mathbb{R}$ and $t \in (0,\infty)$. In addition, the solution $N(x,t) \in [a,b]$

Ex^n Consider the Cauchy problem:

$$\frac{\partial N}{\partial t} = N(1-N) + D\frac{\partial^2 N}{\partial x^2}, \quad x \in \mathbb{R}, \; t \in (0,\infty)$$
$$N(x,0) = N_0(x), \; x \in \mathbb{R}$$

has a unique bounded solution $N(x,t) \in [0,1]$.

Stability analysis of Reaction-diffusion equation are more complicated that ODE as instabilities may arise in the spatial domain. However the stability of solution of PDE can be defined in a manner similar to ODE:

<u>Definition</u>: Let $N(x,t)$ be a solution of an IVP or IBVP satisfying

$$\frac{\partial N}{\partial t} = f(N) + D\frac{\partial^2 N}{\partial x^2}, \quad x \in \Omega, \ t \in (0,\infty)$$

$$N(x,0) = N_0(x), \quad x \in \Omega$$

and for finite domain Ω, B.C. are specified on $\partial\Omega$.

Then $N(x,t)$ is said to stable solution of the IVP or IBVP if, given any $\varepsilon > 0$, $\exists\ \delta > 0$ such that whenever

$$\Phi(x,0) = \Phi_0(x) \text{ satisfies}$$

$$\| N_0(\cdot) - \Phi_0(\cdot) \| < \delta$$

the solution $\Phi(x,t)$ to the same IVP or IBVP with initial condition $\Phi_0(x)$ satisfies

$$\cancel{\| N_0 t}$$

$$\| N_0(\cdot, t) - \Phi(\cdot, t) \| < \varepsilon$$

for all $t > 0$. If not, the solution $N(x,t)$ is unstable.

The solution $N(x,t)$ is said to be locally asymptotic stable if it is stable and in addition,

$$\| N(\cdot, t) - \Phi(\cdot, t) \| \to 0,$$

as $t \to \infty$.

Here the norm is over x variable. For continuous f^n fe

$$\| f(\cdot) \| = \sup_{x \in \bar{\Omega}} f(x).$$

Critical Path Size:

A reaction-diffusion equation is used to estimate the minimum size of the spatial domain needed for population survival. This minimum size is defined as the critical path size.

Phytoplankton are microscopic plants living in the ocean which represent the bottom of the marine food chain. The model of phytoplankton proposed by Kierstead & Slobodkin (1953) was used to determine the critical path size. The proposed model with exponential growth is given by

$$\left.\begin{aligned} &\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} + rN, \quad x \in (0,L), \; t \in (0,\infty) \\ &\text{I.C. } N(x,0) = N_0(x), \; x \in [0,L] \\ &\text{B.C. } N(0,t) = 0 = N(L,t), \; t \in (0,\infty) \end{aligned}\right\} \quad (1)$$

where r, D are +ve constant and $N_0(x)$ is continuous f^n in $[0,L]$.

The solution of (1) is

$$N(x,t) = \sum_{n=1}^{\infty} B_n \sin\left(\frac{n\pi x}{L}\right) \exp\left(rt - D\left(\frac{n\pi}{L}\right)^2 t\right), \quad (2)$$

where
$$B_n = \frac{2}{L}\int_0^L N_0(x) \sin\left(\frac{n\pi x}{L}\right) dx$$

are decreasing coefficient as $n \to \infty$.

From the B.C. above we have assumed that the population cannot survive outside the domain $[0,L]$.

The question posed by Kierstead and Slobodkin that what is the minimum size of the spatial domain so that the plankton pop^n survive.

Here from (2), $\|N(\cdot,t)\| = \sup_{x\in[0,L]} |N(x,t)| \le \sum_{n=1}^{\infty} \hat{B}_n \exp\left(\left[r - D\left(\frac{n\pi}{L}\right)^2\right]t\right)$, — (3)

where $\hat{B} = 2\hat{N}_0$, $\hat{N}_0 = \sup_{x\in[0,L]} |N_0(x)|$.

Thus the population extincts if

$$r - D\left(\frac{n\pi}{L}\right)^2 < 0 \quad \text{—— (4)}$$

as $\lim_{t\to\infty} \|N(\cdot,t)\| \to 0$.

For population extinction, the condition (4) must be satisfied for all n, in particular, for $n = 1$.

That if

$$r < D\left(\frac{\pi}{L}\right)^2 \quad \text{——— (5)}$$

The population will die out after a long time.

For survival of the plankton population, we must have

$$r \geq D\left(\frac{\pi}{L}\right)^2 \quad \text{—— (6)}$$

Condition (6) gives the minimum size of the domain which is called critical patch size (L_c)

is

$$L_c = \pi\sqrt{\frac{D}{r}} \quad \text{——— (7)}$$

The population size increases if $L > L_c$ and decrease if $L < L_c$. If $L = L_c$ the population stay constant.

Here the critical patch size is increases with the increase of the diffusion coefficient and the decrease of the growth rate r. This suggest that the steady state behaviour of the phytoplankton is determined by the relative strength of the diffusive and the reactive terms in (1).

§ Turing instability :

Turing's work in the field of morphogenesis of embryo has had a great impact. His work was published in the year 1952 titled "The chemical basis of morphogenesis", His works explain the origin of different pattern ~~of~~ of stripes in animals. He proposed the reaction-diffusion model for pattern formation. Diffusion was the sourse of instability that cause the pattern. The random diffusion was generally that to give rise to spatially homogeneous solution. However Turing's study result found the opposite effect. There are different biological application demonstrating the formation of pattern in space due to Turing instabilities.

The instability comes from the interaction of ~~or~~ reaction and diffusive terms that govern interacting chemical species that are diffusing within some spatial domain.

Definition of Patterns : Patterns are stable, time-independent, spatially heterogeneous solutions of a reaction-diffusion equation

Definition of Turing instability : An instability of ~~a~~ steady solution (also known as diffusion driven instability) is stable in the absence of diffusion, becomes unstable due to the presence of diffusion.

We consider two species which are two chemicals or morphogens that interact and diffuse. Let $N_1(x,t)$ and $N_2(x,t)$ be the densities at time t, and also satisfy the reaction-diffusion equation

$$\left.\begin{aligned} \frac{\partial N_1}{\partial t} &= f(N_1,N_2) + D_1 \frac{\partial^2 N_1}{\partial x^2} \\ \frac{\partial N_2}{\partial t} &= g(N_1,N_2) + D_2 \frac{\partial^2 N_2}{\partial x^2} \end{aligned}\right\} \quad \text{— (1)}$$

where D_1 and D_2 are the diffusion constants which are +ve'. The ~~xxxxma~~ domain Ω is finite and the boundary conditions are zero flux. i.e $\hat{n}\cdot\nabla(N_1,N_2)=0$.

We suppose that $\bar{N}_1$ and $\bar{N}_2$ are the equilibrium solution such that

$$f(\bar{N}_1,\bar{N}_2)=0, \quad g(N_1,N_2)=0 \quad \text{— (2)}$$

Also the above equilibrium solution is consistent with the zero flux boundary condition.

According to Turing: if the spatially homogeneous equilibrium $(\bar{N}_1,\bar{N}_2)$ is stable in the absence of diffusion but becomes unstable in the presence of diffusion, then spatially nonhomogeneous pattern may arise.

Thus the equilibrium $(\bar{N}_1,\bar{N}_2)$ is stable for the system

$$\left.\begin{aligned} \frac{dN_1}{dt} &= f(N_1,N_2) \\ \frac{dN_2}{dt} &= g(N_1,N_2) \end{aligned}\right\} \quad \text{— (3)}$$

Linearizing the system (3) about the equilibrium $(\bar{N}_1,\bar{N}_2)$ we have

$$\frac{d\vec{u}}{dt} = A\vec{u} \quad \text{— (4)}$$

where $\vec{u} = (u_1, u_2)^T = (N_1 - \bar{N}_1, N_2 - \bar{N}_2)^T$, $A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial N_1} & \frac{\partial f}{\partial N_2} \\ \frac{\partial g}{\partial N_1} & \frac{\partial g}{\partial N_2} \end{pmatrix}$

Since $(\bar{N}_1, \bar{N}_2)$ are stable solution, the Jacobean A has eigenvalues with negative real part and the linear solution approaches to zero iff $Tr(A) < 0$ and $\det A > 0$. ie equivalently

$$a_{11} + a_{22} < 0 \text{ and } a_{11}a_{22} - a_{21}a_{12} > 0 \quad \text{——} (5)$$

We consider equation (1). Then under the above perturbation the system reduces to

$$\frac{\partial \vec{u}}{\partial t} = D\frac{\partial^2 \vec{u}}{\partial x^2} + A\vec{u} \quad \text{——} (6)$$

where $D = \begin{pmatrix} D_1 & 0 \\ 0 & D_2 \end{pmatrix}$

To solve equation (6), we take the Fourier transformation of $\vec{u}$:

$$\vec{u} = \sum_k B_k e^{\lambda t} \vec{v}_k(x) \quad \text{——} (7)$$

$[\vec{u}(x,t) = C(t)\vec{v}(x$

~~where is the $\vec{u}_k$ satisfies the eigenvalue problem~~

$$\cancel{\frac{\partial^2 \vec{u}_k}{\partial x^2} + k^2 \vec{u}_k = 0} \quad \text{—} (8)$$

$$\cancel{(\hat{n}.\vec{\nabla})\vec{u}_k = 0 \text{ on the boundary.}}$$

~~Substituting (7) into (6), we have~~

$\vec{v}_k$ satisfies the eigenvalue problem

$$\left.\begin{aligned} &\frac{\partial^2 \vec{v}}{\partial x^2} + k^2 \vec{v} = 0 \\ &(\vec{n}.\vec{\nabla})\vec{v} = 0 \text{ on the boundary} \end{aligned}\right\} \text{—} (8)$$

where k is the wave numbers which refers to the scale of the pattern.

Substituting (7) into equation (6), we have (using (8))

$$\cancel{\lambda\vec{v} = DA\vec{v} - k^2\vec{v}}$$

$[\vec{u}$

$$\text{ie} \quad \lambda\vec{u} = D\frac{\partial^2 \vec{v}}{\partial x^2} + A\vec{u}$$

$$\text{or} \quad \lambda\vec{u} = -k^2 D\vec{u} + A\vec{u}$$

$$\ldots)\vec{u} = \vec{0} \quad \text{——} (9)$$

The eigenvalues are given by

$$\det(A - k^2D - \lambda I) = 0 \quad \text{(10)}$$

The eigenvalues λ will have negative real part if $Tr(A-k^2D) < 0$ and $\det(A-k^2D) > 0$.

But for diffusive instability at least one of the above inequality reverse ie

$$Tr(A-k^2D) > 0 \quad \text{or} \quad \det(A-k^2D) < 0$$

ie interm of the elements of the matrix, we have

$$(a_{11}+a_{22}) - k^2(D_1+D_2) > 0 \quad \text{(11)}$$

and $\quad \det A - (a_{11}D_2 + a_{22}D_1)k^2 + D_1D_2k^4 < 0 \quad$ (12)

Condition (11) cannot be satisfied as $Tr(A) = a_{11}+a_{22} < 0$.

So, (12) must be satisfied. ie we denote the expression as $h(k^2)$

ie $h(k^2) = D_1D_2k^4 - (a_{11}D_2 + a_{22}D_1)k^2 + \det A$ —(13)

a quadratic expression in k^2.

In order of $h(k^2)$ to be negative, the vertex must be below the k^2-axis. Let us denote the vertex of $h(k^2)$ as $(k^2_{min}, h(k^2_{min}))$.

Then the diffusive instability requires $h(k^2_{min}) < 0$.

~~k^2_{min}~~ $h'(k^2) = 0$ gives minimum value of k^2, then

$$k^2_{min} = \frac{D_2a_{11} + D_1a_{22}}{2D_1D_2} = \frac{1}{2}\left[\frac{a_{11}}{D_1} + \frac{a_{22}}{D_2}\right] \quad \text{(14)}$$

which is the square of wave number

$$\text{Min}\,h = h(k^2_{min}) = \det A - \frac{1}{4D_1D_2}\left(D_2 a_{11} + D_1 a_{22}\right)^2 \quad [\text{By (13)}] \quad \left[\det A - \frac{1}{4D_1D_2}(D_2a_{11}+D_1a_{22})^2\right]$$

Thus the instability criteria is given by

$$\cancel{\det A - \frac{1}{4D_1D_2}\left(D_1\frac{a_{11}}{D_1} + D_1\frac{a_{22}}{D_2}\right)^2 < 0} \quad \cancel{(15)}$$

$$\det A - \frac{1}{4D_1D_2}(D_2a_{11} + D_1a_{22})^2 < 0 \quad \text{(15)}$$

Thus the reaction-diffusion system (1) with Jacobian matrix $A = (a_{ij})_{2\times 2}$ will have diffusion-driven instability if

(i) $\mathrm{Tr}(A) < 0$

(ii) $\mathrm{Det}\, A > 0$

(iii) $\mathrm{Det}\, A < \left(D_2 a_{11} + D_1 a_{22}\right)^2 / 4D_1D_2 \equiv D_2 a_{11} + D_1 a_{22} > 2\sqrt{D_1 D_2 \cdot \mathrm{Det}\, A}$

Some derivation:

Th The reaction-diffusion system (1) with Jacobian matrix $A = (a_{ij})_{2\times 2}$ will have diffusion-driven instability if

(a) $a_{11}a_{22} < 0$

(b) $a_{12}a_{21} < 0$ and

(c) $D_1 \neq D_2$.

The above can be proved easily:

(a) Since $\mathrm{Tr}(A) = a_{11} + a_{22} < 0$ and $D_2 a_{11} + D_1 a_{22} > 0$, we must have $a_{11}a_{22} < 0$.

(b) Since $\mathrm{Det}\, A > 0$ and $a_{11}a_{22} < 0 \Rightarrow a_{11}a_{22} - a_{12}a_{21} > 0$ & $a_{11}a_{22} < 0$

$\Rightarrow a_{12}a_{21} < 0$

(c) If $D_1 = D_2$, condition (iii) above becomes

$$D_1(a_{11} + a_{22}) > 2D_1\sqrt{\mathrm{Det}\, A}$$

Since the $\mathrm{tr}(A) < 0$, this condition does not hold good.

Hence $D_1 \neq D_2$.

Remark: The above conditions suggest the sign of elements of A as for the Turing instability:

(i) $\begin{pmatrix} + & - \\ + & - \end{pmatrix}$, (ii) $\begin{pmatrix} - & + \\ - & + \end{pmatrix}$, (iii) $\begin{pmatrix} + & + \\ - & - \end{pmatrix}$, (iv) $\begin{pmatrix} - & - \\ + & + \end{pmatrix}$.

The above (i), (ii) Jacobian matrices referred to a system known as activator-inhibitor system and (iii) & (iv) refers to a system known as positive feedback system.

If we consider the Lotka-Volterra competitive system, as

$$\frac{dN_1}{dt} = r_1 N_1\left(1 - \frac{N_1}{K_1}\right) - a_{12} N_1 N_2$$

$$\frac{dN_2}{dt} = r_2 N_2\left(1 - \frac{N_2}{K_2}\right) - a_{21} N_1 N_2$$

then the Jacobian matrix A has all elements which are negative. So, the diffusion-driven instability cannot take place in this case system.

DISCARD THIS

TO DO X NOW

Derivation of the critical diffusion coefficient

Again from (14), the min K^2_{min} makes $\frac{dh}{dK^2} = 0$ which implies from (13),

$$2D_1D_2K^2_{min} - (a_{11}D_2 + a_{22}D_1) = 0$$

which gives the critical wave number.

Pattern formation

In the preceding study we have obtained restrictions on the parameters that must be satisfied for Turing instability and it does not give any information for pattern formation. The types of pattern depend on the the domain Ω and the Boundary condition (BC). The eigenvalues and the eigenfunction determines the spatial pattern.

Now from (8), the solution to the eigenvalue problem has eigenvalues

$$K_n^2 = \frac{n^2\pi^2}{L^2}, \quad n = 1, 2, 3, \ldots \quad \text{— (16)}$$

and the eigenfunctions are — (17)

$$v(x) = \cos(K_n x)$$

Hence the solution of the linear system (6) is

$$u_i(x,t) = \sum_{n=1}^{\infty} B_n e^{\lambda(k_n^2)t} \cdot \cos(k_n x) \qquad \text{———} (18)$$

$$= N_i(x,t) - \bar{N}_i$$

For +ve characteristic root of (6), we have minimum value of k_n^2 given by $K_{min}^2 = \frac{1}{2}\left[\frac{a_{11}}{D_1} + \frac{a_{22}}{D_2}\right]$ [by (14)]

Again for the fundamental mode $n=1$, so that

$$K_1^2 = \frac{\pi^2}{L^2} > K_{min}^2 = \frac{1}{2}\left[\frac{a_{11}}{D_1} + \frac{a_{22}}{D_2}\right] = K_+^2 \quad \text{—} (19)$$

Then the minimum length is given

$$L_c = \frac{\pi}{K_+} \qquad \text{———} (20)$$

Thus the solution will be amplified at the wave, ~~$k > k_+$~~. wavenumber $k > k_+$. The solution will be above or below the ~~eqn~~ equilibrium value $\bar{N}_i$ if the component of the eigenfunction $v_i(x)$ are +ve or negative, respectively. Pattern when ~~Cond~~ $\cos\left(\frac{\pi x}{L_c}\right) > 0$ are different from those where $\cos\left(\frac{\pi x}{L_c}\right) < 0$.