Mathematical ecology and biology

PROBLEM SHEET 1. (* means not so easy!)

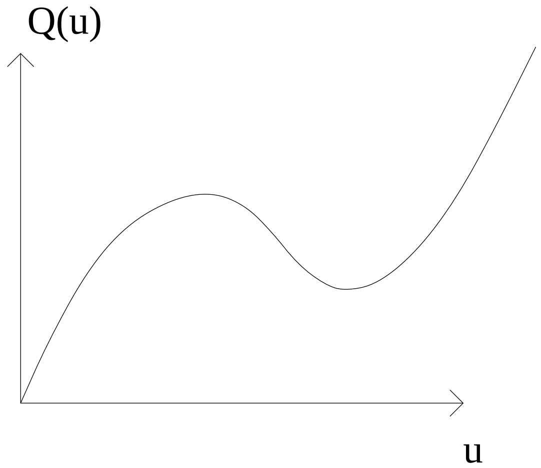
1. A model for a forest-insect system is given by

$$\begin{aligned} \dot{u} &= u[q - Q(u)], & (1) \\ \dot{q} &= \varepsilon[q - \alpha u], & (2) \end{aligned}$$

where u represents the insect population, q represents the tree foliage density, ε is small, α is $O(1)$, and $Q(u)$ is represented by the graph below. Give a simple description of the ecological facts which could motivate this model, and explain what happens if α is very low or very high. Show also that the system will oscillate for values of α in a certain range, which you should describe. What happens if the second equation is changed to

$$\dot{q} = \varepsilon[q(1-q) - \alpha u],$$

and what is the ecological motivation in doing this?



2. The predation $P(N)$ on a population $N(t)$ is very fast and a model for the prey $N(t)$ satisfies

$$\frac{dN}{dt} = RN\left(1 - \frac{N}{K}\right) - P\left\{1 - \exp\left[-\frac{N^2}{\varepsilon A^2}\right]\right\}, \quad 0 < \varepsilon \ll 1,$$

where R, K, P and A are positive constants and ε is a small, dimensionless number. If the units of N are larvae acre^{-1} and those of t are years, what are the dimensions of R, K, P, A and ε? Hence show that $u = \frac{N}{A}$, $\tau = \frac{Pt}{A}$, $r = \frac{AR}{P}$, and $q = \frac{K}{A}$ are non-dimensional. Furthermore, show that the equation is equivalent to

$$\frac{du}{d\tau} = ru\left(1 - \frac{u}{q}\right) - \left(1 - \exp\left[-\frac{u^2}{\varepsilon}\right]\right),$$

where r and q are positive parameters. Demonstrate that, if r, q are $O(1)$, there are three possible nonzero steady states if r and q lie in a domain in r, q space given approximately by $rq > 4$.

*Does this model exhibit hysteresis if r is allowed to vary? Justify your answer. (Hint: put $u = \sqrt{\varepsilon}U$, $r = R/\sqrt{\varepsilon}$, and show that the u–r curve has a 'nose' at $R = 0.638$.)

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PROBLEM SHEET 2

1. It has been suggested that a means of controlling insect numbers is to introduce and maintain a number of sterile insects in the population. One such model for the resulting population dynamics is

$$N_{t+1} = \frac{RN_t^2}{(R-1)\frac{N_t^2}{M} + N_t + S},$$

where $R > 1$ and $M > 0$ are constant parameters, and S is the constant sterile insect population.

Determine the steady states and discuss their linear stability, noting whether any type of bifurcation is possible. Find the critical value S_c of the sterile population in terms of R and M so that if $S > S_c$ the insect population is eradicated. Construct a cobweb map, and hence determine the possible solution behaviour if $0 < S < S_c$.

2. Consider the effect of regularly harvesting the population of a species for which the model equation is

$$u_{t+1} = \frac{bu_t^2}{1+u_t^2} - Eu_t = f(u_t; E), \quad b > 2, \; E > 0,$$

where E is a measure of the effort expended in obtaining the harvest Eu_t. Determine the steady states and hence show that if the effort $E > E_m = (b-2)/2$, no steady harvest can be obtained. If $E < E_m$, show that the model is realistic only if the population u_t always lies between two positive values which you should describe analytically.

With $E < E_m$ evaluate the slope of f at the largest positive steady state. Demonstrate the existence of a saddle node bifurcation as $E \to E_m$.

3. Discuss the global qualitative behaviour of the solutions of the discrete models

(i) $u_{t+1} = u_t \exp\{r(1-u_t)\} \quad (0 < r < 2)$;

(ii) $u_{t+1} = \dfrac{ru_t}{(1+au_t)^b}, \quad a > b, \; b > 0, \; r > 0.$

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PROBLEM SHEET 3

1. Consider a lake with some fish attractive to fishermen. We wish to model the fish-fishermen interaction.

Fish Assumptions:

i. Fish grow logistically in the absence of fishing.

ii. The presence of fishermen depresses fish growth at a rate jointly proportional to the fish and fishermen populations.

Fishermen Assumptions:

i. Fishermen are attracted to the lake at a rate directly proportional to the amount of fish in the lake.

ii. Fishermen are discouraged from the lake at a rate directly proportional to the number of fishermen already there.

(a) Write down a mathematical model for this situation clearly defining your notation.

(b) Show that a nondimensionalised version of the model is

$$\begin{aligned} \frac{du}{dt} &= ru(1-u) - uv \\ \frac{dv}{dt} &= \beta u - v \end{aligned} \qquad (*)$$

where u, v are the nondimensionalised fish and fishermen population respectively.

(c) Calculate the steady states of $(*)$ and determine their stability.

(d) Draw the phase plane, including the nullclines and phase plane trajectories.

(e) What would be the effect of adding fish to the lake at a constant rate?

2. The interaction between two populations with densities N_1 and N_2 is modelled by

$$\begin{aligned} \frac{dN_1}{dt} &= rN_1\left(1-\frac{N_1}{K}\right) - aN_1N_2(1-\exp[-bN_1]), \\ \frac{dN_2}{dt} &= -dN_2 + N_2 f(1-\exp[-bN_1]), \end{aligned}$$

where a, b, d, f, r and K are positive constants. What type of interaction exists between N_1 and N_2? What do the various terms imply ecologically?

Nondimensionalize the system by writing

$$u = \frac{N_1}{K}, \quad v = \frac{aN_2}{r}, \quad \tau = rt, \quad \alpha = \frac{f}{r}, \quad \delta = \frac{d}{r}, \quad \beta = bK.$$

Determine the non-negative equilibria and note any parameter restrictions. Discuss the linear stability of the equilibria. Show that a non-zero N_2-population can exist if $\beta > \beta_c = -\ln(1 - \delta/\alpha)$. *Briefly* describe the bifurcation behaviour as β increases with $0 < \delta/\alpha < 1$.

3. A predator-prey model for herbivore (H)-plankton (P) interaction is

$$\frac{dP}{dt} = rP\left[(K - P) - \frac{BH}{C + P}\right], \quad \frac{dH}{dt} = DH\left[\frac{P}{C + P} - AH\right],$$

where r, K, A, B, C and H are positive constants. Briefly explain the ecological assumptions in the model. Nondimensionalise the system so that it can be written in the form

$$\frac{dp}{d\tau} = p\left[(k - p) - \frac{h}{1 + p}\right], \quad \frac{dh}{d\tau} = dh\left[\frac{p}{1 + p} - ah\right].$$

Sketch the nullclines and demonstrate that at least one positive steady state (p_0, h_0) exists for all $a > 0$, $k > 0$.

Now suppose the positive steady state is unique. By considering the community matrix, show that

(i) for $k < 1$ the positive steady state is stable and

*(ii) that for small enough a, the positive steady state is unstable for $k > 1 + d$, approximately (assuming $k << 1/a$).

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Problem Sheet 4

1. Two dimensionless activator-inhibitor mechanisms have reaction kinetics described by

$$\begin{aligned} &\text{(i)} \quad \frac{du}{dt} = a - bu + \frac{u^2}{v}, \quad \frac{dv}{dt} = u^2 - v, \\ &\text{(ii)} \quad \frac{du}{dt} = a - u + u^2 v, \quad \frac{dv}{dt} = b - u^2 v, \end{aligned}$$

where a and b are positive constants. Which is activator and which the inhibitor in each of (i) and (ii)? What phenomena are indicated by the nonlinear terms? Sketch the nullclines. Is it possible to have positive multiple steady states with these kinetics? Discuss the stability of any non-zero steady states in (i).

What can you say about the number of non-zero steady states if substrate inhibition is included in (i), that is u^2/v is replaced by $u^2/[v(1+ku^2)]$?

2. A protein with concentration g is produced using amino acid S. It is autocatalyzed and degrades linearly according to the kinetics equation

$$\frac{dg}{dt} = s + k_1 \frac{g^2}{1+g^2} - k_2 g = f(g;s),$$

where k_1 and k_2 are positive constants and $s = [S]$ is a given substrate concentration. First show that if $s = 0$ there are two positive steady states if $k_1 > 2k_2$ and determine their stability. Sketch the reaction rate dg/dt as a function of g for $s = 0$ (that is $f(g;0)$). By considering $f(g;s)$ for $s > 0$ show that a critical value s_c exists such that the steady state switches to a higher value for all $s > s_c$. Thus demonstrate that, if $g(0) = 0$ and s increases from $s = 0$ to a sufficiently large value and then decreases to zero again, a biochemical *switch* has been achieved which changes the value of g from 0 to $g_2 > 0$, which you should find.

3. Consider the reaction system whereby two reactants X and Y degrade linearly and X activates Y and Y activates X according to

$$\begin{aligned} \frac{dx}{dt} &= k_1 \frac{y^2}{K + y^2} - k_2 x, \\ \frac{dy}{dt} &= h_1 \frac{x^2}{H + x^2} - h_2 y, \end{aligned}$$

where $x = [X]$, $y = [Y]$ and k_1, k_2, h_1, h_2, K and H are positive constants. Nondimensionalise the system to reduce the relevant number of parameters. Show (i) graphically and (ii) analytically that there can be two or zero (or, exceptionally, one) positive steady states. [Hint for (ii): use Descarte's Rule of Signs: Murray, Appendix 2.]

Mathematical Ecology and Biology

PROBLEM SHEET 5

1. For the MWC dimer (with two protomers) $R \rightleftharpoons T$ with the T form being inactive, show that the fraction of bound sites is given by

$$Y = \frac{S(1+S)}{L + (1+S)^2},$$

where $S = s/K$, s with the substrate concentration, and K and L should be determined.

If a product p is produced at a rate k per bound site, show that the rate of production of p is $2ke_0Y$, where e_0 is the total enzyme present, and S (in the expression for Y) is given by s/K_m, where K_m should be found.

Now suppose a second ligand p can be bound at a site on each protomer (of the active R form), but that binding of p inactivates the reaction with s. Show in this case that the fraction of bound s sites is

$$Y = \frac{S(1+S)(1+P)^2}{L + (1+S)^2(1+P)^2},$$

where $S = s/K_m$ and $P = p/K_p$, and K_m and K_p should be determined. If p is produced at a rate k from sites of R bound with s, deduce that

$$\frac{dp}{dt} = 2ke_0Y,$$

where now $S = sk_+/(k_- + k)$.

2. Consider the model for glycolytic oscillations

$$\begin{aligned} \frac{dS}{dt} &= \mu - \Phi(S,P), \\ \frac{dP}{dt} &= -P + K\Phi, \end{aligned}$$

where

$$\Phi(S,P) = \frac{\beta(S+S^2)(1+P)^2}{L + (1+S)^2(1+P)^2},$$

and $L \gg \beta \gg 1$ (typical values are $L = 10^7$, $\beta = 10^4$).

(i) For the S nullcline, show that if $S, P \gg 1$, then $\dot{S} = 0$ if $SP \approx c(\mu)$ (which need not be determined explicitly). Hence show that the S nullclines are approximate hyperbolas which move to the right in (P,S) space as μ increases.

(ii) For the P nullcline, show that if $S, P = O(1)$, then $\dot{P} = 0$ for

$$S + S^2 \approx \left(\frac{L}{K\beta}\right)\frac{P}{(1+P)^2},$$

and show that when P becomes large, this becomes $S \approx (L/K\beta P)^{1/2}$ (if $1 \ll P \ll L/K\beta$). Draw a rough graph of S against P.

(iii) For the P nullcline, show that if $S, P \gg 1$, then $\dot{P} = 0$ for

$$\frac{1}{\beta K S} \approx \frac{SP}{L + S^2 P^2},$$

and by considering the graph of this equation first in the (PS, S) plane and then in the (P, S) plane, show that the graph is convex upwards, and that as $P \to 0$, $S \approx (L/\beta K P)^{1/2}$.

(iv) Using (ii) and (iii), deduce the composite form of the P nullcline, and deduce the approximate range of μ for which the steady state lies on the negative slope part of $\dot{P} = 0$.

Mathematical Ecology and Biology

Problem sheet 6

1. *(Finals 1992)* A population $u(\mathbf{x}, t)$ has diffusion coefficient $D(u)$ and production rate $g(u)$ per unit volume where $D(u) > 0\ \forall u$. Show that, as a result of Fick's Law, u satisfies the reaction-diffusion equation

$$\frac{\partial u}{\partial t} = \boldsymbol{\nabla}.(D(u)\boldsymbol{\nabla} u) + g(u).$$

Now suppose that $g(0) = g(1) = 0$, $g(u) > 0\ \forall u \in (0, 1)$, $g'(0) > 0$, $g'(1) < 0$ and g and D are continuously differentiable. Show that, for the one-dimensional case if a travelling wave $u = \phi(\xi)$, $\xi = x - ct$ exists from $u = 1$ to $u = 0$, then

$$c = \frac{\int_0^1 g(w)D(w)dw}{\int_{-\infty}^{\infty} D(\phi(s)) \left[\frac{d\phi(s)}{ds}\right]^2 ds}$$

and hence that $c > 0$.

Assuming that such a travelling wave solution is possible, find the lower limit on the wave speed. Sketch the solution $u(x)$ for the travelling wave solution, with the direction of motion clearly marked.

2. *(Finals 1983)* In the reaction sequence

$$X + Y \xrightarrow{k_1} P, \quad A + X \xrightarrow{k_2} 2X, \quad 2X \xrightarrow{k_3} P + A$$

the reactants can diffuse in a one dimensional space with the same diffusion coefficient D. Write down the reaction-diffusion system for X and Y using the law of mass action and with the concentration of A constant.

Using the non-dimensionalisation

$$u = \frac{2k_3[X]}{k_2[A]}, \quad v = \frac{k_1[Y]}{k_2[A]r}, \quad x^* = \left(\frac{k_2[A]}{D}\right)^{\frac{1}{2}} x, \quad t^* = k_2[A]t, \quad b = k_1/2k_3,$$

where r is a positive parameter, show that the reaction-diffusion system becomes

$$\frac{\partial u}{\partial t^*} = u(1 - u - rv) + \frac{\partial^2 u}{\partial x^{*2}}, \quad \frac{\partial v}{\partial t^*} = -buv + \frac{\partial^2 v}{\partial x^{*2}}.$$

This system exhibits travelling wave front solutions with $u(-\infty, t^*) = v(\infty, t^*) = 1$, $u(\infty, t^*) = v(-\infty, t^*) = 0$. Show that in the symmetric situation $u = 1 - v$ the travelling wave fronts are solutions of a Fisher equation if $b = 1 - r$. Hence show that the travelling front wave speed $c \geq 2\sqrt{1 - r}$ if $0 \leq r < 1$.

3. A model for the transmission of the rabies virus in wild fox populations is

$$\frac{\partial S}{\partial t} = -rIS + BS\left(1 - \frac{S}{S_0}\right), \quad \frac{\partial I}{\partial t} = rIS - aI + D\frac{\partial^2 I}{\partial x^2},$$

where S represents the healthy (thus **S**usceptible) population, and I represents the **I**nfected population; r, B, a, D and S_0 are positive constant parameters. Can you explain the meaning of these equations? Nondimensionalize the system to give

$$u_t = u_{xx} + uv - \lambda u, \quad v_t = -uv + bv(1 - v),$$

where u relates to I and v to S, and give the definition of λ. Look for travelling wave solutions with $u > 0$ and $v > 0$ and hence show, by linearizing far ahead of a wavefront where $v \to 1$ and $u \to 0$, that a wave may exist if $\lambda < 1$ and if so the minimum wave speed is $2(1 - \lambda)^{1/2}$.

Mathematical Ecology and Biology

Vacation problem sheet

1. Suppose fishing is regulated within a zone H km from a country's shore (taken to be a straight line) but outside of this zone over-fishing is so excessive that the population is effectively zero. Assume that the fish reproduce logistically, disperse by diffusion and within the zone are harvested with an effort E. Justify the following model for the fish population $u(x,t)$:

$$u_t = ru\left(1 - \frac{u}{K}\right) - Eu + Du_{xx},$$

$$u = 0 \quad \text{on} \quad x = H, \quad u_x = 0 \quad \text{on} \quad x = 0.$$

where $r, K, E\ (< r)$ and D are positive constants.

If the fish stock is not to collapse show that the fishing zone H must be greater than $(\pi/2)\ [D/(r-E)]^{1/2}$ km. Briefly discuss any ecological implications.

2. Consider the general reaction-diffusion system

$$\begin{aligned} \frac{\partial u}{\partial t} &= f(u,v) + D_1 u_{xx} \\ \frac{\partial v}{\partial t} &= g(u,v) + D_2 v_{xx} \end{aligned}$$

where f and g describe the reaction kinetics and D_1, D_2 are positive constants. Assume (u_0, v_0) is such that $f = g = 0$ at (u_0, v_0), where u_0, v_0 are const.

(i) Write down the conditions for diffusive driven instability (DDI).

(ii) From (i) show that DDI is only possible if $f_u g_v,\ f_v g_u < 0$ at the steady state (u_0, v_0).

Consider now the scheme where

$$\begin{aligned} f(u,v) &= \frac{\rho u^2}{(1+\kappa u^2)v} - \mu u, \\ g(u,v) &= \rho' u^2 - \nu v \end{aligned}$$

where ρ, κ, μ, ν and ρ' are positive constants.

Show that there is a unique steady state (u_0, v_0) with $u_0 > 0$, $v_0 > 0$.

(iii) Draw a phase portrait of this scheme in the absence of diffusion and show that DDI is only possible if the nullclines intersect in a certain way.

(iv) Write down the conditions for DDI for these particular kinetics.

(v) Show that when DDI is possible, bifurcation to solutions oscillating in space as well as time is not possible.

3. The amoebae of the slime mold *Dictyostelium discoideum*, with density $n(x,t)$, secrete a chemical attractant, cyclic-AMP, and spatial aggregations of amoebae start to form. One of the models for this process gives rise to the system of equations, which in their one-dimensional form, are

$$n_t = D_n n_{xx} - \chi(n a_x)_x, \quad a_t = hn - ka + D_a a_{xx},$$

where a is the attractant concentration and h, k, χ and the diffusion coefficients D_n and D_a are all positive constants. Nondimensionalise the system, to obtain

$$\begin{aligned} n_t &= n_{xx} - \mu(n a_x)_x, \\ a_t &= n - a + \delta a_{xx}, \end{aligned}$$

and give the definitions of μ and δ.

Consider (i) a finite domain with zero flux boundary conditions and (ii) an infinite domain. Examine the linear stability about the steady state (which introduces a further parameter here), derive the dispersion relation and discuss the role of the various parameter groupings. Hence obtain the conditions on the parameters and domain size for the mechanism to initiate spatially heterogeneous solutions.

Experimentally the chemotactic parameter χ increases during the life cycle of the slime mold. Using χ as the bifurcation parameter determine the critical wave length when the system bifurcates to spatially structured solutions in the finite domain. Also examine the bifurcating instability as the domain length increases. Show that the minimum (dimensional) domain length for instability is given by

$$L_{\min}^2 = \frac{\pi^2 D_n D_a}{\chi h n_0 - k D_n}$$

where n_0 is the unperturbed (dimensional) amoeba concentration.