MATHEMATICAL MODELLING

HOMEWORK SOLUTIONS

November 25, 2015

Exercise 22

(a) Denote D_m the diffusion coefficient of the roaming prey. Denote D_p, q the diffusion and taxis coefficient of the predator, respectively. Note that the taxis is positive and movement is towards higher *prey* density, i.e., $J_{\text{taxis}} = +qp\partial_x m_1$. The equations are

$$\begin{aligned}
\partial_t p &= D_p \partial_{xx} p - q\partial_x (p\partial_x m_1) \\
\partial_t m_1 &= -\alpha p m_1 + \frac{1}{\tau} m_2 + D_m \partial_{xx} m_1 \\
\partial_t m_2 &= +\alpha p m_1 - \frac{1}{\tau} m_2
\end{aligned}$$

The reflecting boundary condition for m_1 is

$$J_1 = -D_m \partial_x m_1 = 0 \Leftrightarrow \partial_x m_1 = 0 \quad \text{for } x = 0, L$$

and for p we obtain

$$\begin{aligned}
J_p = -D_p \partial_x p + qp\partial_x m_1 = 0 \quad \text{for } x = 0, L \\
\Leftrightarrow \partial_x p = 0 \quad \text{for } x = 0, L
\end{aligned}$$

(b) Assume that reactions are fast (substitute α with α/ε and τ with $\varepsilon\tau$). In the fast time $\vartheta = t/\varepsilon$ the fast dynamics is

$$\begin{cases}
\frac{1}{\varepsilon}\partial_\vartheta p = D_p \partial_{xx} p - q\partial_x (p\partial_x m_1) \\
\frac{1}{\varepsilon}\partial_\vartheta m_1 = -\frac{\alpha}{\varepsilon} p m_1 + \frac{1}{\varepsilon\tau} m_2 + D_m \partial_{xx} m_1 \\
\frac{1}{\varepsilon}\partial_\vartheta m_2 = +\frac{\alpha}{\varepsilon} p m_1 - \frac{1}{\varepsilon\tau} m_2
\end{cases}
\quad \xRightarrow{\varepsilon \to 0} \quad
\begin{cases}
\partial_\vartheta p = 0 \\
\partial_\vartheta m_1 = -\alpha p m_1 + \frac{1}{\tau} m_2 \\
\partial_\vartheta m_2 = +\alpha p m_1 - \frac{1}{\tau} m_2
\end{cases}$$

Consider now the total population density $m = m_1 + m_2$. This is a slow variable, indeed

$$\partial_\vartheta m = \partial_\vartheta m_1 + \partial_\vartheta m_2 = 0.$$

The equilibrium of the fast dynamics is

$$0 = -\alpha p \overline{m}_1 + \frac{1}{\tau}(m - \overline{m}_1) \quad \Rightarrow \quad \overline{m}_1 = \frac{m}{\tau\alpha p + 1}$$

We now write the slow equations for p and m:

$$\begin{cases}
\partial_t m = D_m \partial_{xx} \overline{m}_1 = D_m \partial_{xx} \left(\frac{m}{\tau\alpha p+1}\right) \\
\partial_t p = D_p \partial_{xx} p - q\partial_x \left(p\partial_x \overline{m}_1\right) = D_p \partial_{xx} p - q\partial_x \left(p\partial_x \left(\frac{m}{\tau\alpha p+1}\right)\right)
\end{cases} \tag{1}$$

We impose zero-flux boundary conditions. The boundary condition for m gives

$$0 = -D_m \partial_x \left(\frac{m}{\tau \alpha p + 1} \right) \Leftrightarrow \partial_x \left(\frac{m}{\tau \alpha p + 1} \right) = 0 \quad \text{for } x = 0, L \tag{2}$$

and we can use this to simplify the boundary condition for p:

$$0 = -D_p \partial_x p + qp \partial_x \left(\frac{m}{\tau \alpha p + 1} \right) = -D_p \partial_x p \Leftrightarrow \partial_x p = 0 \quad \text{for } x = 0, L$$

We can now go back to (2) and simplify further:

$$0 = \partial_x \left(\frac{m}{\tau \alpha p + 1} \right) = \frac{(\tau \alpha p + 1)\partial_x m - \tau \alpha m \partial_x p}{(\tau \alpha p + 1)^2} = \frac{\partial_x m}{\tau \alpha p + 1} \Leftrightarrow \partial_x m = 0 \quad \text{for } x = 0, L$$

(c) Consider system (1). For the first equation,

$$\partial_t m = D_m \partial_{xx} \left(\frac{m}{\tau \alpha p + 1} \right) = \partial_x \left(D_m \frac{(\tau \alpha p + 1)\partial_x m - \tau \alpha m \partial_x p}{(\tau \alpha p + 1)^2} \right)$$

For the second equation,

$$\partial_t p = D_p \partial_{xx} p - \partial_x \left(qp \partial_x \frac{(\tau \alpha p + 1)\partial_x m - \tau \alpha m \partial_x p}{(\tau \alpha p + 1)^2} \right)$$

Therefore, we can rewrite system (1) as

$$\begin{cases} \partial_t m = -\partial_x \left[-D_1(p) \partial_x m + K(p) m \partial_x p \right] \\ \partial_t p = -\partial_x \left[-D_2 \partial_x p + Q_1(p) p \partial_x m + Q_2(m,p) p \partial_x p \right] \end{cases}$$

with

$$\begin{aligned}
D_1(p) &= \frac{D_m}{\tau \alpha p + 1} && \text{density-dependent diffusion of prey} \\
K(p) &= \frac{D_m \tau \alpha}{(\tau \alpha p + 1)^2} && \text{density-dependent positive taxis} \\
D_2 &= D_p && \text{diffusion of predator} \\
Q_1(p) &= \frac{q}{\tau \alpha p + 1} && \text{density-dependent positive taxis} \\
Q_2(m,p) &= -\frac{q \tau \alpha m}{(\tau \alpha p + 1)^2} && \text{density-dependent negative auto-taxis}
\end{aligned}$$

Exercise 23

Consider the predator–prey system

$$\begin{aligned} \varepsilon \partial_t m &= a - bm - \beta mp \\ \partial_t p &= \gamma \beta mp - \delta p + D \partial_{xx} p \end{aligned}$$

with $0 < \varepsilon \ll 1$.

(a) The quasi-equilibrium of the m-dynamics is (assuming p constant)

$$0 = a - b\overline{m} - \beta\overline{m}p \Leftrightarrow \overline{m}(p) = \frac{a}{b + \beta p}$$

Therefore, the equation for p (slow dynamics) becomes

$$\partial_t p = \frac{a\gamma\beta p}{b + \beta p} - \delta p + D\partial_{xx}p, \quad t \geq 0, x \in \mathbb{R}$$

(b) We look for travelling wave solutions, i.e., we want to check if the equations admits a solution of the form

$$p(x,t) = p(x - ct). \tag{3}$$

We substitute (3) into the equation for p and we get

$$-cp' = \frac{a\gamma\beta p}{b + \beta p} - \delta p + Dp''$$

We are not interested in solving explicitly this second-order equation. Instead, we want to find travelling waves that satisfy suitable boundary conditions: we are interested in the qualitative behaviour of the system. Therefore we look at the *phase plane* of the system of equations

$$\begin{aligned} p' &= H \\ H' &= \frac{\delta}{D}p - \frac{a\gamma\beta p}{D(b + \beta p)} - \frac{c}{D}H \end{aligned}$$

The equilibria are $(0,0)$ and $(\overline{p}, 0)$ such that

$$\delta = \frac{a\gamma\beta}{b + \beta\overline{p}} \Leftrightarrow \overline{p} = \frac{a\gamma\beta - b\delta}{\beta\delta}$$

Notice that $\overline{p} > 0$ under the assumption $a\gamma\beta > b\delta$. The isoclines are

$$\begin{aligned} p' = 0 &\Leftrightarrow H = 0 \\ H' = 0 &\Leftrightarrow H = \frac{p}{c}\left(\delta - \frac{a\gamma\beta}{b + \beta p}\right) \end{aligned}$$

Notice that the shape of the H-isocline and the sign of the vertical arrows depend on the sign of the speed c: in order to plot the phase-plane, we separate two cases (see picture below). Since we are looking for travelling waves, we want to look if the system admits some orbits that are *bounded*: for instance, orbits that go from one equilibrium to the other, or turn around in a periodic orbit.

In both cases, from the arrows it is easy to see that the equilibrium $(\overline{p}, 0)$ is a saddle point. What about the origin $(0,0)$? The arrows are turning around, so we cannot conclude about stability from the phase plane. We compute the jacobian and we apply the trace–determinant criterion for two-dimensional systems.

$$J_{(0,0)} = \begin{pmatrix} 0 & 1 \\ \frac{\delta}{D} - \frac{a\gamma\beta D(b+\beta p) - a\gamma\beta p D\beta}{D^2(b+\beta p)^2} & -\frac{c}{D} \end{pmatrix}\Bigg|_{(0,0)} = \begin{pmatrix} 0 & 1 \\ \frac{\delta b - a\gamma\beta}{Db} & -\frac{c}{D} \end{pmatrix}$$

$$\mathrm{tr} J = -\frac{c}{D} \quad \text{(sign depends on } c\text{)}$$

$$\det J = \frac{a\gamma\beta - b\delta}{Db} > 0.$$

If $c > 0$, the origin is stable. Therefore, the only possible waves $p(x - ct)$ are those that depart from $(\overline{p}, 0)$ and end up at $(0, 0)$. This means that (at every time t) such waves satisfy the boundary conditions

$$p(-\infty) = \overline{p}, \quad p(+\infty) = 0,$$

i.e., the population is at the stable equilibrium on the left spatial boundary, and there is no population to the right. Moreover, since we are considering positive speed $c > 0$, the wave is moving towards the right, and therefore the population is *invading* the spatial domain (see picture below). To ensure that such a travelling wave exists and it is biologically acceptable, we should check that the corresponding orbit does not become negative: i.e., we should check if the origin is a stable node or focus. In this case we have

- stable node if $\det < \mathrm{tr}^2/4 \Leftrightarrow c > \sqrt{\frac{4D}{b}(a\gamma\beta - \delta b)} =: c^*$. In this case, by looking at the arrows in the phase plane we conclude that a possible travelling wave is the orbit that departs from $(\overline{p}, 0)$ goes down and left, then crosses the $H-$isocline horizontally to the left and ends up at $(0, 0)$ without crossing the vertical axis. Therefore, we should check that the unstable manifold of $(\overline{p}, 0)$ and the stable manifold of $(0, 0)$ are connected (the arrows are not enough).

  In order to prove that the orbit departing from $(\overline{p}, 0)$ actually ends up in $(0, 0)$, we could try to find a "trapping region" and then use Poincaré–Bendixson theorem to prove that the orbits cannot cross the vertical axis. We should find a curve $H = g(p)$ passing through $(0, 0)$ and such that $H'/p' < g'(p)$ for $p > 0, H < 0$, so that the orbit is "more steep" than the curve. (but in this case it is nontrivial)

- stable focus if $\det > \mathrm{tr}^2/4 \Leftrightarrow 0 < c < c^*$. In this case no travelling wave is possible, because it would cross the vertical axis and therefore p would become negative.

If $c < 0$, the origin is unstable. In this case, the only possible waves are those departing from $(0, 0)$ and ending up in $(\overline{p}, 0)$. Such waves satisfy the boundary conditions

$$p(-\infty) = 0, \quad p(+\infty) = \overline{p},$$

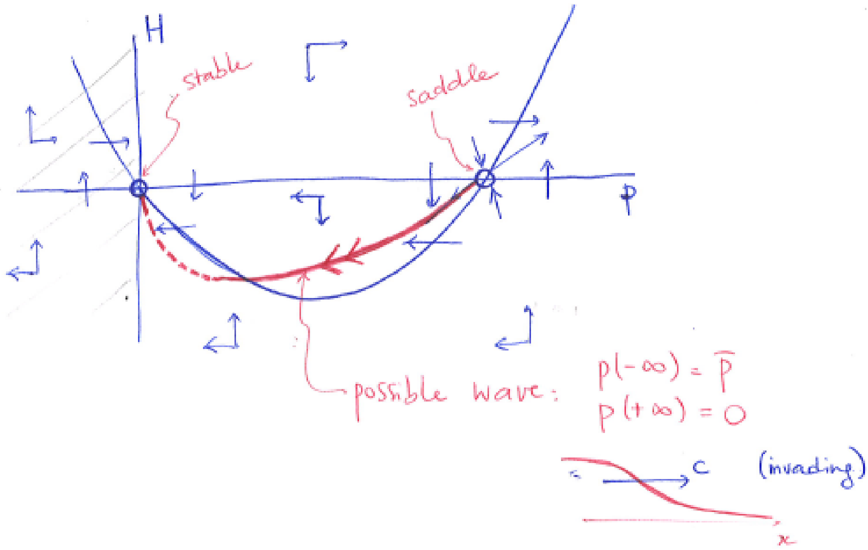
i.e., the population is absent on the left boundary, and it is at the positive equilibrium on the right. Moreover, since the speed is negative, this means that the wave is moving towards the left, and the population is again *invading* the spatial domain (this time from right to left). The situation is analogous to the previous one: we should check that $(0, 0)$ is a *node*, and then check that the unstable manifold departing from $(0, 0)$ connects to the stable manifold of $(\overline{p}, 0)$.

If $c = 0$ we are actually looking for stationary waves $p = p(x)$, i.e., equilibria of the system. In this case, the isoclines are

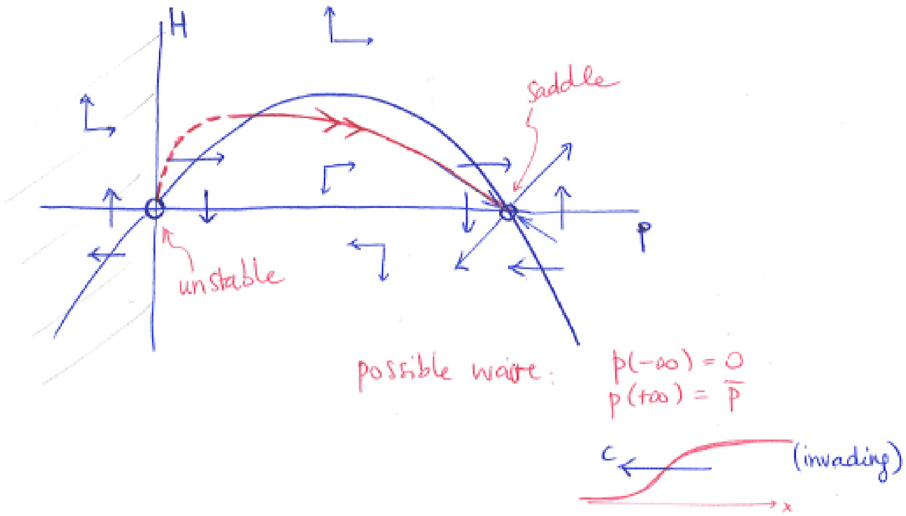
$$\begin{aligned} p' = 0 \Leftrightarrow & H = 0 \\ H' = 0 \Leftrightarrow & \frac{p}{c}\left(\delta - \frac{a\gamma\beta}{b + \beta p}\right) = 0 \Leftrightarrow p = 0 \text{ or } p = \overline{p}. \end{aligned}$$

The origin is a (stable or unstable) focus, and therefore every orbit in the phase-plane satisfying finite boundary conditions crosses the vertical axis and becomes biologically impossible. Therefore, there are no stationary waves except the trivial ones $p(x) = 0$ and $p(x) = \overline{p}$.

$\boxed{c > 0}$



$\boxed{c < 0}$



$\boxed{c = 0}$