INTRODUCTION TO MATHEMATICAL BIOLOGY

HOMEWORK SOLUTIONS

October 3, 2016

Exercise 3.1

We consider a logistic population of prey which is harvested by a fixed number P of predators with Holling type II functional response:

$$\frac{dN}{dt} = r_0 N \left(1 - \frac{N}{K}\right) - \frac{\beta N}{1 + \beta T N} P$$

As usual, let $f(N)$ be the right hand side of this ODE and let $g(N) = f(N)/N$ be the *per capita* growth rate,

$$f(N) = g(N)N, \quad g(N) = r_0 \left(1 - \frac{N}{K}\right) - \frac{\beta}{1 + \beta T N} P$$

Any bifurcation can occur only if $f'(\hat{N}) = 0$ holds at the equilibrium. Recall that with $f'(\hat{N}) < 0$ the equilibrium is asymptotically stable, and with $f'(\hat{N}) > 0$ the equilibrium is asymptotically unstable; in both cases it is hyperbolic. The condition for having a bifurcation is that we have an equilibrium and it is not hyperbolic:

$$f(\hat{N}) = 0, \quad f'(\hat{N}) = 0$$

Let us first consider a nontrivial equilibrium ($\hat{N} \neq 0$). The equilibrium equation $f(\hat{N}) = 0$ then simplifies to $g(\hat{N}) = 0$, which is equivalent to

$$P = \frac{r_0}{\beta} \left(1 - \frac{\hat{N}}{K}\right) (1 + \beta T \hat{N})$$

and the condition for non-hyperbolicity $f'(\hat{N}) = 0$ simplifies to $g'(\hat{N}) = 0$, which yields

$$P = \frac{r_0}{\beta} \frac{1 + \beta T \hat{N}}{\beta T K}$$

Solve the last two equations for the equilibrium $\hat{N}$:

$$\hat{N} = \frac{\beta T K - 1}{2\beta T}$$

This is the equilibrium density at which the bifurcation happens. Notice that it is positive if $\beta T K > 1$, i.e., if the handling time is sufficiently long. To get the critical value of the parameter P where the bifurcation happens, substitute the critical density into P above to obtain

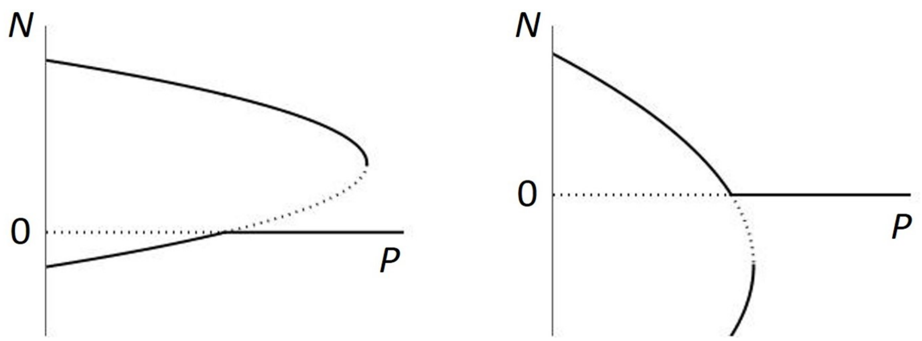
$$P_{crit} = \frac{r_0}{\beta} \frac{(1+\beta TK)^2}{4\beta TK}$$

At this bifurcation point, the conditions of the fold bifurcation theorem are satisfied: the derivative of the right hand side of the ODE with respect to the *parameter*, P, does not vanish when $N > 0$, and the second derivative with respect to N also does not vanish (as long as $r > 0$). Hence the nontrivial equilibrium undergoes a fold bifurcation at $P = P_{crit}$.

Consider now the trivial equilibrium $\hat{N} = 0$. This satisfies the equilibrium condition $f(\hat{N}) = 0$. The non-hyperbolicity condition $f'(\hat{N}) = 0$ simplifies to $g(0) = 0$, which promptly yields $P_{crit} = r_0/\beta$. Note that with $N = 0$, the derivative of the right hand side of the ODE with respect to the parameter, P, vanishes. The trivial equilibrium undergoes a transcritical bifurcation at $P = r_0/\beta$.

Notice that the critical P value for a fold bifurcation coincides with the critical P value of the transcritical bifurcation if $\frac{(1+\beta TK)^2}{4\beta TK} = 1$; this is the case if (and only if) $\beta TK = 1$. In this case, the fold and transcritical bifurcations "combine", and the model exhibits a more exceptional (higher codimension) bifurcation.

The figure below shows the bifurcation diagram of $\hat{N}$ with respect to P for $\beta KT > 1$ (left) and $\beta KT < 1$ (right). The stability of the equilibria is easily deduced from the fact that stable and unstable equilibria alternate and the trivial equilibrium is unstable for $P < r_0/\beta$ (to the left of the transcritical bifurcation) and stable above. The special case $\beta TK = 1$ corresponds to the situation inbetween, when the fold bifurcation does not happen above or below the horizontal axis, but exactly on it.



In conclusion, the prey population goes extinct if there are too many predators. If $\beta TK > 1$ (long handling time), then extinction happens through a fold bifurcation, i.e., in a catastrophic way. When the handling time is short, and therefore the Holling II functional response is not too different from a linear functional response over the relevant range of prey population sizes (e.g. for $N < K$), then extinction happens through a transcritical bifurcation.

Exercise 3.2

We first write the differential equation for the density of searching predators $S(t)$, by summing up three contributions: searching predators that start pursuing the prey (notice that a predator pursuing a prey does not count as searching any more); predators that just finished digesting the prey and become searching again; predators whose prey has just escaped. We assume the prey density is constant equal to N. The equation for the searching predators is

$$\frac{dS}{dt} = -\beta N S(t) + p\beta N S(t - T_1 - T_2) + (1-p)\beta N S(t - T_1).$$

We assume that the predator dynamics is at equilibrium $\hat{S}$. In this case, the differential equation does not tell us any more information about $\hat{S}$, so we use the conservation law and require that at any time t the total number of searching, pursuing, and handling predators is a constant P:

$$P = S(t) + \int_0^{T_1} \beta N S(t-\tau)d\tau + \int_{T_1}^{T_1+T_2} p\beta N S(t-\tau)d\tau$$

At equilibrium, this reads

$$P = \hat{S} + \int_0^{T_1} \beta N \hat{S} d\tau + p\int_{T_1}^{T_1+T_2} \beta N \hat{S} d\tau$$
$$\Leftrightarrow \hat{S} = \frac{P}{1 + \beta N(T_1 + pT_2).}$$

Finally, we determine the functional response of the predator by considering

$$\beta N \hat{S} = \frac{\beta N P}{1 + \beta N(T_1 + pT_2)} = \underbrace{\left[\frac{\beta N}{1 + \beta N(T_1 + pT_2)}\right]}_{\phi(N)} P.$$

Notice that the term in round brackets equals the expected handling time of predators, i.e., $p(T_1 + T_2) + (1-p)T_1$. In particular, this exercise is a special case of Exercise 3.3, where the handling time T has a discrete distribution:

$$H = \begin{cases} T_1 & \text{with probability } 1-p \\ T_1 + T_2 & \text{with probability } p \end{cases}$$

Exercise 3.3

We proceed in a way very similar to exercise 3.2 and compute the conservation law for total density of predators:

$$P = S(t) + \int_0^{\tau_{\max}} \beta N S(t-\tau)\text{Prob(still handling at } t\text{)}$$
$$= S(t) + \int_0^{\tau_{\max}} \beta N S(t-\tau)(1 - F(\tau))d\tau$$

and at equilibrium, integrating by parts, we get

$$\begin{aligned}P &= \hat{S} + \beta N \hat{S}\left(\tau_{\max} - \int_0^{\tau_{\max}} F(\tau))d\tau\right) \\ &= \hat{S} + \beta N \hat{S}\left(\tau_{\max} - [\tau F(\tau)]_0^{\tau_{\max}} + \int_0^{\tau_{\max}} \tau F'(\tau))d\tau\right) \\ &= \hat{S} + \beta N \hat{S} T\end{aligned}$$

where $T = \int_0^{\tau_{\max}} \tau F'(\tau)d\tau$ is the expected handling time. Hence,

$$\hat{S} = \frac{P}{1 + \beta N T}$$

Exercise 3.4

A fold bifurcation point is characterized by $\partial f/\partial x(\hat{x}_0, \mu_0) = 0$ (and $\partial f/\partial \mu(\hat{x}_0, \mu_0) \neq 0$, $\partial^2 f/\partial x^2(\hat{x}_0, \mu_0) \neq 0$). The stability of the equilibrium is determined by the sign of $\partial f/\partial x$, which we can guess from $\partial^2 f/\partial x^2$ (e.g., $\partial^2 f/\partial x^2 > 0$ means that $\partial f/\partial x$ is increasing, which means that $\hat{x}$ is stable if $\hat{x} < \hat{x}_0$, unstable otherwise).

For understanding the shape of the bifurcation diagram, we study the curve $\mu(x)$. In particular,

$$\frac{d^2\mu}{dx^2}(\hat{x}_0, \mu_0) = \frac{-\partial^2 f/\partial x^2}{\partial f/\partial \mu}(\hat{x}_0, \mu_0)$$

and hence the concavity of the curve depends on the relative sign of $\partial^2 f/\partial x^2$ and $\partial f/\partial \mu$.

In summary:

- $\partial^2 f/\partial x^2 > 0$: lower branch is stable, upper branch is unstable. If $\partial f/\partial \mu > 0$, then two equilibria exist for $\mu < \mu_0$; if $\partial f/\partial \mu < 0$, two equilibria exist for $\mu > \mu_0$.
- $\partial^2 f/\partial x^2 < 0$: lower branch is unstable, upper branch is stable. If $\partial f/\partial \mu > 0$, then two equilibria exist for $\mu > \mu_0$; if $\partial f/\partial \mu < 0$, two equilibria exist for $\mu < \mu_0$.

Exercise 3.5

Remember that, at the transcritical bifurcation point, the following conditions are satisfied:

$$\frac{\partial f}{\partial x}(0, \mu_0) = g(0, \mu_0) = 0, \qquad \frac{\partial^2 f}{\partial \mu^2}(0, \mu_0) = 0.$$

We can understand the stability of the zero equilibrium by studying how the derivative $\partial f/\partial x$ depends on μ, i.e., by looking at

$$b := \frac{\partial^2 f}{\partial x \partial \mu}(0, \mu_0).$$

For instance, $b > 0$ means that $\partial f/\partial x$ is increasing with μ, hence 0 is stable for $\mu < \mu_0$ and unstable otherwise.

To understand the shape, we look at the zeros of the quadratic form

$$ax^2 + 2b(\mu - \mu_0)x = 0$$

where

$$a := \frac{\partial^2 f}{\partial x^2}(0, \mu_0) = 2\frac{\partial g}{\partial x}(0, \mu_0).$$

In particular,

$$x = \frac{-b(\mu - \mu_0) \pm |b(\mu - \mu_0)|}{a}.$$

Notice that one solution will always correspond to the trivial branch $x = 0$, while the position of the second branch depends on the sign of a and b.

In summary:

- $b = \frac{\partial^2 f}{\partial x \partial \mu} > 0$: zero equilibrium is stable for $\mu < \mu_0$, unstable for $\mu > \mu_0$; if $a > 0$ the nontrivial equilibrium is positive (and unstable) for $\mu < \mu_0$ (*subcritical bifurcation*), if $a < 0$, the nontrivial equilibrium is positive (and stable) for $\mu > \mu_0$ (*supercritical bifurcation*)

- $b = \frac{\partial^2 f}{\partial x \partial \mu} < 0$: zero equilibrium is unstable for $\mu < \mu_0$, stable for $\mu > \mu_0$; if $a > 0$ the nontrivial equilibrium is positive (and unstable) for $\mu > \mu_0$ (*subcritical bifurcation*), if $a < 0$ the nontrivial equilibrium is positive (and stable) for $\mu < \mu_0$ (*supercritical bifurcation*)