Year 3 — Mathematical Biology and Ecology

Based on lectures by Dr Ozgur Akman and Dr Marc Goodfellow

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These notes are not endorsed by the lecturers, and I have modified them (often significantly) after lectures. They are nowhere near accurate representations of what was actually lectured, and in particular, all errors are almost surely mine.

Contents

1 Continuous Models for a single species

We are going to model simply how we model population dynamics for a single species. We are going to call $N(t)$ our population size at a certain time. We are going to say that $N(t)$ is continuous. We also say $N \in \mathbb{R}$ and so it's going to be a density measure. We are going to constrain this $N \geq 0, \forall t$. We can measure this and create a model, *Lecture 2*

$$\frac{dN}{dt} = f(N, t, \boldsymbol{\mu})$$

We call N the variable, then $\boldsymbol{\mu}$ the parameter. We let $t \in \mathbb{R}$ and $t > 0$.

Let's start off by thinking about an actual population of individuals, we have observed that there is some sort of growth dynamics. We can write a mechanistic model, by including mechanisms that affect the population.

$$\frac{dN}{dt} = +\text{births} + \text{resources} + \text{net migration} - \text{deaths}$$

If the positive things are greater, the population will grow, otherwise if they are smaller they decline, or they stay equal.

Now we make some assumptions, so we can write down a mathematical model.

(i) Births and deaths predominate:

$$\frac{dN}{dt} = \text{births} - \text{deaths}$$

(ii) Births and deaths are proportional to N:

$$\frac{dN}{dt} = \alpha N - \beta N \qquad \alpha, \beta \in \mathbb{R}^+$$

where we call α the birthrate and β the deathrate and $\boldsymbol{\mu} = (\alpha, \beta)$.

If we consider, as an aside,

$$\frac{dN}{dt} = \alpha N - \beta N + \gamma \qquad \gamma \in \mathbb{R}$$

this adds something like independent migration, where we assume migration is constant, this could be γN if it's proportional to N.

We can solve this equation nicely,

$$\begin{aligned} \frac{dN}{dt} &= N(\alpha - \beta) \\ \int \frac{1}{N}\frac{dN}{dt}\, dt &= \int (\alpha - \beta) dt \\ \ln N &= (\alpha - \beta)t + C \\ N(t) &= Ae^{(\alpha-\beta)t} \end{aligned}$$

Now assume this is an initial value problem, $N_0 = A$ and so,

$$N(t) = N_0 e^{(\alpha-\beta)t}$$

We are also interested in the long term dynamics of these models, the asymptotic dynamics. Hence, we consider $t \to \infty$.

$$\lim_{t\to\infty} N(t) = \begin{cases} \infty & \text{if } \alpha > \beta \\ 0 & \text{if } \alpha < \beta \\ N_0 & \text{if } \alpha = \beta \end{cases}$$

We call the case where $\alpha = \beta$ a steady state solution.

You don't usually see just a t in the equation, but we may want to use a forcing term, i.e. periodic migration in Cornwall.

$$\frac{dN}{dt} = \alpha N - \beta N + \cos(t)$$

We are not going to consider these non-autonomous systems. Hence we can write,

$$\frac{dN}{dt} = f(N, \boldsymbol{\mu})$$

We have a nice thing to make sure our growth doesn't go exponential. It's the logistic map,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) \qquad r, k > 0 \quad N \geq 0$$

where $f(N) = rN\left(1 - \frac{N}{k}\right)$ is called the logistic model. This model has a level of self regulation, so if N is high, then it will decrease later. Firstly, look at $f(N)$,

$$f(N) = rN\left(1 - \frac{N}{k}\right)$$

We start by graphing it,

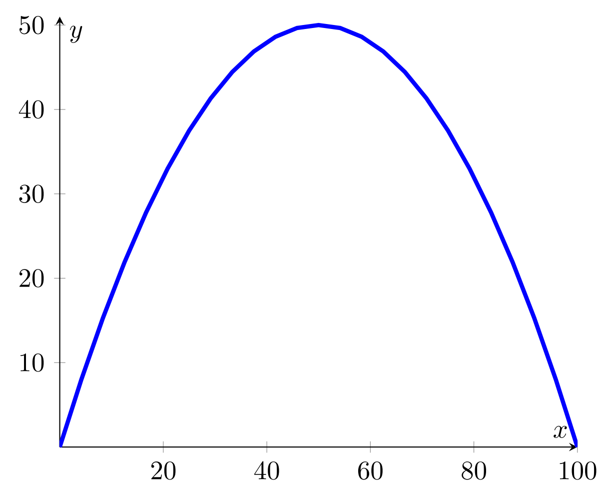


Figure 1: $y = 2x\left(1 - \frac{x}{100}\right)$

Exercise. Solve $\frac{dN}{dt} = rN(1 - \frac{N}{k})$

The solution to this equation is,

$$N(t) = \frac{N_0 k e^{rt}}{k - N_0 + N_0 e^{rt}}$$

As $t \to \infty$, we can consider it and see that it will depend on N_0. If $N_0 = 0$, then we get that $N(t) = 0, \forall\, t$. If we then take $N_0 > 0$, then we get,

$$\begin{aligned} N(t) &= \frac{N_0 k}{\frac{k - N_0}{e^{kt}} + N_0} \\ &= k \qquad\qquad\qquad\qquad\qquad\qquad t \to \infty \end{aligned}$$

lets try and formalise some of these ideas. So consider, *Lecture 3*

$$\frac{dN}{dt} = f(N)$$

where $N \in \mathbb{R}, t \in \mathbb{R}, f : \mathbb{R} \to \mathbb{R}$. Then we define steady states as, where $f(N^*) = 0$. These are also reffered to as fixed points or equilibrium. When a system in the first place depends on whether the state is attracting.

Definition 1.1 (Attrracting)**.** A steady state N^* is attracting if all trajectories that start close to N^* approach it as $t \to \infty$.

We consider $N = N^* + n$, recall the taylor series is an approximation to a function at a point,

$$f(x) \approx f(a) + f'(a)(x-a) + \frac{f''(a)(x-a)^2}{2!} + \dots$$

as we consider small values of n we can throw away higher terms. Hence, we can linearise it.

$$\begin{aligned}
\frac{dN}{dt} &= f(N) \\
\frac{dN^* + n}{dt} &= f(N^* + n) \\
\frac{dn}{dt} &= f(N^* + n) \\
\frac{dn}{dt} &\approx f(N^*) + f'(N^*)(N^* + n - N^*) + f''(a)\frac{(N^* + n - N^*)}{2!} + \dots \\
\frac{dn}{dt} &\approx 0 + f'(N^*)n + \frac{f''(N^*)}{2!}n^2 + \dots \\
\frac{dn}{dt} &\approx f'(N^*)n
\end{aligned}$$

and so we can model it by,

$$\frac{dn}{dt} = f'(N^*)n$$

which can be solved as,

$$n(t) \approx n_0 e^{f'(N^* t}$$

If $f'(N^*) > 0$, then we just have an exponential (unstable), but if $f'(N^*) < 0$ then we have a decaying exponential (stable).

Example. We shall consider,

$$\frac{dx}{dt} = rN\left(1 - \frac{N}{k}\right)$$

and so we want $f(N^*) = 0$ and hence we get that $N^* = 0$ and $N^{**} = k$. Then we find $f'(N) = r\left(1 - \frac{2N}{K}\right)$. Hence we can find $f'(0) = r$ and $r'(k) = -r$ and as $r > 0$, $f'(N^*) > 0$ hence N^* is unstable and as $f(N^{**}) < 0$ then N^{**} is stable.

We are going to recap last lectures, and study, *Lecture 4*

$$\frac{dN}{dt} = N(N-\alpha)(N-\beta)$$

where $N \in \mathbb{R}^+$ and $0 < \alpha < \beta$. We are going to focus on long term dynamics, i.e. $t \to \infty$. The steady state will give us information about that, once we know what they are and their stability, we know everything. Steady states are going to be where, $\frac{dN}{dt} = f(N) = 0$, then we can see that this is just $N^* = 0$, $N^{**}\alpha$, $N^{***} = \beta$.

Definition 1.2 (Trajectory)**.** From an initial N_0, a trajectory is how $N(t)$ evolves.

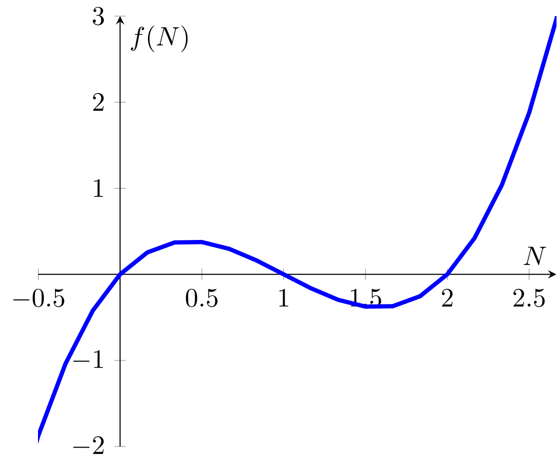


Figure 2: $y = N(N - \alpha)(N - \beta)$

Then we consider the small perturbations around the steady states and it was a linear ODE that resulted in exponential decay or just an exponential. We don't need to do this though, as we can look at the phase space as it has split up the graph into regions. These regions are $(-\infty, 0]$, $[0, \alpha]$, $[\alpha, \beta]$.

- For $(-\infty, 0]$ the system declines and so we draw arrows going away from 0 to the left.
- Then it's going to move towards α from 0 where it stops at the steady state α.
- From α to β, the particle is going to move from β to α.
- Anything larger than β, it shoots off to infinity.

From this, we can talk about the stability of the stable states. We can call 0 and β unstable and we can say α is a stable fixed point. So now we ask how do we describe $N(t)$ from this information?

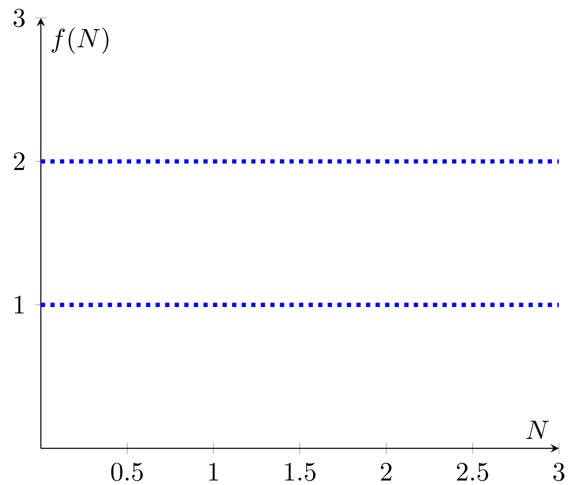


Figure 3: Steady States of the system

2 Modelling Spruce Budworm

Spruce Budworm eats spruce trees and populations have been watched and there exists some oscillatory behavior. Let's formulate some sort of model, firstly with a cartoon and then the assumptions to create a mathematical model. We consider $N =$ population density $\in \mathbb{R}$. We assume that;

- bounded growth, the logistic growth model (e.g. limited resources)
- predation (by birds)

and so we can write,

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - p(N)$$

and now a few assumptions for p,

- no predation if no prey, $p(0) = 0$
- predator population is not infinite, this means the rate of predation saturates as $n \to \infty$.
- If n is small, $p(N)$ is small.

We want a sigmoidal form of function so we can encode these assumptions.

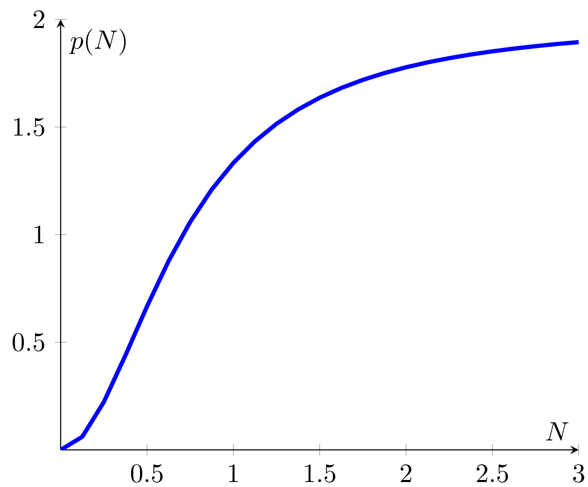


Figure 4: Sigmoidal Function, $p(N)$

We will let $p(N) = \frac{BN^2}{A^2+N^2}$, which will work quite nicely. This is a function seen all over Maths Biology. Hence, we write,

$$\frac{dN}{dt} = r_B N\left(1 - \frac{N}{k_B}\right) - \frac{BN^2}{A^2 + N^2}$$

where $r_B, k_B, B, A > 0$ and $N \geq 0$. In mathematical Biology we don't really have any big ideas about what our parameters are, we talk more generally about what our parameters actually mean. This makes it harder to know what's going on with multiple parameters.

2.1 Scaling and Non-dimensionalisation

The goal is to scale variables and time such that we get an equivalent system with fewer parameters, equivalent is in relation to the steady states and their stabilities.

Our stategy is to find constants α and β so that $u = \alpha$ and $\tau = \beta t$ yields a simpler system. The first thing we do is write down a new system, $\frac{du}{d\tau}$.

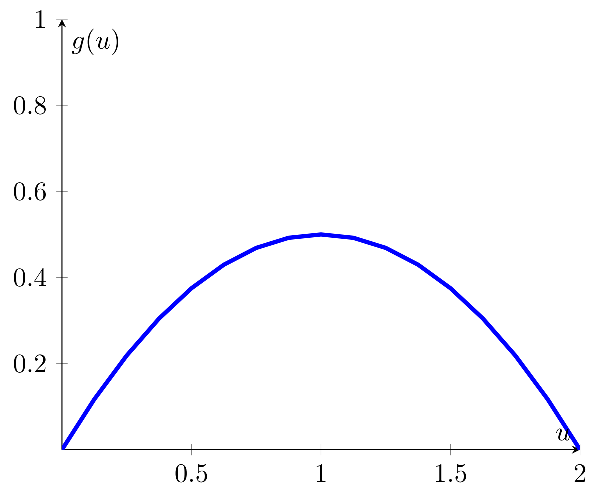
$$\frac{du}{d\tau} = \frac{dN}{dt}\frac{dt}{d\tau}\frac{du}{dN}$$

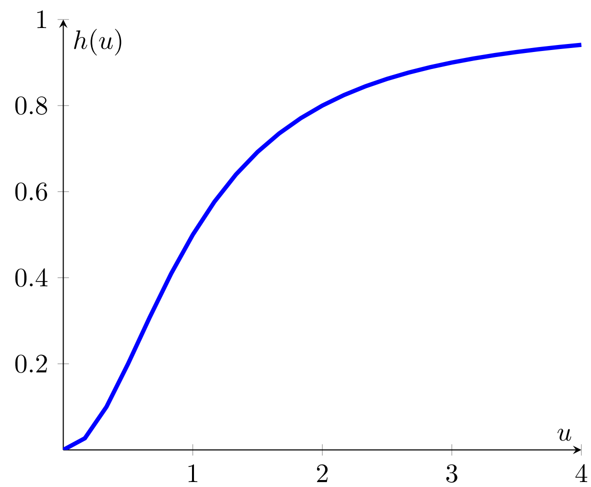
and so we can do some algebra (ommited), then we get to a point where we want to choose some values for our placeholders of α and β, given the form of the system, we choose that $\alpha = \frac{1}{A}$ and $\beta = B\alpha = \frac{B}{A}$ and hence the system simplifies to,

$$\frac{du}{d\tau} = ru\left(1 - \frac{u}{q}\right) - \frac{u^2}{1+u^2}$$

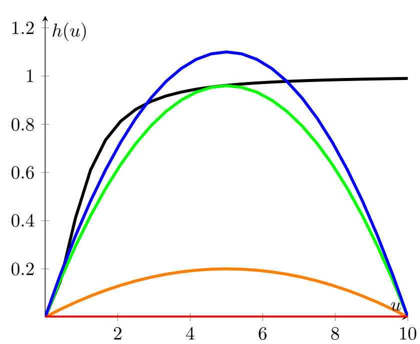
We are now going to look at our non-dimensionalised system by looking at the steady states and look at the stability. *Lecture 5*

Previously we just plotted the functions. However, this is slightly harder to do, but we write out, $f(u) = g(u) + h(u)$ and then plot them individually





and now we can consider them on the same axis,



Where we can say that there is an equilibrium when $g(u) = 0$ and this is a unstable equilibrium. Now for a $r \neq 0$, then we have the orange curve, then we have that the equilibrium at 0 is still unstable and there is a new steady state which we find to be stable. We have a third value (green), where we have u^{**}, where we have another unstable fixed point. Finally, when we move our function higher again, (blue) and we get a u^{***} that's stable. There is another interesting point, where there is a tangent between the two graphs above this one $u^{**} = u^{***}$ and hence we have three steady states.

We shall note the geometric approach, we can graph the functions and consider the derivatives around critical points. We can summarise this in a bifurcation diagram.

2.2 Bifurcation Diagram

Imagine we have those snapshots and put them on a diagram. where a filled dot is stable and unfilled is

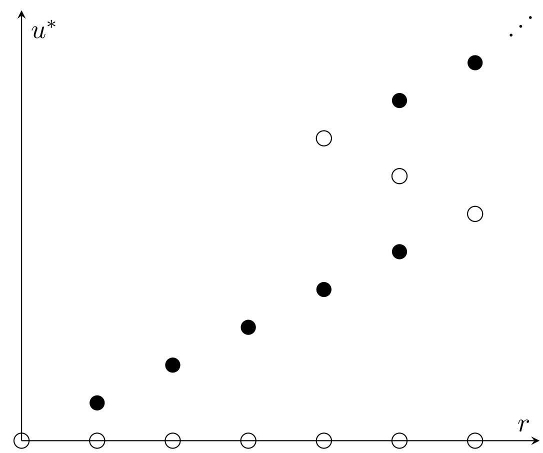


Figure 5: Bifuration Diagram for our system

unstable. We can further this by drawing smooth curves along where we have placed the dots and produce said bifurcation diagram.

Hence, let us think about trajectories of the system. The bifurcation diagram has split us into three different areas. From an initial condition, in a region one (before the unstable area) we have an unstable fixed point and an unstable fixed point. Hence, aslong as you start with a positive initial condition we converge to u^*. Moreover, Region 2 is even more interesting, in the unstable area.

We can move back to our model. Let B be the population dynamics of predators, and consider $r = \frac{r_B A}{B}$ *Lecture 6* and consider a slow change in B. Consider a decrease in B, hence an increase in r and u. As soon as you

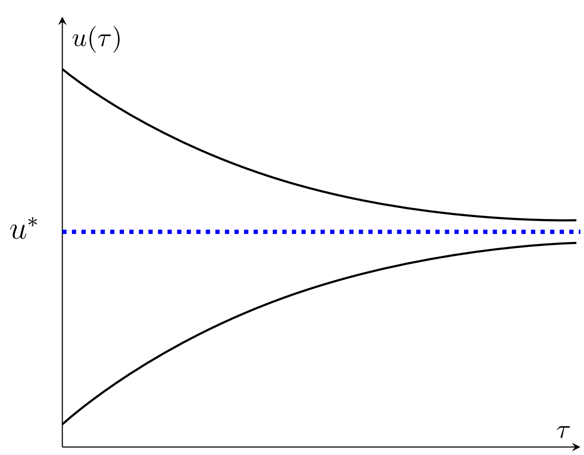


Figure 6: Steady States of the R_1

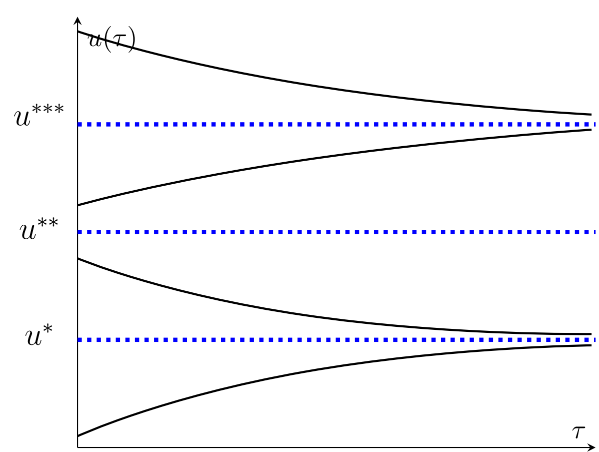


Figure 7: Steady States of the R_1

reach an unstable steady state, you jump up to the higher state and carries on as usual.

Now we are at a higher level, we have depopulation. So, what happens now as B increases, well then r and u decrease and we follow the branch back down.

This phenomena is called Hysteresis. This occurs when the bifurcation diagram has a sudden jump and then a 'reason' for the population to decrease again. We also introduced a potential way that oscillatory behavior can occur.

If we have a stable and an unstable fixed point and as you increase r, you must reach one of them eventually, as the two stable states get closer and closer they must collide, when you get a tangency. Our case is a saddle-node bifurcation.

Definition 2.1 (Saddle-node bifurcation)**.** Consider $\frac{dN}{dt} = f(N, k)$ where k is a parameter and there is a critical value of k, k_c. So that when $k = k_c$, $f'(N^*) = 0$ for an equilibrium N^*.

Then the bifurcation at $k = k_c$ is a saddle-node bifurcation if a stable-unstable pair of equilibrium are either created or destroyed.

Our system is $f = g - h$ and so, $f' = g' - h'$ is our condition for the Budworm equations.

2.3 Bistability

If we cosider our bifurcation diagram and when r is in Region 2, we have two steady states, and they coexist. If we draw the trajectories of the system; with stable, unstable, stable, unstable.

Consider some unmodeled factors, so some noise. We may use a stochastic differential equation to model. Then the noise may be enough for it to jump to the other stable steady state and so converge there.

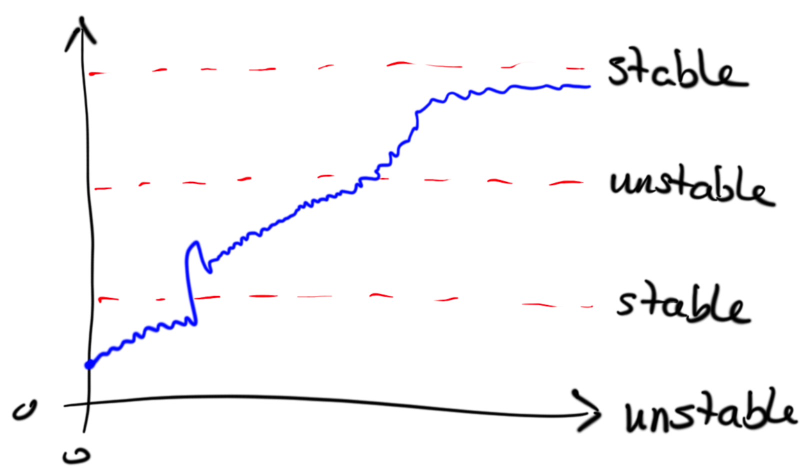


Figure 8: Noise on a trajectory

3 Harvesting a single natural population

We are now going to move into another example and consider different types of bifurcation. We are going to now consider a harvesting, *Lecture 7*

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right) - h(N)$$

where $h(N)$ is our harvesting rate. Initially we are going to keep it simple and let h be our harvesting rate, $h(N) = hN$. Now look for steady states,

$$rN\left(1 - \frac{N}{k}\right) - hN = 0$$

which has solutions, $N^* = 0$ and $r - \frac{rN^{**w}}{k} - h = 0$, hence, $N^{**} = k\left(1 - \frac{h}{r}\right)$.
We can consider $f(N) = F(N) - G(N)$ where $F(N) = rN\left(1 - \frac{N}{k}\right)$ and $G(N) = hN$ and then plot them.

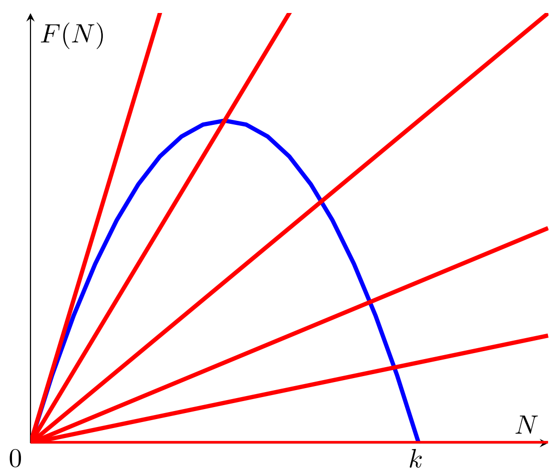


Figure 9

We can find the stability, firstly consider $f'(N) = r - h - \frac{2t}{k}N$ and see $f'(0) = r - h$ and $f'(N^*) = h - r$. We notice that for a positive steady state at N^{**} we need $h < r$. So assume that $h < r$, then we can see that we have $f'(0) > 0$ and $f'(N^*) < 0$ and so we call the $h < r$ sustainable harvesting.
In actuality, we want some yield. We denote yield, $Y(h) = nN_h$ where $N_h = N^{**}$. Hence we write $y(h)$,

$$y(h) = hk\left(1 - \frac{h}{r}\right)$$

this is a quadratic and so we have a control parameter h. Given it's a parabola we can find a maximum yield bt finding the maxima of the parabola. This occurs at $h = \frac{r}{2}$ and the yield is, $\frac{rk}{4}$. We can also find the value of N_h, which is $N_h = \frac{k}{2}$. These are the two values we expect for the logistic curve.

We can vary h and when $h = 0$ we can just see that they intersect at $(0, k)$ and it's not that interesting. Then as h increases it heads towards the $\frac{k}{2}$ and this is a critical value, as we see in Figure 9. Now imagine we increase the slope further then we reach the point where they are tangential. Over the varying of h we can see that the stability changes, after the tangential behavior they meet again for negative N and creates a new saddle point.

3.1 Transcritical Bifurcation

Before, we reached a point where the steady states absorb eachother. Here we have places where they meet and then don't absorb eachother. Here is the diagram;

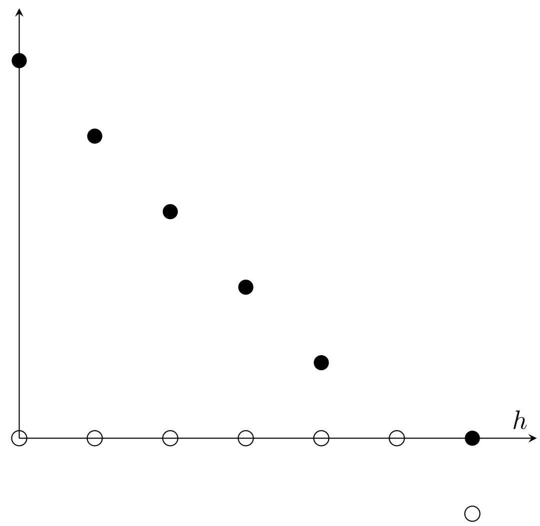


Figure 10: Bifuration Diagram for our system

Consider $\frac{dN}{dt} = f(N, k)$ where k is a parameter. There is a critical value of k, k_c such that when $k = k_c$ then $f'(N^*) = 0$ for some N^*.

Definition 3.1 (Transcritical Bifurcation)**.** Then the bifurcation at k_c is transcritical if as k passes through the stable-unstable pair of equilibria collide and exchange stability.

Whenever $k < k_c$ we have stable node and an unstable node. We go from harvesting state was supporting the population to depletion at $k = k_c$.

We now consider another factor, the time response. We define this as $T_R = \frac{1}{|f'(N^*)|}$. We say that the sign of the derivative denotes the stability of the point but the inverse maginitude is the time it takes the perturbation to return to normal. If we remove something from the population, will it take ages to get back to normal? Firslt consider the non-zer steady state. We saw that $f'(N_h) = h - r$, and we know that $h < r$ and so, $T_R(h) = \frac{1}{r-h}$ and when $h = 0$, $T_r(h = 0) = \frac{1}{r}$.

Definition 3.2 (Relative Recovery Time)**.** We define simply the relative recovery time as,

$$\frac{T_R(h)}{T_R(h=0)}$$

and s the relative recovery time for our system at N_h is simply,

$$RRT = \frac{r}{r-h}$$

We can now start to look at the relation between yield and the relative recovery time and yield.

3.2 RRT and yield

We remember that $y(t) = hk\left(1 - \frac{h}{r}\right)$ and we can then write $h^2 - rh + \frac{rY}{k} = 0$. Hence by the quadratic formula, $h = \frac{r}{2}\left(1 + \sqrt{1 - \frac{4Y}{rK}}\right)$ and now as we know our maximum yield is simply just $\frac{rk}{4}$, then we can say,

$h = \frac{r}{2}\left(1 + \sqrt{1 - \frac{Y}{Y_{max}}}\right)$. Hence, now we go to recovery time.

$$T_R(h) = \frac{1}{r-h} = \frac{1}{r - \frac{r}{2}\left(1 \pm \sqrt{1 - \frac{Y}{Y_{max}}}\right)}$$

and now the relative recovery time.

$$RRT(Y) = \frac{2}{1 \pm \sqrt{1 - \frac{Y}{Y_{max}}}}$$

We split our RRT into two branches, L_+ and L_-. We also note that $0 \leq \frac{Y}{Y_{max}} \leq 1$. If $\frac{Y}{Y_{max}} = 1$, then, $L_+ = 1$. Hence, we can plot this RRT function. *Lecture 7*

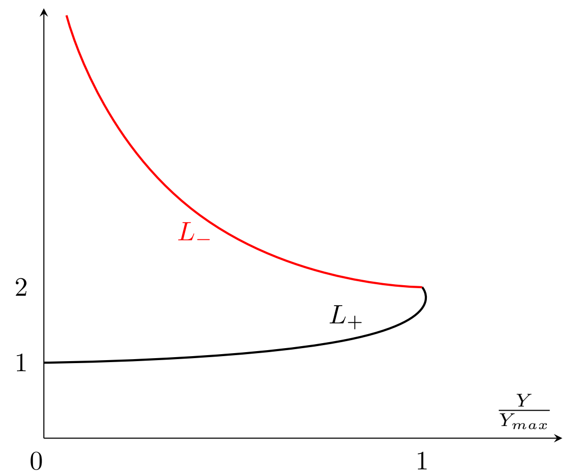


Figure 11: RRT for different values of $\frac{Y}{Y_{max}}$

This relates to as you go further and further towards the $(0, 0)$ steady state you go off to infinity.

3.3 Constant Yield Harvesting

We use the same model as before, but now we let $f(N) = N_0$. Then we can find the steady states and we get a quadratic which we can them solve and get our steady states $N = \frac{1}{2}\left(k \pm \sqrt{k^2 - \frac{4kY_0}{r}}\right) = \frac{k}{2}\left(1 \pm \sqrt{1 - \frac{4Y_0}{kr}}\right)$ and now again we consider $f(N) = g(N) - Y_0$.

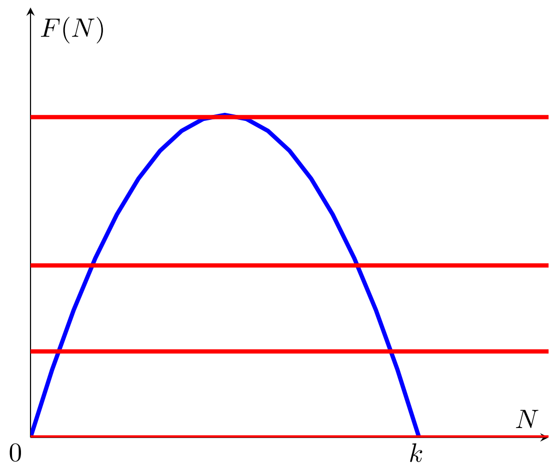


Figure 12

When $Y_0 = 0$, we get two steady states, one saddle point at 0 and a stable node at N^*. When we have a tangent line, then $f'(N) = 0$ at that point and we have a bifurcation there. We notice here, again, we have a saddle node bifurcation.

Now we consider the time response, we can see that $f'(N) = r - \frac{2rN}{k}$ and so,

$$T_R(N_+) = \frac{1}{r\sqrt{1 - \frac{Y_0}{Y_{max}}}}$$

$$RRT = \frac{1}{\sqrt{1 - \frac{Y_0}{Y_{max}}}}$$

and then we get an asymptote and so RRT goes to infinity. However there are several problems to what we are going here, as we head towards the tangential line, there may be a point where it jumps from one point to another. At other points, it can't jump as it's further apart.

4 Interactive Populations

We are now going to jump to 2D,

Example. Let's model the density of $N(t)$ which is our population of prey and $P(t)$ be the population of predators.

$$\begin{aligned}\frac{dN}{dt} &= rN\left(1 - \frac{N}{k}\right) - NPR(N)\\ \frac{dP}{dt} &= sN\left(1 - \frac{P}{hN}\right)\end{aligned}$$

We know need to choose $R(N)$, so we want a curve where we start at $(0, 0)$ and asymptotes for large N. We let it be a $R(N) = \frac{k}{N+D}$, hence our system is:

$$\begin{aligned}\frac{dN}{dt} &= rN\left(1 - \frac{N}{k}\right) - \frac{kNP}{N+D}\\ \frac{dP}{dt} &= sN\left(1 - \frac{P}{hN}\right)\end{aligned}$$

We can now consider the steady states of $diNt$ and so we can seek to non-dimensionalise it.