Contents

1 INTRODUCTION

This note is based on a Mathematical Modelling seminar in 1995 dealing with population models. The note is rather concise and assumes that the reader already has some knowledge in analysis of non-linear systems of differential equations. At the end of the note, you can find some of the references that the material is collected from, and an appendix which shows how to make a simple MATLAB program for examining some of the treated systems.

2 THE LOGISTIC EQUATION

The *logistic equation* is a non-linear first order differential equation that can be written

$$\frac{dN^*}{dt^*}\frac{1}{N^*} = r\left(1 - \frac{N^*}{K}\right). \tag{1}$$

The equation describes the number of individuals N^* in a single population as a function of time t^*. The constant K is called the sustainable level or capacity, while r is a growth rate. If $N^* \ll K$, the solution is approximately exponential $N^* = N_0 \exp(rt^*)$, with natural time scale $1/r$. The capacity K, which is also a stationary solution, gives us a scale for N^*. This leads to the scaled equation

$$\frac{dN}{dt} = N - N^2. \tag{2}$$

The most natural is to solve the equation by separation, but the simplest is to introduce $U = 1/N$, which gives the linear equation $\dot{U} + U = 1$, with general solution

$$U(t) = 1 + Ae^{-t}. \tag{3}$$

Thus,

$$N(t) = (1 + Ae^{-t})^{-1}. \tag{4}$$

Depending on the sign of A, the solution may be expressed as

$$s(t) = \frac{1}{1 + e^{-(t-t_0)}} \tag{5}$$

for $A > 0$, and

$$s(t) = \frac{1}{1 - e^{-(t-t_0)}} \tag{6}$$

for $A < 0$.

We see that *all* solutions in the interval $\langle 0, 1 \rangle$ are expressible by the single function

$$s(t) = \frac{1}{1 + e^{-t}}, \tag{7}$$

which is called the logistic curve, or the *sigmoid*. Solutions in the interval $\langle 1, \infty \rangle$ evolve according to the single function $1/(1 - e^{-t})$, as shown in figure 1.

We immediately see that $N \equiv 1$ is a stable equilibrium solution, while $N \equiv 0$ is unstable (*Physically*, $N = 0$ is of course stable!). One feature of the sigmoid is that no matter how much time it has taken a population to reach a certain level, e.g. $K/10$, it will only take time $\mathcal{O}(1/r)$
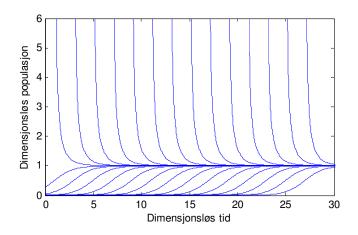
Figure 1: Solutions of the dimensionless logistic equation.

to reach saturation. We also note that no matter how high the starting level is, we will reach equilibrium in time $\mathcal{O}(1/r)$. Thus, changing K significantly has dramatic consequences.

It is useful to apply the trick of introducing $U = 1/N$ even when r and K vary with time. Let us change the notation above for a moment and write $K^*(t^*) = K\kappa(rt^*)$, $r^* = r\rho(rt^*)$. After scaling, we get the equation

$$\frac{dN}{dt} = \rho(t)N\left(1 - N/\kappa(t)\right), \tag{8}$$

or

$$\frac{dU}{dt} + \rho(t)U = \rho(t)/\kappa(t), \tag{9}$$

which is a linear first order equation. As a simple example, consider $\rho(t) = 1$ and $1/\kappa(t) = 1 + a\sin(\omega t)$. Then, after all transients have died out, the solution is

$$N(t) = \left\{1 + \frac{a}{\sqrt{1+\omega^2}}\sin\left(\omega t - \phi\right)\right\}^{-1}, \quad \phi = \arcsin\left(\frac{\omega}{\sqrt{1+\omega^2}}\right). \tag{10}$$

The behaviour when $\omega \to 0$ and $\omega \to \infty$ is as expected.

2.1 Hunting and Catching

It is easy to incorporate hunting or catching into the logistic model, e.g. the fish stock in a certain part of the ocean. The model starts from the logistic equation and additionally assumes a level of fishing per unit of time which is proportional to the fish stock and the number of boats u^* participating,

$$\frac{dN^*}{dt^*} = rN^*\left(1 - \frac{N^*}{K}\right) - \alpha N^* u^*. \tag{11}$$

By a similar scaling as above, the equation becomes

$$\frac{dN}{dt} = N - N^2 - \mu N, \quad \mu = \alpha u^*/r. \tag{12}$$

The equilibrium solutions become $N_1 = 0$, $N_2 = 1 - \mu$. Standard linear stability analysis gives that the solution $N_1 = 0$ is stable for $\mu > 1$ and unstable for $\mu < 1$, while $N_2 = 1 - \mu$ is stable when $\mu < 1$. The case $\mu = 1$ is left for the reader.

3

A steady withdrawal per time unit can be expressed as

$$\frac{dQ}{dt^*} = \alpha N_2 u^* = \alpha u^* K(1 - \mu) = rK\mu(1 - \mu), \tag{13}$$

which reaches a maximum for $\mu = 1/2$, i.e. $u^* = r/(2\alpha)$ and $N_2^* = K/2$. Hence, optimal resource management is attained when the stock is kept at a level with maximal growth, i.e. at half the maximal stock level. This is a well known "law" in resource management.

2.2 Delayed reaction

Delay in a logistic model enters naturally in systems where the growth is dependent on the conditions some time back. The equation is

$$\frac{dN^*}{dt^*}\frac{1}{N^*} = r\left(1 - \frac{N^*(t^* - \tau^*)}{K}\right) \tag{14}$$

which becomes, after scaling in the same way as before,

$$\frac{dN(t)}{dt} = N(t)\left(1 - N(t - \tau)\right). \tag{15}$$

In May 1973 the Norwegian Nobel prize winner in economics, Ragnar Frisch, was the first to start applying such models. In general, it is not possible to solve the equation analytically, but we still have the equilibrium equation $N(t) \equiv 1$. Linear stability analysis is about introducing $N(t) = 1 + a(t)$ and neglecting terms that are $O(a^2)$. This gives us the prototypical delay equation

$$\dot{a}(t) = -a(t - \tau). \tag{16}$$

The equation is linear, so the sum of two solutions is still a solution. Thus, it is reasonable to study the behaviour of Fourier components, and by inserting a component of the form $a(t) = a_0 e^{zt}$, $z = x + iy$, we get a complex equation for z,

$$z = -e^{-z\tau}, \tag{17}$$

or the following pair for (x, y):

$$\begin{aligned} x &= -e^{-x\tau}\cos(y\tau), \\ y &= e^{-x\tau}\sin(y\tau) \end{aligned} \tag{18}$$

Since $e^{-zt} = e^{-xt}e^{-iyt}$, the stability properties are determined by the value of x. It is easy to show that if $0 \leq \tau < 1/e$, the solution is real with $-e < x < -1$. In other words, $N(t) = 1$ is stable. In the interval $1/e < \tau \leq \pi/2$, the dominant solution will still have negative real part, but it will now be complex. This gives damped oscillations, which in the limit with small amplitude is exponentially damped. When $\tau = \pi/2$, the linearised equation has a periodic solution, and for larger τ there will be solutions where $x > 0$. Then, $N(t) = 1$ is no longer stable.

For further studies of delay equations, see the literature, e.g. Hairer, Nørsett and Wanner (1993). It has been said that this type of equations explains the dramatic population cycle of lemmings (see figure 2). Note that there are freely available program packages on the Internet for solving delay equations in MATLAB.
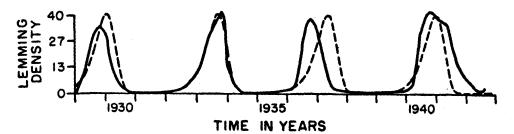
4

FIG. 2. Shelford's (1943) data on the lemming population in the Churchill area in Canada (expressed as numbers of individuals per hectare), compared with a naive theoretical curve (dashed line) obtained from the simple time delayed logistic equation (3); the time delay T is taken to be a little under one year ($T = 0.72$ yr.).

Figure 2: Lemming density in Churchill, Canada, adapted to a delay of 9 months (one winter) (May, 1978).

3   THE GROWTH OF THE EARTH POPULATION

In laboratory studies of closed bacterial cultures, it has proven hard to find a behaviour following the logistic model. Instead, the population eventually tends to zero because of *self-poisoning*. It's not improbable that something similar will hold for humanity. The poisoning may be caused by PCBs, long-lived radioactive isotopes, or hormone copycats affecting fertility. This has already occurred for our neighbours in the Arctic.

In a world where social benefits are more equally distributed, it would be natural that the amount of pollution released per unit time is proportional to the number of individuals. The total amount of pollution at time t^* is then proportional to

$$\int_{-\infty}^{t^*} N^* (s^*) \, ds^* \tag{19}$$

if the pollution does not brake down with time. In addition, we assume that the negative effect on the growth rate is proportional to the amount of pollution. This gives us the following modified model:

$$\frac{1}{N^* (t^*)} \frac{dN^* (t^*)}{dt^*} = r \left(1 - \frac{N^* (t^*)}{N_m} \right) - c \int_{-\infty}^{t^*} N^* (s^*) \, ds^*, \ c > 0. \tag{20}$$

(Note: This is not a new and original model, but the exact reference to the literature is missing).

Is it possible that a population following this equation would survive in the long term? Assume that $\lim_{t^* \to \infty} N^* (t^*) = a > 0$, and that the population development starts at $N_s < N_m$. The solution will stay below N_m and thus,

$$\frac{dN^* (t^*)}{dt^*} < N_m \left(r - c \int_{-\infty}^{t^*} N^* (s^*) \, ds^* \right). \tag{21}$$

Since $\lim_{t^* \to \infty} N^* (t^*) = a$, the right-hand side will tend to $-\infty$ when $t^* \to \infty$, which is completely incompatible with $N^* (t^*) \to a$.

A simple alternative model which doesn't have as dramatic consequences, is

$$\frac{1}{N^*(t^*)}\frac{dN^*(t^*)}{dt^*} = r\left(1 - \frac{N^*(t^*)}{N_m}\right) - c\int_{-\infty}^{t^*} e^{-(t^*-s^*)/\tau} N^*(s^*)\,ds^*. \tag{22}$$

Here, the pollution (or the effect on the growth rate) is broken down with time constant τ, and it seems that a certain population level can survive (Details are left for the reader).

Let us go back to equation 20 and scale it in the usual way. This results in

$$\frac{1}{N}\frac{dN}{dt} = 1 - N - \alpha\int_{-\infty}^{t} N(s)\,ds, \ \alpha = \frac{cN_m}{r^2}. \tag{23}$$

The equation reduces to a 2nd order equation by introducing $C(t) = \int_{-\infty}^{t} N(s)\,ds$, but it can probably not be solved analytically. If α is large, and we start with a small population, we can expect that N never reaches 1. Then, if we neglect the second term on the right-hand side, we obtain an equation which gives us an upper limit for the population developing according to the complete equation,

$$\frac{1}{N_u}\frac{dN_u}{dt} = 1 - \alpha\int_{-\infty}^{t} N_u(s)\,ds. \tag{24}$$

We introduce $P(t) = \alpha\int_{-\infty}^{t} N_u(s)\,ds$, which leads to the equation

$$P'' = P'(1 - P). \tag{25}$$

The equation can be integrated once,

$$P'(t) = P - \frac{P^2}{2} + A, \tag{26}$$

where A is a constant.

If we restrict to the situation where both $P(t)$ and $P'(t)$ tend to 0 when $t \to -\infty$, we must have $A = 0$, and we get a logistic equation. The solution for N is then

$$N(t) = \frac{1}{\alpha}P'(t) = \frac{1}{2\alpha}\cosh^{-2}\left(\frac{t - t_0}{2}\right). \tag{27}$$

This function is not dissimilar to a Gaussian bell curve with a maximum for $t = t_0$. As expected, small α gives large maximum population.

If one were to adapt the model to actual data, one could start with the inflection points of the function. Let

$$N_0(\tau) = \cosh^{-2}(\tau/2). \tag{28}$$

It is easy to show that $N_0''(\tau) = 0$ for $\tau = \pm 2\operatorname{atanh}(1/3) = \pm 1.3170\ldots$ Hence, if we set $\tau_0 = -2\operatorname{atanh}(1/3)$, we find

$$N_0(\tau_0) = \frac{2}{3},$$
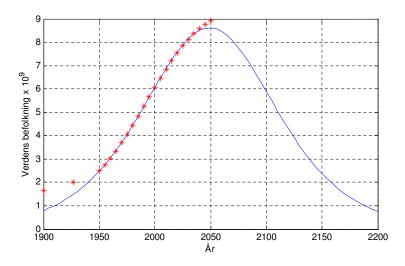$$N_0'(\tau_0) = \frac{2}{9}\sqrt{3}. \tag{29}$$

Figure 3: The time evolution of the Earth's population for a logistic model with pollution (solid curve). Actual population evolution and the UN's estimates (stars).

The population of the Earth is claimed to have passed the inflection point $N''(t_s) = 0$ in 1996, when we, according to my sources, had

$$N(t_s) = 5.75 \times 10^9 \text{ individuals,}$$

$$\frac{dN}{dt}(t_s) = 8.3 \times 10^7 \text{ years}^{-1}. \tag{30}$$

By letting

$$N^*(t^*) = N_{\max} N_0 \left(\frac{t^* - t_{\max}}{B} \right), \tag{31}$$

we obtain

$$N_{\max} = \frac{3}{2} 5.75 \times 10^9 = 8.62 \times 10^9,$$

$$B = \frac{8.62 \times 10^9}{8.3 \times 10^7} \frac{2}{9} \sqrt{3} \text{ years} = 40 \text{ years} \tag{32}$$

$$t_{\max} = 1996 + 1.3170 \times 40 = 2049.$$

In figure 3, $N^*(t^*)$ is plotted against year, and it is compared to data and predictions (created by the UN) which are available on *Wikipedia*. As expected, the curves coincide between 1950 and 2040, but one can clearly not trust such a model too much.

4 COMPETITION FOR THE SAME RESOURCES

In 1934, the Russian biologist Georgyi Frantsevitch Gause (1910–1986) wrote the book *The Struggle for Existence*, where he formulated *The Competitive Exclusion Principle*, which states that two species cannot coexist in the long term if they compete for the same limited resource (applicable to the current situation in the Middle East?). A simple model which reflects such a
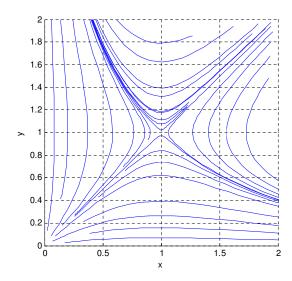
Figure 4: Numerical solutions for Gause's model with $\varepsilon = 1$.

situation is the following:

$$\frac{1}{N_1^*}\frac{dN_1^*}{dt^*} = r_1\left(1 - \alpha N_2^*\right), \tag{33}$$

$$\frac{1}{N_2^*}\frac{dN_2^*}{dt^*} = r_2\left(1 - \beta N_1^*\right). \tag{34}$$

Two obvious time scales appear, namely $1/r_1$ and $1/r_2$. If the difference between the time scales is large, this will be a stiff system, with behaviour characteristic for singular perturbation. The scaling is easy, and leads to a dimensionless system of the form

$$\frac{dx}{dt} = x\left(1 - y\right),$$
$$\frac{dy}{dt} = \varepsilon y\left(1 - x\right),$$

where the parameter ε expresses the relationship between the time scales. From the symmetry of the equations, we see that all conclusions reached about small ε can be rewritten to corresponding statements for large ε. Thus, it is enough to consider $\varepsilon < 0 \le 1$. The system has equilibrium points in $(1,1)$ which is a saddle point, and $(0,0)$ which is an unstable node. If one of the populations is 0, the other grows without limits, so the model is not especially realistic.

A numerical solution of the system for $\varepsilon = 1$ is shown in figure 4. We see that the first quadrant splits into four areas delimited by the coordinate axes and two curves crossing each other in $(1,1)$. These curves are called *separatrices*. Systems close to the separatrix $y = x$ live dangerously: A small disturbance may cause the movement to jump over to the other side, and we get a fundamentally different development of the population.

It is easy to find an implicit equation for the trajectories by dividing the equations by each other and separating the variables:

$$\left(\frac{1}{y} - 1\right) dy = \varepsilon\left(\frac{1}{x} - 1\right) dx. \tag{35}$$

8

This gives all non-trivial trajectories, expressed as

$$ye^{-y} = C\left(xe^{-x}\right)^{\varepsilon}, \ 0 < \varepsilon \le 1, \tag{36}$$

where C is a positive constant. For given values of ε and C we see from xe^{-x} that there exist four pairs of solutions. Pairs of these lie on the same trajectories. The maximum value of the left-hand side is e^{-1}. If $\max_x C(xe^{-x})^{\varepsilon} > e^{-1}$, i.e. $C > e^{\varepsilon-1}$, we describe the trajectories to the right and left of the equilibrium (1,1). Otherwise, we describe the trajectories over and under (1,1). The separatrices are given implicitly by

$$ye^{-y} = e^{\varepsilon-1}\left(xe^{-x}\right)^{\varepsilon}. \tag{37}$$

Corresponding models have also been made for warfare. One should take care when making conclusions from such primitive models, as there exist systems in nature that apparently violate Gause's principle (among others, plankton, according to Wikipedia).

5   THE LOTKA–VOLTERRA EQUATIONS

The Lotka–Volterra equations, also known as the predator-prey equations were formulated by Alfred J. Lotka and Vito Volterra independently, around 1925. Since the equations are described in detail in most books about non-linear differential equations, the presentation below is very brief. In the same way as the equations above, they can be written as a system

$$\frac{1}{N_1^*}\frac{dN_1^*}{dt^*} = r_1\left(1 - \alpha N_2^*\right), \tag{38}$$

$$\frac{1}{N_2^*}\frac{dN_2^*}{dt^*} = r_2\left(-1 + \beta N_1^*\right), \tag{39}$$

where N_1^* is the prey density and N_2^* is the predator density. As in the preceding paragraph, after scaling the system attains the form

$$\frac{dx}{dt} = x\left(1 - y\right), \tag{40}$$

$$\frac{dy}{dt} = \varepsilon y\left(-1 + x\right), \tag{41}$$

with equilibria in (1,1) and (0,0) independent of the size of ε. The first is a centre, and the second a saddle point. The trajectories are shown in figure 5.

Here, the implicit equation for the trajectories is

$$ye^{-y}\left(xe^{-x}\right)^{\varepsilon} = C, \quad 0 < C. \tag{42}$$

Since the left-hand side is limited from above by $e^{-1-\varepsilon}$, we must have $C < e^{-1-\varepsilon}$. For a given possible value of C, x will also be restricted to the interval around $x = 1$ which satisfies $(xe^{-x})^{\varepsilon} \ge Ce$. We get a similar interval for y defined by $ye^{-y} \ge Ce^{\varepsilon}$. Thus, the trajectory is inside a rectangle which is defined by equality of the respective inequalities. The shape of the rectangle is determined by ε and C. When C approaches its maximum value, the trajectories shrink towards $(1,1)$ and become approximately elliptical with centre $(1,1)$. When $C \ll 1$ the trajectory shifts towards the coordinate axes, unless $y \approx -\varepsilon x - \ln(C)$, which is the trajectory far away from the coordinate axes. The orbit shape is roughly triangular.
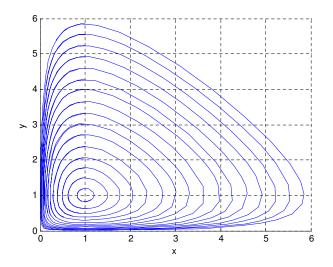
Figure 5: Paths of the Lotka–Volterra system when $\varepsilon = 1$ calculated numerically. The numerical solution goes around the orbits several times and does not connect perfectly.

Limitations in growth as in the logistic equation leads to scaled equations of the form

$$\frac{dx}{dt} = x\left(1 - y - \alpha x\right), \tag{43}$$

$$\frac{dy}{dt} = \varepsilon y\left(-1 + x - \beta y\right) \tag{44}$$

with equilibria in the origin and (x_0, y_0) where

$$x_0 = \frac{1 + \beta}{1 + \alpha\beta} \ , \ y_0 = \frac{1 - \alpha}{1 + \alpha\beta}. \tag{45}$$

We leave to the reader to show that (x_0, y_0) becomes a stable focus when α and β are small. What else happens?

If we return to the original Lotka–Volterra equations and utilise that the trajectories are periodic with period T, we get

$$\frac{1}{r_1} \int\limits_{t^*=0}^{T} \frac{dN_1^*}{N_1^*} = \int\limits_{t^*=0}^{T} \left(1 - \alpha N_2^*\right) dt^* = T - \alpha \int\limits_{t^*=0}^{T} N_2^* dt^*, \tag{46}$$

and correspondingly for the other equation. But, since

$$\frac{1}{r_1} \int\limits_{t^*=0}^{T} \frac{dN_1^*}{N_1^*} = \frac{1}{r_1} \left(\ln(N_1^*(T) - \ln(N_1^*(0)\right) = 0, \tag{47}$$

so

$$\frac{1}{T} \int\limits_{t^*=0}^{T} N_2^* dt^* = \frac{1}{\alpha}, \tag{48}$$

$$\frac{1}{T} \int\limits_{t^*=0}^{T} N_1^* dt^* = \frac{1}{\beta}. \tag{49}$$

10

The average levels become equal to the values in the equilibrium point.

If one studies the predator-prey models a little more in depth, one will see that the Lotka–Volterra equations are special. Typically, such models will have stable equilibrium points. If one observes oscillations in nature, these will not be periodic solutions about a neutral equilibrium point, but so-called *stable limit cycles* that are more stable to perturbations.

Delays in the Lotka–Volterra models have also been studied, and such equations can, unlike ordinary equations actually have *chaotic* behaviour.

It is also possible to study what hunting means to a Lotka–Volterra system. If we assume constant capture relative to population, this can be modelled as

$$\frac{dN_1^*}{dt^*} \frac{1}{N_1^*} = r_1 \left(1 - \alpha N_2^*\right) - f_1, \tag{50}$$

$$\frac{dN_2^*}{dt^*} \frac{1}{N_2^*} = r_2 \left(-1 + \beta N_1^*\right) - f_2. \tag{51}$$

Since we can write

$$\frac{dN_1^*}{dt^*} \frac{1}{N_1^*} = (r_1 - f_1) \left(1 - \frac{r_1 \alpha}{r_1 - f_1} N_2^*\right), \tag{52}$$

$$\frac{dN_2^*}{dt^*} \frac{1}{N_2^*} = (r_2 + f_2) \left(-1 + \frac{r_2 \beta}{r_2 + f_2} N_1^*\right), \tag{53}$$

we see that as long as the parameters are constant, the behaviour will be like for a Lotka–Volterra system with modified parameters. In particular,

$$\frac{1}{T} \int_{t^*=0}^{T} N_2^* dt^* = \frac{1}{\alpha} \frac{r_1 - f_1}{r_1}, \tag{54}$$

$$\frac{1}{T} \int_{t^*=0}^{T} N_1^* dt^* = \frac{1}{\beta} \frac{r_2 + f_2}{r_2}. \tag{55}$$

The model is not necessarily realistic if one looks at the average catch per time unit:

$$F_1 = \left\langle N_1^* \right\rangle f_1 = \frac{1}{\beta} \frac{r_2 + f_2}{r_2} f_1, \tag{56}$$

$$F_2 = \left\langle N_2^* \right\rangle f_2 = \frac{1}{\alpha} \frac{r_1 - f_1}{r_1} f_2. \tag{57}$$

We observe that if we just catch predators ($f_1 = 0$), we will be able to capture an unlimited amount, without the average level changing. In contrast, the average of the prey population will grow (!). There is much that one could study for such systems, for example, how the behaviour is when one has time dependent catch with variations that are long and short relative to the period of the stock variations.
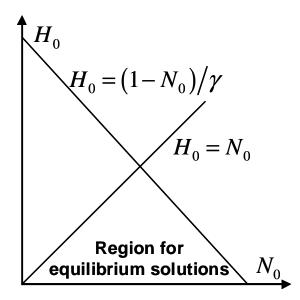
Figure 6: All equilibrium solutions lie within the shaded area when f_N and f_H are between 0 and 1.

6   WHALES AND KRILL

Around 1980, R. M. May made a model for the whale-krill system in Antarctica, where N^* is the krill population and H^* the whale population:

$$\frac{dN^*}{dt^*}\frac{1}{N^*} = r\left(1 - \frac{N^*}{K_N}\right) - a_2 H^* - u_N F_N, \tag{58}$$

$$\frac{dH^*}{dt^*}\frac{1}{H^*} = q\left(1 - \frac{H^*}{\alpha N^*}\right) - u_H F_H \tag{59}$$

As seen, the maximum sustainable level of the whale stock is proportional to the krill level. The growth rates r and q must be expected to be quite different, and so that $1/r \ll 1/q$, i.e. $\varepsilon = q/r \ll 1$. If we scale based on the time scale for changes in the whale population, we end up with the following singularly perturbed system:

$$\varepsilon \dot{N} = N\left(1 - N - \gamma H - f_N\right), \tag{60}$$

$$\dot{H} = H\left(1 - H/N - f_H\right) \tag{61}$$

We assume that f_N and f_H are constants between 0 and 1. Then the model has a stationary point in

$$N_0 = \frac{1 - f_N}{1 + \gamma(1 - f_H)}, \tag{62}$$

$$H_0 = \frac{(1 - f_N)(1 - f_H)}{1 + \gamma(1 - f_H)}, \tag{63}$$

and all singular points lie inside a triangle, as pointed out in figure 6.

The equilibrium solutions are stable focuses, as shown in figure 7. When ε is small, the solutions bear the characteristic sign of *singular perturbation*.
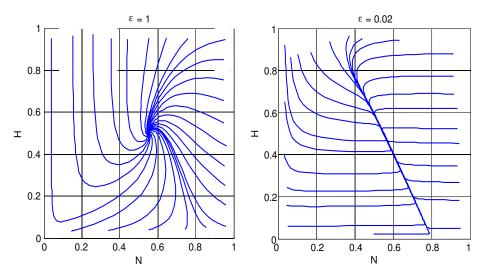
Figure 7: Phase plot of the whale-krill system with $f_N = 0.2$ and $f_H = 0.1$, $\gamma = 0.5$ with $\varepsilon = 1$ to the left, $\varepsilon = 0.02$ to the right.

This behaviour is not so striking in areas where $N = O(\varepsilon)$ or $N \ll H$, since one then also will have other small terms in the equations. If the population of whales is lower than the equilibrium level, one sees how the system quickly approaches a "quasi-static equilibrium", approximately given by $1 - N - \gamma H - f_N = 0$, and then follows it towards the equilibrium point. Obviously, this is due to the krill population reacting quickly compared to the whale stock.

For a given catch rate, the amount caught per time unit is

$$P_N = f_N N_0 = \frac{f_N(1 - f_N)}{1 + \gamma(1 - f_H)}, \tag{64}$$

$$P_H = f_H H_0 = \frac{f_H(1 - f_H)(1 - f_N)}{1 + \gamma(1 - f_H)} \tag{65}$$

We see that the maximum amount of krill we can take out is given by $f_N = 1/2$ whatever the catch of whales, while the maximum amount of whales is $f_H = \left(1 + \gamma\sqrt{1 + \gamma}\right)/\gamma$. It is not possible to increase whaling by fishing krill, while it of course is beneficial to catch whales to be able to catch more krill.

It is easy to imagine economic issues related to such a model. If one catches both whales and krill, one is interested in maximising profits. If the prices are p_N and p_H, one would like to maximise economic return per time unit, $p_N P_N + p_H P_H$. At the same time there's a limit to the weight of catch over a period T that can be transported with available tonnage, $(w_N P_N + w_H P_H)t \leq L$.

If catch rates are proportional to the inverse of the populations, i.e. a fixed quantity is fished per unit of time irrespective of the size of the stocks, the equations are more cumbersome. Any equilibrium solutions can be found from

$$N\left(1 - N - \gamma H - a_N/N\right) = N - NH^2 - \gamma HN - a_N = 0, \tag{66}$$

$$H\left(1 - H/N - a_H/H\right) = H - H^2/N - a_H = 0. \tag{67}$$

13

If we assume that $\gamma = 1$ and that we only catch whales, we deduce that

$$N_0 = 1 - H_0,$$

$$H_0 = \frac{1 + a_H \pm \sqrt{(1 + a_H)^2 - 8a_H}}{4}. \tag{68}$$

In other words, if $0 < a_H < 3 - 2\sqrt{2}$, we have two equilibrium points. We leave details to the reader.

An important aspect of such models is whether they are stable against disturbances, and how well the catch can be controlled by decree, etc. As one understands, there is unlimited potential for both mathematical, numerical and economic analysis.

7 SPECIES THAT BENEFIT FROM EACH OTHER

There are many examples of systems where the species have mutual benefit of each other. Plants that depend on pollinators is one such example. Pollinators on the other hand receive nectar from the plant. In some situations the pollinators are specially adapted to one type of plants (or perhaps the reverse is true?).

It is easy to see that the following simple model, where P is plant population and B is the pollinator, leads to an absurdity:

$$\frac{dB^*}{dt^*} \frac{1}{B^*} = (-1 + \alpha P^*), \tag{69}$$

$$\frac{dP^*}{dt^*} \frac{1}{P^*} = \varepsilon(-1 + \beta B^*). \tag{70}$$

It is a bit more surprising that

$$\frac{dB^*}{dt^*} \frac{1}{B^*} = (-1 + \alpha P^* - \gamma B^*), \tag{71}$$

$$\frac{dP^*}{dt} \frac{1}{P^*} = \varepsilon(-1 + \beta B^* - \delta P^*) \tag{72}$$

does not work either.

The following model, which is taken from May (1978), starts with a logistic equation for the pollinators, where the sustainable population level depends on the plant population:

$$\frac{dB^*}{dt^*} = rB^* \left(1 - \alpha \frac{B^*}{P^*} \right). \tag{73}$$

The plant quantity in turn satisfies an equation of the form

$$\frac{dP^*}{dt^*} = -qP^* + I \frac{\hat{B}}{\hat{B} + C}, \tag{74}$$

where $\hat{B}$ is the effective density of pollinators. If there are very few plants, it is not certain that the pollinators can find plants ($\hat{B} \ll B^*$), while if there are many plants, all pollinators find enough plants ($\hat{B} \approx B^*$). A possible model for $\hat{B}$ can then be

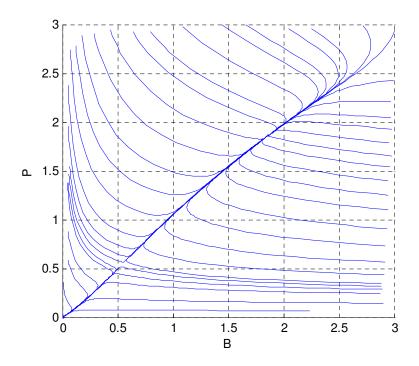$$\hat{B} = B^* \frac{P^*}{P^* + D}. \tag{75}$$

Figure 8: Phase diagram for pollinators (B) and plants (P) for a situation where we have one stable and one unstable equilibrium point.

Together, this gives the equations

$$\frac{dB}{dt}\frac{1}{B} = 1 - a\frac{B}{P},$$
$$\frac{dP}{dt}\frac{1}{P} = -\varepsilon + b\frac{B}{BP + P + 1}, \tag{76}$$

where we have scaled in the following way:

$$P^* = DP,\ B^* = CB,\ \ a = \alpha C/D,\ \ b = I/(rD),\ \ t^* = tr,\ \ \varepsilon = q/r. \tag{77}$$

By solving for the equilibria, we end up with

$$B_0 = \frac{1}{2a\varepsilon}\left(b - \varepsilon a \pm \sqrt{(b - \varepsilon a)^2 - 4a\varepsilon^2}\right), \tag{78}$$
$$P_0 = aB_0. \tag{79}$$

There will be two equilibria in the first quadrant if $0 < b - \varepsilon a,\ \ 0 < (b - \varepsilon a)^2 - 4a\varepsilon^2$, or

$$0 < (I - q\alpha C)/D, \tag{80}$$
$$0 < \frac{(I - q\alpha C)^2 - 4\alpha q^2 CD}{D^2}. \tag{81}$$

Figure 8 illustrates a random set of parameters that give two equilibria ($\varepsilon = 1/2, a = 1, b = 1.7$).

If the system is left of the separatrix, it dies out. Isolated systems of this kind are common only in areas with stable climatic conditions. According to the reference, there are e.g. no such ant-plant systems north of $24°$, no nectar-eating bats (!) north of $33°$, or orchid-bees north of $24°$ in America.

8   AFTERWORD

The mathematical theory underlying the models we have seen is a part of what is called *dynamical systems.* This is a field with large and interesting activity that not only includes differential equations, but also time-discrete and stochastic models. In special cases, e.g. for some systems of ordinary differential equations with more than two variables, discrete models, or equations with delay, the solutions exhibit so-called *chaotic* behaviour. In nature, both systems that seem to be fairly robust to disruptions (e.g. described by the before-mentioned stable limit cycles), and the completely opposite occur (e.g. the equations for atmospheric turbulence, which controls the weather).

9   BIBLIOGRAPHY

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10 APPENDIX: EQUATION SOLVER IN MATLAB

There are many interactive solvers for two-dimensional ODE systems on the *Internet.* Below is a simple solver in MATLAB, so that one can test out the systems that are discussed in the text. The solver consists of two m-files. The first is the program itself, while the second computes the derivatives (right-hand side) of the equations. See the documentation of MATLAB for more information about `ode45`. The MATLAB function `ginput` makes it possible to point in the plot with the mouse to set the initial values (Text after `%` in the code are comments).

```
tspan = [0 10];              % Define a time interval
axis([-3 3 -2 4]); grid;  % Define the axes
hold on                         % Lock the coordinate system
for loop = 1:100          % Allow for up to 100 repetitions
  x0 = ginput(1);          % Pick the initial value by pointing with the mouse
  [t,x]=ode45('xder',tspan,x0);  % Integrate the equation
  plot(x(:,1),x(:,2))     % Draw the path
end;

function xd=xder(t,x)
s = x(1);
c = x(2);
xd(1)=-s*(1-c)+c;
xd(2)=s*(1-c)-c+(1-c).^2;
xd = xd';  % column vector
```

Figure 9 shows an example of how the trajectories look for the equation above with a random selection of initial values.
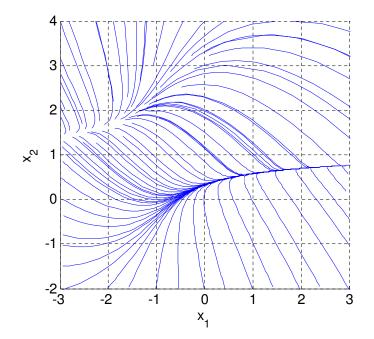
Figure 9: Trajectories of the equation as defined in the MATLAB file `xder.m` in the text. Starting points are selected with the mouse so that it is possible to examine specific areas of the graph in detail.