Modelling with ordinary differential equations

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1 Introduction

1.1 Preliminaries

This course is concerned with differential equations (DEs) having just one *independent variable*, which are known as ordinary differential equations (ODEs). The course Partial Differential Equations and Waves (Semester 2) tackles differential equations with multiple independent variables. We will consider scalar ODEs having a single dependent variable and vector ODEs, equivalently systems of ODEs, having vector (or multiple) dependent variables.

1.2 Dynamics, modelling and computation

Dynamics, modelling and computation are the key ingredients of this course.

1.2.1 Dynamics

Dynamics refers to the temporal structure of a quantity.

Typically, we seek the behaviour of a function u(t), which describes some physical quantity u (location, temperature, population, etc), as a function of time t. To do this we will use an ODE with one or more *initial conditions* (ICs), giving an *initial value problem* (IVP).

Alternatively, we may seek the *spatial structure* of a quantity, i.e. u(x), where x denotes location. For this we need an ODE with one or more boundary conditions, and the problem will be a *boundary value problem* (BVP).

1.2.2 Modelling

Mathematical modelling is the process of deriving equations for realword problems, with associated initial and/or boundary conditions.

Differential equations model an enormous range of phenomena in many applications areas in physics, chemistry, biology, sociology, engineering and games. We 'solve' differential equations to predict and understand behaviours and complex interactions in such applications.

Visit:

4 1 Introduction

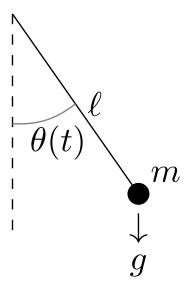


Fig. 1.1: A simple pendulum; a mass m oscillating under gravity g at the end of a (weightless) string of length ℓ .

for examples of how researchers in the School of Mathematical Sciences (i.e. your lecturers) are using ODEs (and PDEs) to model a range of real-world problems.

Example 1.1 The simple gravity pendulum

In this example we will derive the ODE model

$$\frac{d^2\theta}{dt^2} + \frac{g}{\ell}\sin\theta = 0, \tag{1.1a}$$

for the motion of the pendulum shown in Fig 1.1, with initial conditions

$$\theta = \theta_0$$
 and $\frac{d\theta}{d\tau} = 0$ for $t = 0$. (1.1b)

1.2.3 Computation

Ideally, we would like to calculate an *exact solution* to a given ODE, as exact solutions contain no error. However, for most interesting ODEs we can't find exact solutions. In fact, we don't necessarily know if a solution exists, or if solutions are unique!

If we do know that a unique solution exists, then we can compute an approximate solution, which contains some error. The amount of error that can be tolerated depends on the application. In general there is a trade-off between computational error and computational time. You should choose a method that gives the required accuracy without wasting time and resources. If you want a 'ball park' answer, use a fast method with low-order accuracy; if you need a very accurate answer you will need to use a slower method with high-order accuracy. Remember that mathematical models themselves are approximations of the real world!

Example 1.2 Back to example 1.1

Can we calculate an exact solution of the pendulum IVP (1.1)? How could we calculate an approximate solution?

1.2.4 Analysis

Analysis underpins all aspects of dynamics, modelling and computation.

For an applied mathematician, analysis refers to finding general patterns and understanding what they tell us. Analysis can be in terms of the mathematical properties of the ODE alone, but for all ODE models it is essential to analyse the properties of the ODE in order to interpret the what the model predicts for the real-world problem we began with.

Example 1.3 Back to example 1.1 again

Can we spot some solutions of the pendulum ODE (1.1)? If so, what do they tell us?

2 One-dimensional autonomous ODE models

2.1 Autonomous scalar equations

A first-order scalar ODE is of the form

$$\frac{dx}{dt} = f(x(t), t).$$

If the function f does not depend explicitly on t, i.e.

$$\frac{dx}{dt} = f(x). (2.1)$$

then the equation is *autonomous*. For such equations, *phase-line* analysis determines the *qualitative* behaviour of solutions without having to calculate the solution x(t).

Note that we will often use the standard notation

$$\dot{x} \equiv \frac{dx}{dt}$$
 or $x' \equiv \frac{dx}{dt}$. (2.2)

2.2 Fixed points, phase line analysis, and stability criteria

The steady states, fixed points or equilibria of (2.1), are the values of x such that

$$\frac{dx}{dt} = 0$$
 \Leftrightarrow $f(x) = 0.$

Consider the logistic growth equation

$$\frac{dx}{dt} = f(x), \quad f(x) = r x \left(1 - \frac{x}{k}\right), \tag{2.3}$$

which models population size x. Here rx is the growth term (growth proportional to population size, r = growth rate), rx^2/k is the death term due to competition between in the population, k is the carrying capacity of the population domain. The right-hand side f(x) is plotted in Fig. 2.1. The fixed points are x = 0 and x = k.

Suppose that the system is at one of the fixed points, which we shall denote x^* . If the system is given a small 'kick', i.e. perturbed slightly, so that it moves a little away from $x = x^*$ then the sign of f(x) tells us the direction of travel from the perturbed state. If f(x) > 0 then x increases with time, as shown by an arrow to the right. Conversely, if f(x) < 0 then x decreases with time, as shown by an arrow to the left.

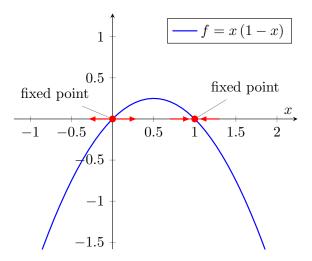


Fig. 2.1: Phase-line analysis of the logistic equation with r = k = 1. The arrows show the direction of travel if x is perturbed away from a fixed point.

From the plot, we see that if the system moves slightly from x = 0, it will continue to move away from this fixed point. The fixed point x = 0 is said to be *unstable*. If the system moves slightly from x = k it will move back to this fixed point. The fixed point x = k is said to be *stable*.

This is an easy, graphical way to determine the stability of fixed points. We need only to plot the right-hand side of the ODE (2.1) and consider its sign either side of the fixed points f(x) = 0. This gives qualitative information about the solution.

Sometimes we might want a more quantitative way of establishing stability, e.g. if we were using a computer program for this. So, let x^* be a steady state of (2.1), and suppose the system is initially at $x = x^*$, and then perturbed to $x^* + \delta x$. We use

$$\dot{x}(x^* + \delta x) \approx \delta x f'(x^*), \tag{2.4}$$

to deduce:

- If $f'(x^*) < 0$ then x is decreasing for $\delta x > 0$ and increasing for $\delta x < 0$, i.e. the system moves back towards x^* and the steady state $x = x^*$ is a stable.
- If $f'(x^*) > 0$ then x is increasing for $\delta x > 0$ and decreasing for $\delta x < 0$, i.e. the system moves further away from x^* and the steady state is unstable.
- If $f'(x^*) = 0$, i.e. x^* is a stationary point of f(x), we need to consider the next order non-zero term in our expansion. There are three possibilities:
 - 1. in the neighbourhood of $x = x^*$, f(x) is a decreasing function of x so that the fixed point is stable;

- 2. in the neighbourhood of $x = x^*$, f(x) is an increasing function of x so that the fixed point is unstable;
- 3. $x = x^*$ is a turning point of f(x) and the fixed point is semi stable or half stable because the direction of travel is towards the fixed point from one side and away from it on the other side. Because we can never determine which way a system will be perturbed, we must assume that such a point is, essentially, unstable.

From this we conclude that:

A fixed point
$$x = x^*$$
 is stable if $f'(x^*) < 0$.

Example Find the fixed points of the following autonomous differential equations, and determine their stability:

(a)
$$\frac{dx}{dt} = x^2$$

(b)
$$\frac{dx}{dt} = x(1-x)(2-x)$$

Plotting the *vector field* gives an even better qualitative understanding of the solution:

- Evaluate the slope of the solution x(t) at many points (t, x) given by f(x).
- At each point (t, x) draw a short arrow indicating the slope at that point.
- Solution curves are tangential to these short arrows.

Vector fields are readily plotted using Matlab's quiver command.

2.3 Fisheries management

As demand for fish and seafood grows worldwide, it is becoming increasingly important that fisheries are managed so as to avoid over-fishing, which could lead to catastrophic disruption of the ecosystem, and total collapse of fish numbers. Mathematical models allow fisheries managers to understand the dynamics of the fish populations, and the impact of various management strategies.

Consider an isolated population of fish. What is the best fishing strategy to maximise the yield, whilst also maintaining the population? We explore this using the model

$$\frac{dN}{dt} = \underbrace{BN}_{birth} - \underbrace{DN^2}_{death} - \underbrace{g(N)}_{yield} \quad \text{and} \quad N(0) = N_0, \tag{2.5}$$

where N is the number of fish. The 'birth' term tells us that the population increases at a rate proportional to the population size; B is the birth rate per individual. The 'death' term tells us that the population decreases at a rate proportional to the square of the population size, which measures the number of interactions between individuals in a large well-mixed population; the individuals are all competing for the same resources (in particular food) and the larger the population the more competition and deaths. The 'yield' term tells us the depletion in the fish population per unit time due to fishing; we need to decide on a functional form for this term. If g(N) = 0, we have just a logistic growth model.

2.3.1 Nondimensionalisation

IVP model (2.5) has at parameters B (the birth rate), D (the death rate), N_0 (the initial population), and any parameters that arise in the function g(N). It is always a good idea to non-dimensionalise your model!

Define dimensionless variables, \hat{N} and \hat{t} , by

$$N = N_c \,\hat{N} \quad \text{and} \quad t = t_c \,\hat{t}, \tag{2.6}$$

for some (characteristic) scales N_c and t_c , which we must choose.

By choosing $t_c = 1/B$ and $N_c = K$, the model becomes

$$\frac{d\hat{N}}{d\hat{t}} = \hat{N} \left(1 - \hat{N} \right) - \hat{g}(\hat{N}) \quad \text{and} \quad \hat{N}(0) = \hat{N}_0 \equiv \frac{N_0}{N_c}, \tag{2.7}$$

which has fewer parameters than the original model.

In tutorial 1 we consider a constant yield fishing term, g(N) = Y. Then

$$\hat{g}(\hat{N}) = \frac{t_c Y}{N_c} = \frac{Y}{B K} = \frac{Y D}{B^2} = y,$$

and we have the dimensionless equation

$$\frac{d\hat{N}}{d\hat{t}} = \hat{N}\left(1 - \hat{N}\right) - y \tag{2.8}$$

with just one parameter y.

Note: if g(N) = 0 we have a dimensionless logistic equation with no parameters. This one equation gives the solution for all physical logistic-growth problems, but is subject to an initial condition that adds a parameter.

Once we have the solution to our dimensionless problem we need to know the values K and B to convert answers to physical results,

$$N = K \hat{N}$$
 and $t = \frac{\hat{t}}{B}$. (2.9)

Scaling or non-dimensionalising equations is a very important part of modelling.

- 1. Typically, it reduces the number of parameters, which makes analysis easier.
 - (a) It is easier to see the type of equation and identify a solution method.

- (b) It is preferable to see how a solution changes with parameters if there are fewer parameters. In the example above, we can see how the solution changes with the parameters y and \hat{N}_0 , rather than with four parameters B, K, Y and N_0 . For the logistic equation there are no parameters, so we just have to find the solution to one equation and we effectively have the solution for all logistic-growth problems in terms of the initial condition parameter. This is especially useful if we have to find the solution numerically, all the more so if the simulation takes a long time.
- (c) Results can be presented more compactly we can plot N versus t for different values of y or N_0 at a given final time t_f versus y.
- (d) Solutions obtained for one system can be applied to another with different parameter values but which obeys the same scaled equation - there is no need to recalculate the solution.
- 2. It aids experimental validation of a model using a smaller-scale version; from the dimensionless equations we can see how to choose parameters for an experiment while not changing the behaviour of the model.
- 3. Whether the number of parameters are reduced or not, we can see the relative importance of the different terms in the equation(s) and, perhaps, use this to simplify the equation(s) to be solved. For example, if y in (2.8) is a very small number, say $O(\epsilon) \ll 1$, then we can drop it and conclude that the rate of fishing is so small relative to the growth rate of the population that fishing is unimportant for determining the population size.

It is important to choose scales appropriately based on the information we have and what we wish to investigate.

2.3.2 Constant yield; saddle-node bifurcation

Tutorial 1 shows that model (2.8) has a bifurcation at y = 1/4. For y > 1/4 there were no (real) steady states, for y = 1/4 there was one and for y < 1/4 there were two. It was called a saddle-node bifurcation. This is the basic mechanism by which fixed points are created and destroyed. As a parameter (y) is varied, two fixed points move toward each other, collide, and mutually annihilate.

More generally, if a small variation of a parameter causes a profound change in the qualitative behaviour of the solution, we call it a bifurcation.

Definition: For the ODE $\dot{x} = f(x : \mu)$, where μ is a scalar parameter, \bar{x} is a bifurcation point and $\bar{\mu}$ is a bifurcation value if

$$f(\bar{x}:\bar{\mu}) = 0$$
 and $\frac{\partial f}{\partial x}(\bar{x}:\bar{\mu}) = 0,$ (2.11)

where $\frac{\partial f}{\partial x}$ denotes the partial derivative with respect to x.

The canonical form for a saddle-node bifurcation is the first order ODE

$$\dot{x} = \mu - x^2. {(2.12)}$$

The right-hand side is just the simplest quadratic polynomial with a constant parameter. In (2.8) we have a slightly more complicated quadratic polynomial.

The right-hand-side of (2.12) has no real roots for $\mu < 0$, one (x = 0) for $\mu = 0$ and two $(x = \pm \sqrt{\mu})$ for $\mu > 0$ (see Fig. 2.2). We have a saddle-node bifurcation as μ increases from negative to positive.

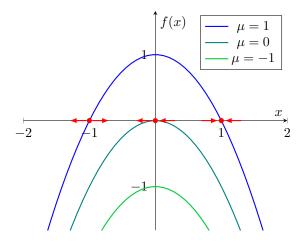


Fig. 2.2: Phase-line analysis of $f(x) = \mu - x^2$ for $\mu = -1, 0, 1$.

For $\mu > 0$, which root is stable and which is unstable?

Once we have determined the stability of the fixed point as functions of μ , we plot the *bifurcation diagram* shown in Fig. 2.3, which shows the roots $x^* = \pm \sqrt{\mu}$ versus μ , with stability indicated on the two branches.

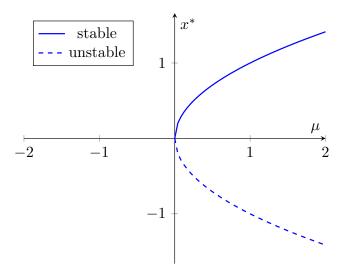


Fig. 2.3: The bifurfaction diagram for $f = \mu - x^2$, showing the fixed points x_* versus parameter μ , with stability indicated.

A saddle-node bifurcation is sometimes called a *fold bifurcation* or a *turning point bifurcation*. The term "saddle-node" derives from

an analogous bifurcation in higher-dimensional space.

2.3.3 Constant effort model; transcritical bifurcation

We now consider the model with a "constant effort" fishing term:

$$\frac{dN}{dt} = \underbrace{BN}_{birth} - \underbrace{DN^2}_{death} - \underbrace{EN}_{fishing}. \tag{2.13}$$

The parameter E is the effort put into fishing; the higher the effort, the more fish are caught per unit time. Thus effort includes factors such as the number of fishermen, boats, their working hours, etc.

The scaled or dimensionless model, using

$$t_c = \frac{1}{B}$$
, and $N_c = K$ where $K = \frac{B}{D}$, (2.14)

is

$$\frac{d\hat{N}}{d\hat{t}} = \hat{N}\left(1 - \hat{N}\right) - e\,\hat{N}, \quad e = \frac{E}{B}.\tag{2.15}$$

Here we have one parameter e instead of three (B, D, E).

This equation is of the form

$$\dot{x} = \mu \, x - x^2,\tag{2.16}$$

where $x \equiv \hat{N}$ and $\mu = 1 - e$.

What happens as μ goes from negative to positive?

Eqn. (2.16) is the canonical form for a transcritical bifurcation.

With a transcritical bifurcation, two branches of equilibria exchange their stability as μ passes through the bifurcation value (here $\mu=0$). Fig. 2.4 showns the bifurcation diagram, i.e. the steady states versus μ .

What does this tell us about model Eqn. (2.15)? In particular, what is the maximum yield that can be achieved?



An alternative scaling

We could have scaled Eqn. (2.15) differently by using

$$t_c = \frac{1}{B - E}$$
 and $N_c = k$ where $k = \frac{B - E}{D}$. (2.17)

Then the model equation is just the logistic-growth equation,

$$\frac{d\hat{N}}{d\hat{t}} = \hat{N} \left(1 - \hat{N} \right), \tag{2.18}$$

with no parameters at all!

Note that we are, implicitly assuming E < B or k > 0.

This is nice but how do we examine how the fishing rate affects the yield, now that the fishing rate is involved in the scaling of the problem?

This example shows that we can scale a problem in different ways. How we scale the problem will affect the way information can be obtained. In this last example we used dimensional, rather than dimensionless yield. It is easier to see how changing the fishing rate changes the yield, using the dimensionless model, if we don't include the fishing rate in the scaling of the problem.

Choosing scaling for a problem and understanding the dimensionless results is not always easy; it takes practice.

2.4 Pitchfork bifurcation; jumps and hysteresis

There is a third kind of bifurcation that can arise in one-dimensional autonomous ODEs, called a *pitchfork bifurcation*. They are common in physical problems that have symmetry. Fixed points tend to appear and disappear in symmetrical pairs. Consider, for example, a thin sheet that is being compressed, as illustrated in Fig. 2.5.

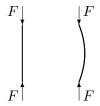


Fig. 2.5: Buckling of a rod under compression

If the compressive force F becomes large enough the sheet will buckle and deflect to the left or the right. The vertical position has gone unstable and two new symmetrical fixed points, corresponding to the left- and right-buckled configurations, have been born.

There are two very different types of pitchfork bifurcation: supercritical and subcritical pitchfork bifurcations. The first of these is simplest.

2.4.1 Supercritical pitchfork bifurcation

The supercritical pitchfork bifurcation has the canonical form

$$\dot{x} = f(x : \mu)$$
 where $f(x : \mu) = \mu x - x^3$, (2.19)

where μ is a real parameter. Note that this equation is *invariant* under the change of variable $x \to -x$. This is the mathematical expression of left–right symmetry.

Fig. 2.6 shows $f(x : \mu) = \mu x - x^3$ for different values of μ , from which we can infer the fixed points, stabilities and bifurcation.

We can also calculate these properties using the above definitions.

Fig. 2.7 shows the bifurcation diagram, and it is clear why it is called a pitchfork bifurcation.

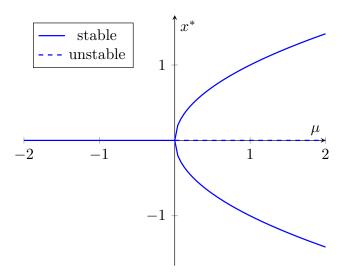


Fig. 2.7: Supercritical pitchfork bifurcation diagram.

Example Equations similar to $\dot{x} = -x + \mu \tanh x$ arise in models

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of magnets and neural networks. Show that this equation undergoes a supercritical bifurcation as μ is varied and plot the bifurcation diagram.

2.4.2 Subcritical pitchfork bifurcation

In the supercritical case $\dot{x} = \mu x - x^3$, the cubic term is *stabilising*, acting as a restoring force that pulls x(t) back toward x = 0. The subcritical pitchfork bifurcation has canonical form

$$\dot{x} = f(x : \mu)$$
 where $f(x : \mu) = \mu x + x^3$. (2.23)

Now the cubic term is destabilising.

We want to calculate the fixed points, stabilities and bifurcations.

Hysteresis

In real physical systems, such an explosive instability is usually opposed by the stabilising influence of higher-order terms. Assuming the system is symmetric under $x \to -x$, we extend ODE (2.23) to

$$\dot{x} = \mu x + x^3 - x^5, \tag{2.24}$$

by adding the stabilising term $-x^5$. The bifurcation diagram for this ODE is shown in Fig. 2.8. For small x^* this looks like the bifurcation diagram for ODE (2.23). The new feature is that the unstable branches turn around and become stable at $\mu = \mu_s$, where $\mu_s < 0$. These stable large-amplitude branches exist for all $\mu > \mu_s$.

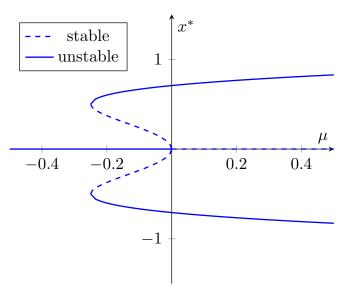


Fig. 2.8: Bifurcation diagram for $\dot{x} = \mu x + x^3 - x^5$.

How do we interpret this bifurcation diagram? We have to consider a number of cases. In the following discussion we denote the large-amplitude steady states at some value of the parameter μ by $x^* = \pm X_{\mu}$ and the unstable non-zero steady states by $x^* = \pm x_{\mu}$.

- Case 1: $\mu < \mu_s$. $\lim_{t \to \infty} x(t) = 0$ for all initial conditions $x(0) = x_0$.
- Case 2: $\mu_s < \mu < 0$. If $-x_{\mu} < x_0 < x_{\mu}$ then $\lim_{t \to \infty} x(t) = 0$. If $x_0 < -x_{\mu}$ then $\lim_{t \to \infty} x(t) = -X_{\mu}$, and if $x_0 > x_{\mu}$ then $\lim_{t \to \infty} x(t) = X_{\mu}$.
- Case 3: $\mu > 0$. If $x_0 < 0$ then $\lim_{t \to \infty} x(t) = -X_{\mu}$, and if $x_0 > 0$ then $\lim_{t \to \infty} x(t) = X_{\mu}$.

Now suppose the state of the system is $x^* = 0$ and $\mu < \mu_s$ and we then slowly increase μ . The state remains unchanged as the system travels along the stable $x^* = 0$ branch of the bifurcation curve until $\mu = 0$. When $\mu = 0^+$ the state will *jump* to one or other of the large-amplitude stable branches and then continue along that branch. Physically such a jump might be interpreted as a catastrophic event.

If we next slowly decrease the value of μ , the state will remain on the large-amplitude branch until $\mu = \mu_s$. When $\mu = \mu_s^-$ the state will again jump, back to the trivial steady state.

This lack of reversibility as a parameter (here μ) is varied is called *hysteresis*.

Note that the bifurcation at $\mu = \mu_s$ is a saddle-node bifurcation; stable and unstable fixed points are born as μ is increased.

2.5 The spruce-budworm model

2.5.1 The model

The spruce budworm is a significant pest species in Canada, as it can defoliate coniferous trees and devastate the forestry industry (Fig. 2.9). The first reported outbreak was in 1909 in British Columbia, and outbreaks have continued to occur in Canada and the US over increasingly large areas ever since. Some outbreaks subside naturally after a few years, but others have persisted for up to 30 years. In 1978, Ludwig et al. developed and studied the following model for the dynamics of the budworm population

$$\frac{dN}{dt} = RN\left(1 - \frac{N}{K}\right) - p(N) \quad \text{and} \quad N(0) = N_0,$$

where N(t) denotes the budworm population at time t. We assume that, in the absence of predators, the budworm population grows according to the logistic ODE, where R is the (linear) birth rate of the budworm and K is the carrying capacity (which is related to the density of foliage available on the trees).



Fig. 2.9: The spruce budworm. http://en.wikipedia.org/wiki/Spruce_Budworm

The p(N) term represents predation, e.g. by birds, and takes the form:

$$p(N) = \frac{BN^2}{A^2 + N^2}.$$

Sketch the function and interpret it.

The model can be written in the dimensionless form

$$\frac{d\hat{N}}{d\hat{t}} = r \,\hat{N} \left(1 - \frac{\hat{N}}{k} \right) - \frac{\hat{N}^2}{1 + \hat{N}^2} \quad \text{and} \quad \hat{N}(0) = \hat{N}_0, \qquad (2.25a)$$

where

$$k = \frac{K}{A}, \quad r = \frac{AR}{B}, \quad \hat{N} = \frac{N}{A}, \quad \hat{t} = \frac{Bt}{A}, \quad \hat{N}_0 = \frac{N_0}{A}.$$
 (2.25b)

Exercise: show this.

For notational convenience, we will rewrite IVP (2.25a) as

$$\dot{x} = f(x:r,k)$$
 where $f(x:r,k) = r x \left(1 - \frac{x}{k}\right) - \frac{x^2}{1 + r^2}$. (2.26)

We will use this model to determine the conditions under which the budworm population will be under control and the conditions which will lead to an outbreak of budworms.

What do we mean by an "outbreak"? The idea is that as parameters drift, the budworm population suddenly jumps from a low level to a high level. $N \approx A$ or $x \approx 1$ is defined to be a low population level, so $x \gg 1$ is a high level.

2.5.2 Analysis for constant k

The right-hand-side, which we denote f(x), is relatively complicated as it involves two parameters, r and k. Initially, to make things simpler, we will fix k = 6.

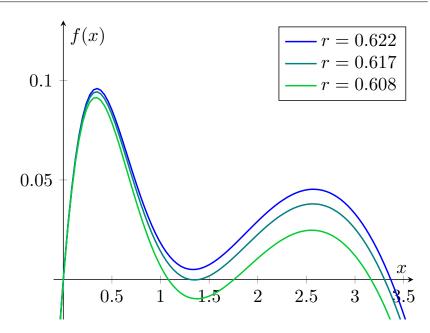


Fig. 2.10: Finding the fixed points for the spruce budworm model

We plot f(x) for three particular values of r in Fig. 2.10. We can see that:

- 1. For r = 0.608 there are four fixed points: $0 < x_1^* < x_2^* < x_3^*$, which are unstable, stable, unstable and stable, respectively.
- 2. For r = 0.617 there are three fixed points: $0 < x_1^* < x_2^*$ which are unstable, semi-stable and stable, respectively.
- 3. For r = 0.622 there are two fixed points: 0 (unstable) and x_1^* (stable).

We can see that as r increases from 0.608, the behaviour of the model changes fundamentally, i.e. a bifurcation occurs. What type of bifurcation is this? At first there are four fixed points. When r=0.617, the curve just touches the x-axis in Fig. 2.10, and there are then only 3 fixed points; r=0.617 is a bifurcation value. For r>0.617, there are just two fixed points. We show the behaviour of the fixed points for a greater range of r on a bifurcation diagram.

Sketch the bifurcation diagram and explain why it possesses a hysteresis.

2.5.3 Analysis for two varying parameters

Write

$$f(x:r,k) = x\left\{r\left(1 - \frac{x}{k}\right) - \frac{x}{1+x^2}\right\}.$$
 (2.27)

A fixed point exists at $x^* = 0$, and it is unstable for all parameter values because

$$f(0^+) \approx rx > 0$$
 and $f(0^-) < 0$. (2.28)

Other fixed points are given by

$$r\left(1 - \frac{x}{k}\right) = \frac{x}{1 + x^2},\tag{2.29}$$

which is easiest to analyse graphically, noting that the left-hand side is a simple function (linear) but contains parameters, and the right-hand side is a relatively complicated function but contains no parameters. Fig. 2.11 graphs the left and right sides of (2.29). The number of fixed points depends on both r and k. For r sufficiently large there will be one, two or three fixed points. For small r there will be one or two fixed points.

Bifurcations occur when (2.29) holds, and

$$\frac{d}{dx}\left[r\left(1-\frac{x}{k}\right)\right] = \frac{d}{dx}\left(\frac{x}{1+x^2}\right). \tag{2.30}$$

Solving for r and k gives

$$r = \frac{2x^3}{(1+x^2)^2}$$
 and $k = \frac{2x^3}{x^2-1}$. (2.31)

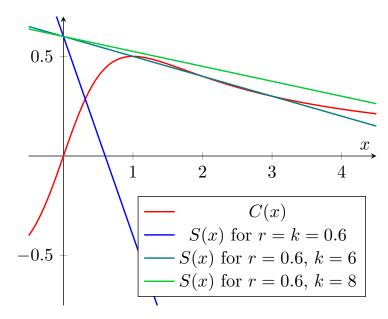


Fig. 2.11: Plots of C(x) (red), and S(x) for different parameter values.

Since we must have k > 0, then x > 1 (x < 0 makes no physical sense). The two expressions in Eq. (2.31) define the bifurcation curves, i.e. curves along which bifurcations occur. For each x > 1 we plot the point (k(x), r(x)) in the (k, r) plane. The resulting curves are shown in Fig. 2.12.

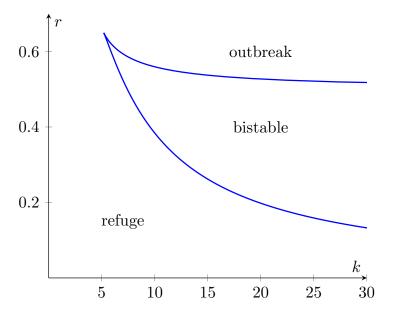


Fig. 2.12: Bifurcation curves for the spruce-budworm model.

For k small there is just one non-zero stable fixed point for any value r and there are no bifurcations. As k increases we enter the region where there are two bifurcations; on each of the upper and

lower bifurcation curves there are two fixed points, between them there are three fixed points and above and below there is one.

We can also sketch of what happens in (k, r)-space.

Interpretation

In practical terms, the bifurcation analysis suggests that an outbreak of the pest corresponds to a small change in the environment causing a slight change in the parameter values (an increase in birth rate, say), which results in the population jumping from the lower to the upper stable branch. The outbreak subsides when the solution jumps from the upper to the lower branch. The model suggests

that control of the outbreak would require us either to reduce r, or reduce k, so that the solution moves away from the bistable region in Fig. 2.12, and into the region where there is only one stable equilibrium.

See Strogatz (2000) for more discussion on the physical application of the model.

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