# 4 First-Order Non-Linear Difference Equations

## 4.1 Introduction

- First-order non-linear difference equations.
- *Motivation*: population models for a single species.
- Population of the next generation ($N_{t+1}$) depends upon its current value ($N_t$).

$$N_{t+1} = f\left(N_t\right), \tag{4.1}$$

**Note**: this is an *autonomous* equation.



The critical issue from the perspective of population biology is to identify the long-time behaviour of the population, e.g. does the population become extinct?

**Question 4.1** *Explain why for some species the autonomous model*

$$N_{t+1} = f\left(N_t\right). \tag{4.2}$$

*should be replaced by the non-autonomous model*

$$N_{t+1} = f\left(N_t, t\right). \tag{4.3}$$

First-Order Non-Linear Difference Equations: An Introduction

## 4.2 Aims

1. Derive the linear population model (LPM), explaining all assumptions.
2. Explain the defects of the LPM.
3. Explain the features of a realistic growth model.
4. Understand how to use cobwebbing.
5. Explain what *fixed-points* are and know how to derive them.
6. Appreciate the importance of finding the fixed points of the map

$$x_{t+1} = f(x_t)$$

as the first step towards understanding the dynamics of the population model.

7. To be able to derive the *logistic difference equation* and find its fixed points.

## 4.3 A linear model for population growth

### 4.3.1 Derivation of Model

To motivate the use of a *non-linear* model for a population we first consider the following *linear* model.

**Example 4.1 (Ecology)** *The average birth rate of carp in a lake per individual per yearris The fractional death rate of carp in the year is d per year. The number of carp in the lake at year* $n = 0$ *is* $N_0 = N$. *Find an expression for the size of the population after year n* ($N_t$).

We must convert this **word** problem into a **difference equation** (c.f. with the carp problem from chapter 2.2).

First-Order Non-Linear Difference Equations: An Introduction

Let $N_t$ be the population size of carp in year $n$.

$$\left\{ \begin{array}{c} \text{change in} \\ \text{population} \end{array} \right\} =$$

### 4.3.2 Assumptions of the Model

#### 4.3.2.1 Birth-rate

We have assumed that:

1. The birth-rate is a linear function of the population size.
2. The number of new born in year $N_{t+1}$ is $rN_t$ where $r$ is the average birth-rate per individual (also known as the *static birth rate*).
3. Obviously $r \geq 0$.



#### 4.3.2.2 Death-rate

We have assumed that:

1. A constant fraction of the population dies each year.
2. The total number of deaths each year is $dN_t$.
3. Obviously $0 \leq d \leq 1$.

In what follows we shall always assume that $d = 1$.

**Question 4.2** *What does it mean biologically to assume that $d = 1$?*

#### 4.3.2.3 Other processes

**Question 4.3** *Are there any general processes besides births and deaths that we could add to our model?*

First-Order Non-Linear Difference Equations: An Introduction

### 4.3.3 Solution of the linear model

Assuming that $d = 1$ we have derived the *linear population model*

$$N_{t+1} = rN_t, \quad N_0 = N. \qquad (4.4)$$

Equation (4.4) accurately describes the population growth for only short ____ times, when the population is small (dilute). It has been used, with some justification, for the early stages of growth of certain bacteria.

This eq$^{\mathrm{n}}$ is of the same form as those that we studied in chapter 2.4. In that chapter we learnt that the solution of the eq$^{\mathrm{n}}$

$$x_n - ax_{n-1} = 0,\ n \geq 1 \quad \text{is}$$

$$x_n = \_\_\_\_$$

$$x_0 a^n$$

The solution of equation (4.4) is,

$N_{t+1} =$

$$\rule{6cm}{0.4pt} \quad (4.5)$$

**Question 4.4** *How does the solution to equation (4.4) depend upon the value of $r$?*

$r > 1$

________________________________

$r = 1$

________________________________

$r < 1$

________________________________



**Question 4.5** *Consider the population model*

$$N_t = rN_{t-1}, \quad N_0 = N, \quad 0 < r < 1.$$

*How long does it take for the population to become extinct?*

**Answer 1**

The solution of the model is $N_t = r^t N$. Thus $\lim_{t\to\infty} N_t = 0$, i.e. the population becomes extinct only in the limit of an infinite number of iterations.

*First-Order Non-Linear Difference Equations: An Introduction*

**Question 4.5** *Consider the population model*

$$N_t = rN_{t-1}, \quad N_0 = N, \quad 0 < r < 1.$$

*How long does it take for the population to become extinct?*

**Answer 2**.

The population becomes extinct when the size of the population drops below one. Thus we require

$$\begin{aligned} r^t N &< 1, \\ \Rightarrow r^t &< \frac{1}{N}, \\ \Rightarrow t \ln r &< \ln \frac{1}{N}, \\ \Rightarrow t &> -\frac{\ln N}{\ln r}. \end{aligned}$$

Note that $0 < r < 1 \Rightarrow \ln r < 0$.

First-Order Non-Linear Difference Equations: An Introduction

**Question 4.6** *Does the behaviour of the model (4.4) when $r < 1$ suggest a possible mechanism for the eradication of a pest?*

**Question 4.7** *Is the constant population $N_t = N_0$, corresponding to the case $r = 1$, a 'solution' that is likely to occur in the 'real' world?*

Yes. If the static birth-rate is reduced below one the pest will eventually become extinct.

First-Order Non-Linear Difference Equations: An Introduction

## 4.4 The failure of the linear model: The need for nonlinear models

As a population grows the dilute approximation fails. Individuals within the population compete for resources, e.g. food, and self-regulation occurs due to crowding. Better population models reflect the fact that such processes reduce the birth rate and replace the static birth rate by an *effective*, or dynamic, birth rate

$$N_{t+1} = r_{\text{eff}}(N_t)N_t, \tag{4.6}$$

with $r_{\text{eff}}(N_t) < r$.

This leads us to study difference equations of the form

$$N_{t+1} = N_t F(N_t), \quad (4.7)$$
$$= f(N_t), \quad (4.8)$$

where $f(N_t)$ has the qualitative form shown in figure 4.1. The form of the function $f(N_t)$ shown in figure 4.1 has *four* important features that make it a realistic function to describe population dynamics.

First-Order Non-Linear Difference Equations: An Introduction

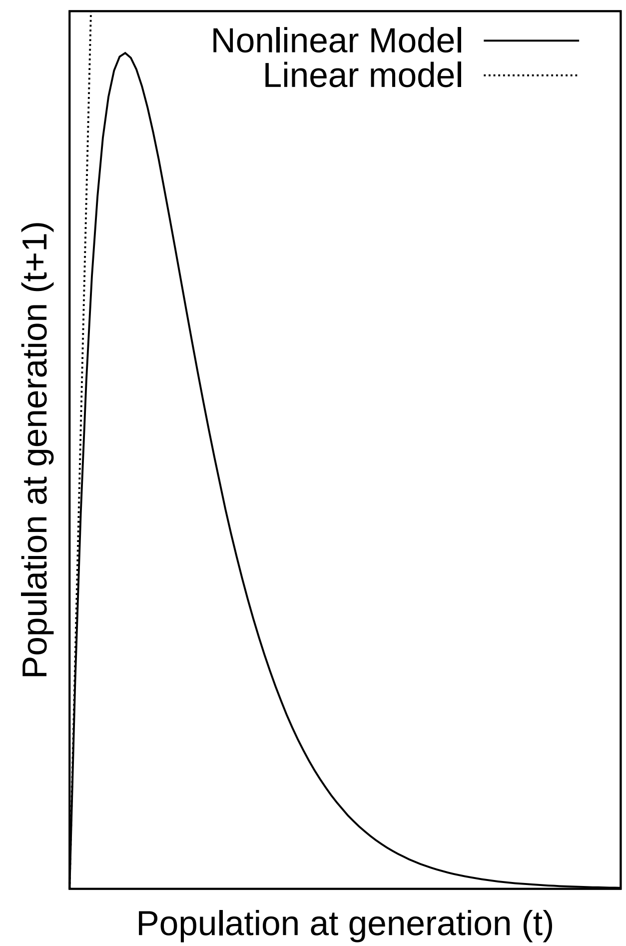



Figure 4.1: Typical growth form in the model $N_{t+1} = f(N_t)$.

1. $f(0) = \underline{0}$. Why?

2. If the population is small the *effective birth rate* should equal the *static birth rate*, i.e.

$$\lim_{N \to 0} \quad \underline{r_{\text{eff}}(N_t) = r.}$$

3. The function $f(N_t)$ is *bounded*. It increases to a *maximum* and then *decreases*.

4. As the nutrients and volume available to a population are limited we expect that for sufficiently large population size the effective growth rate approaches zero, i.e.

$$\lim_{N \to \infty} \quad \underline{r_{\text{eff}}(N_t) = 0.}$$



## 4.5 Cobwebbing: A Graphical Solution

Equations arising in population biology of the form described by equation (4.8) and figure 4.1 are usually impossible to solve analytically but we can extract a considerable amount of information about the population dynamics without an analytical solution. Of course, whatever the form of $f(N_t)$, we shall only be interested in non-negative populations.

From a practical point of view it is a straightforward matter to evaluate $N_{t+1}$ in equation (4.1) and subsequent generations computationally by using equation (4.1) recursively. However, we can elicit a considerable amount of information about the population growth behaviour by a simple graphical technique known as *cobwebbing*. To determine the successive iterates of an initial point $x_0$ to the nonlinear map $x_{t+1} = f(x)$.



1. Draw a vertical segment along $x = x_0$ until we intersect the curve $y = f(x)$, intersecting at $P$. This gives us the value $x_1 = f(x_0)$.
2. Draw a horizontal segment from $P$ to $y = x$. The abscissa of this point of intersection is $x_1$. Why?
3. Repeated (1) and (2) to obtain $x_{t+1}$ from $x_t$.

| |
|---|
| Use this procedure to complete figure 4.2. |

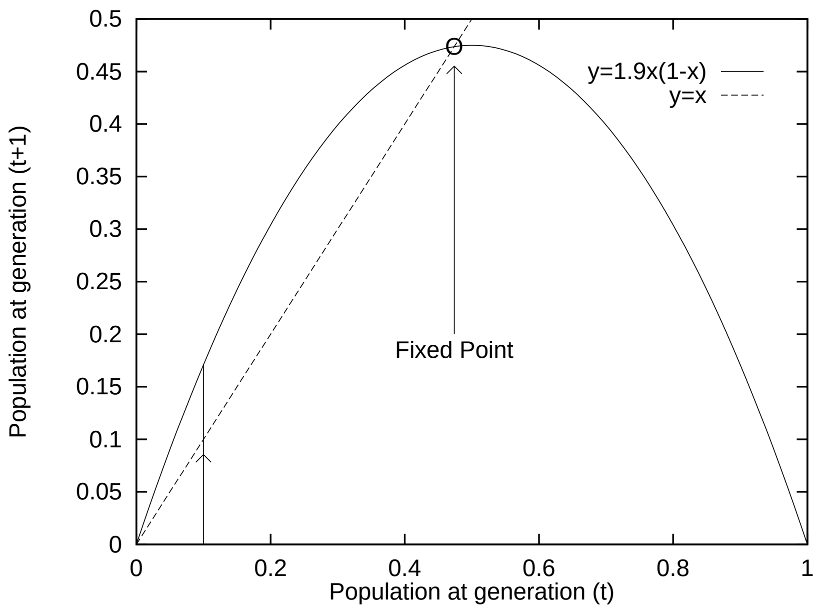



Figure 4.2: Determination of population dynamics using cobwebbing.

**Question 4.8** *What happens to the dynamic evolution of the initial point in figure 4.2?*

First-Order Non-Linear Difference Equations: An Introduction

## 4.6 Fixed points

Points where the line $y = x$ intersects the line $y = f(x)$ are known as *fixed points* (or *period-1* solution). The *first-step* in understanding the long-time behaviour of a nonlinear difference equation is to find the *fixed-points* of the function $f(x)$.

> To find the fixed points ($x^*$) of the difference equation
>
> $$x_{t+1} = f(x_t),$$
>
> we solve the equation
>
> $$x^* = f(x^*).$$

First-Order Non-Linear Difference Equations: An Introduction

**Example 4.2** *Find the fixed points of the equation*

$$x_{n+1} = 2x_n (1 - x_n) .$$

**Solution** We must solve the equation

$$x^* = 2x^* (1 - x^*) .$$

For convenience during the working we write $x^*$ as $x$.Thus

$$\begin{aligned} 0 &= 2x(1-x) - x, \\ &= x[2(1-x) - 1], \\ &= x(1-2x) . \end{aligned}$$

Thus the fixed points are $x = 0$ and $x = \frac{1}{2}$ or, in our original notation, $x^* = 0$ and $x^* = \frac{1}{2}$.

First-Order Non-Linear Difference Equations: An Introduction

**Question 4.9**

1. *Why do you think a fixed point is called a fixed point?* **Hint.** *Consider the problem*

$$x_{t+1} = f(x_t), \quad x_0 = x^*,$$

   *where $x^*$ is a fixed-point of the function $f(x_t)$.*

2. *What does a fixed-point represent biologically?*

## 4.7 The logistic equation

A simple specific form for the specific birth rate is

$$r_{\text{eff}} = r - \frac{N_t}{K}, \tag{4.9}$$

where the parameter $K$ is known as the *carrying capacity* and the parameter $r$ is known as the *per-capita death rate*, so that

$$N_{t+1} = r_{\text{eff}}(N_t)\, N_t \tag{4.10}$$

$$= \left(r - \frac{N_t}{K}\right) N_t \tag{4.11}$$

*First-Order Non-Linear Difference Equations: An Introduction*

By defining

$$x_t \equiv \frac{1}{rK} \cdot N_t, \tag{4.12}$$

we obtain the standard form

$$x_{t+1} = \tag{4.13}$$

$$\underline{\qquad\qquad\qquad}. \tag{4.14}$$

This is the *logistic equation.*

**Question 4.10** *Sketch the function* $y = rx(1-x)$ *with* $0 \le x \le 1$.

A drawback of the logistic model is that if $x_t > 1$ then $\underline{x_{t+1} < 0}$. Thus the logistic model only makes biological sense if $0 < x_t < 1$. This requirements restricts the values that $r$ can take.

**Question 4.11** *Show that if* $0 < x_t < 1$ *and* $0 \le r \le 4$ *then* $0 < x_{t+1} < 1$.



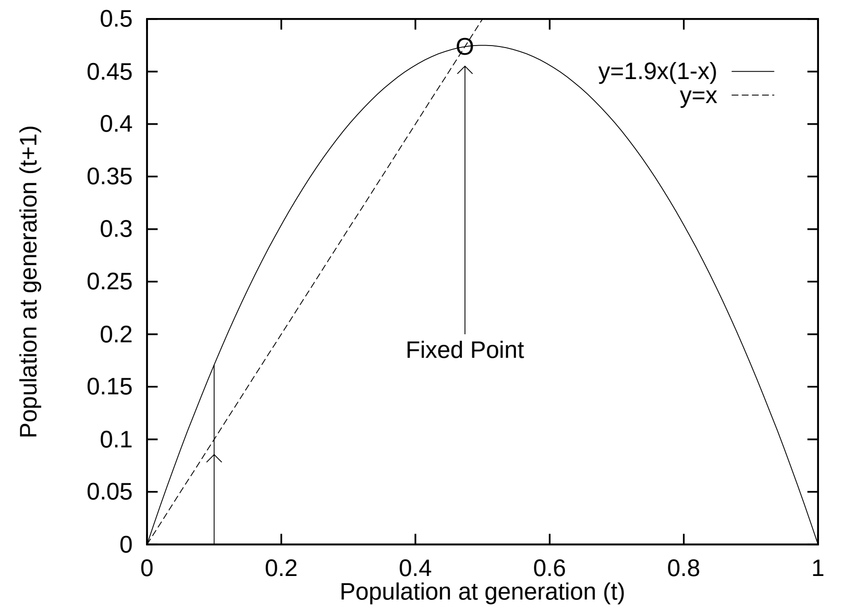
**Question 4.12** *Find the fixed point(s) of the logistic map when*

1. $r = 0.95$
2. $r = 1$
3. $r = 1.2$
4. $r = 1.9$
5. $r = r$.

*Comment on the biological interpretation of your answers.*

When studying a model it is often useful to first do some preliminary investigations to get an idea of what behaviour is exhibited by it. These investigations usually take the form of numerical simulations. For one-variable discrete models such as the logistic equation we can also use the technique of cobwebbing described in section 4.5. In fact we have already used cobwebbing for the logistic equation. Figure 4.2 shows that the dynamic evolution of the initial condition $x_0 = 0.1$ when $r = 1.9$.

First-Order Non-Linear Difference Equations: An Introduction




**Question 4.13** *Consider figure 4.2. What can you say about the evolution of any initial condition* $x_0$ *with* $0 < x_0 < 1$*? How does this answer compare to your calculation in question 4.12* $(r = 1.9)$*?*

**Question 4.14** *Using cobwebbing determine the long-term behaviour of the logistic equation for any initial condition* $0 < x_0 < 1$ *with* $r$ *in the range* $0 < r < 1$. *What is the biological interpretation of your result? By considering what* $r < 1$ *means biologically explain why your interpretation 'makes sense'.*

First-Order Non-Linear Difference Equations: An Introduction

**Question 4.15** *Using cobwebbing determine the long-term behaviour of the logistic equation when* $r = 1.2$ *for initial conditions in the range* $0 < x_0 < \frac{1}{6}$ *and* $\frac{1}{6} < x_0 < 0.2$ *where* $\frac{1}{6}$ *is the value of the non-trivial fixed point. Comment on the biological meaning of your results. Use figure 4.3 (a& b).*

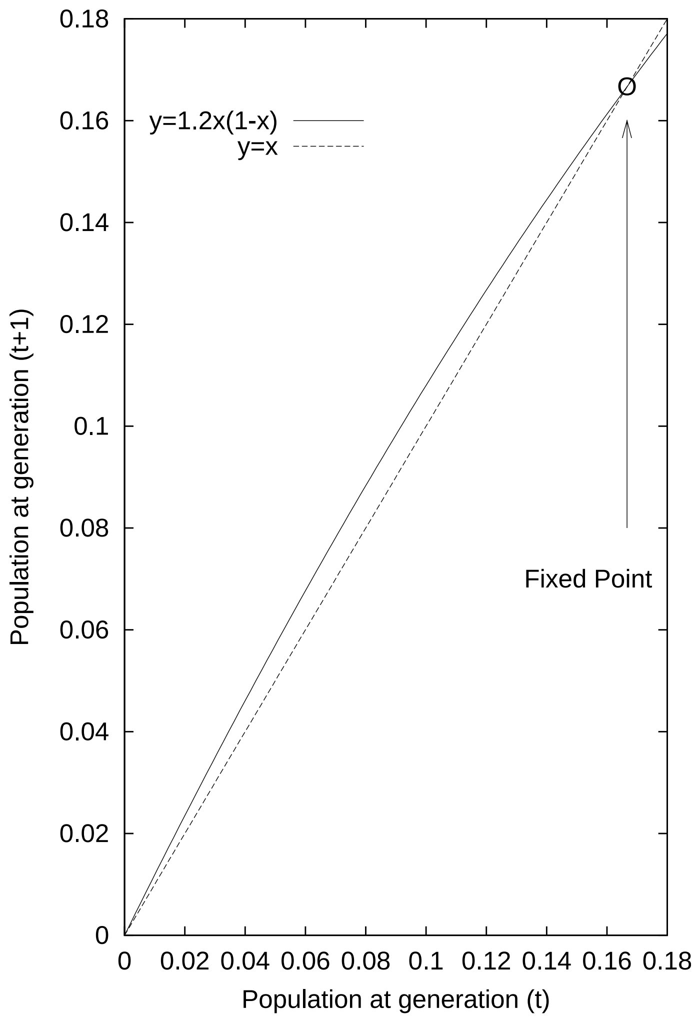



Figure 4.3: (a) Cobwebbing: $0 < x_0 < \frac{1}{6}$

*First-Order Non-Linear Difference Equations: An Introduction*

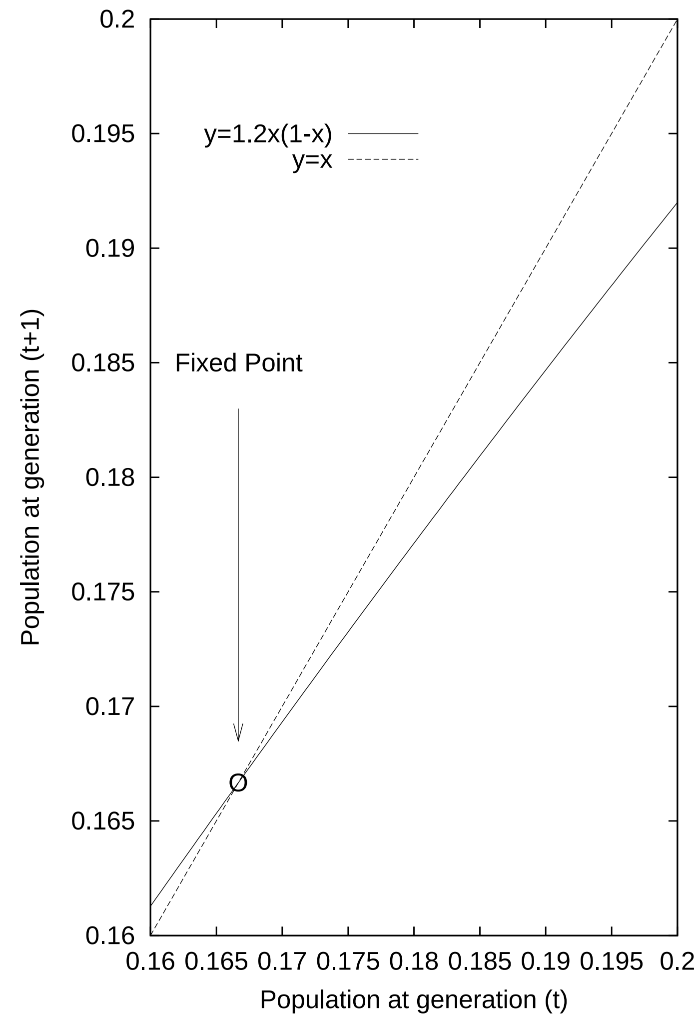



Figure 4.3: (b) Cobwebbing: $\frac{1}{6} < x_0 < 0.2$

## 4.8 Cobwebbing and fixed points: Putting them together

In this section we apply what we have learnt about cobwebbing and fixed-points to study fly dynamics in a remote part of Canada...

**Example 4.3 (Fly dynamics in Canada)** *In a remote region in Canada, the dynamics of a fly population has been studied and found to satisfy the difference equation*

$$x_{n+1} = 1 - 0.01x_n^2,$$

*where $x_n (> 0)$ is the fly population density at generation $n$,*



(a) *Determine the fixed point(s) of this model.*

First-Order Non-Linear Difference Equations: An Introduction

*To find the fixed points of the equation*

$$x_{n+1} = f\left(x_n\right),$$

*we have to solve the equation*

$$x^* = f\left(x^*\right).$$

*Replacing* $x^*$ *by* $x$ *we have*

$$x = 1 - 0.01x^2,$$

$$0.01x^2 + x - 11 = 0.$$

*The fixed points are* $x_1^* = -110$ *and* $x_2^* = 10$.

*(b) Assume that the initial fly population density is 30. By drawing a cobweb diagram determine what happens to the fly population after a very long time (i.e. as $n \to \infty$).*

First-Order Non-Linear Difference Equations: An Introduction

*The cobwebbing diagram shows that* $\lim_{n\to\infty} x_n = 10$.

*(c) Assume that the initial fly population density is 40. By drawing a cobweb diagram and carefuly considering the meaning of the RHS of the equation*

$$x_{n+1} = 1 - 0.01x_n^2,$$

*determine what happens to the fly population after a very long time (i.e. as $n \to \infty$).*

First-Order Non-Linear Difference Equations: An Introduction

*The key idea is that $x_1 = -5$ must be changed on biological grounds to $x_1 = 0$. It then follows that* $\lim_{n\to\infty} x_n = 10$.

## 4.9 Revision of key ideas

## 4.10 Concept map

Draw a concept map for this chapter relating the aims/key ideas of the chapter. If you are unfamiliar with the idea of a concept map see appendix A.