UNIVARIATE DYNAMICS

A state wildlife management agency decides to create a sport fishery in a particular lake. They will begin by draining the lake and dredging the bottom. They will introduce desirable plants and create an ideal habitat for the desired species of fish. They will then fill the lake with water and introduce a small population of fish. Fishing will be prohibited until the fish population has reached an acceptable level. Now suppose our job is to model the growth of the population of fish in this hypothetical lake. Our goal is to construct a mathematical model to predict how the fish population will change. The model will be useful in designing a strategy for managing the fishery.

An economic development program is planning to bring dairy cattle to small villages in developing countries. The cattle will be fed primarily on the local grasses. Suppose our job is to decide how many cows should be kept in a particular area so as to make full use of the local resources without overgrazing. As in the fishery scenario, we will need a mathematical model to predict the effect of the cows on the grass resource.

In this chapter, we use the fishery and grazing scenarios as settings in which to develop and study a number of models for the change of populations with time. We restrict ourselves for now to **univariate models**, which are models that require careful monitoring of only one population, the fish in the first case and the grass in the second. There are two main categories of univariate models, discrete and continuous, differing in the assumption made about how to mark time. **Discrete models** assume that time can be broken up into distinct uniform intervals. The length of the interval depends on the life history of the organism being modeled. Salmon have yearly spawning periods, so a time interval of one year is chosen for a discrete salmon model. Flour beetles have a complicated life cycle that can be approximated as a two-week larva stage, a two-week pupa stage, and an adult stage of variable length. Discrete models for flour beetles use a time interval of two weeks. A discrete model consists of mathematical formulas that describe how a population changes from one census to the next. **Continuous models** consist of mathematical formulas that describe the rate at which a population changes at any particular time and population level.

The primary goal of this chapter is to empower the reader with tools for the analysis of both discrete and continuous models. A secondary goal is to guide the reader to an appreciation of how to interpret discrete and continuous models and how to judge which kind of model is more suitable for a given biological setting. Generally, discrete models are to be preferred when similar events happen simultaneously, such as in populations that have a specific season for births. Continuous models are generally preferable when similar events are spread over time and occur simultaneously with other events. In most disease situations, for example, some members of the population are just getting sick while others are recovering, and the sick individuals are at different stages of the disease; a continuous model is likely to be more appropriate than a discrete model.

Sections 1 and 2 serve as introductions to discrete models and continuous models, respectively. Section 3 presents the principal graphical method for each type: *cobweb analysis* for discrete models and *phase line analysis* for continuous models. Section 4 presents *linearized stability analysis*, a particularly useful application of the derivative that works for both discrete and continuous models, although in different ways. Section 5 ties the two kinds of models together by showing how continuous models can be used to derive discrete models and by examining the similarities and differences between discrete and continuous models.

1 Discrete Population Models

In the fishery scenario described in the chapter introduction, our goal is to construct a mathematical model to predict how a fish population will change. We assume that we know the number of fish in year zero. We also assume that fish born at the beginning of year t are ready to spawn at the beginning of year $t+1$.

Population models are created by careful accounting. We need to list the different sources of fish in the year $t+1$ census. We then choose a reasonable mathematical formula to predict the number of fish in each group as a function of the year t population. The sum of the different component populations is the total year $t+1$ population. In our simple model, there are two sources of year $t+1$ fish. There are fish that were counted in the year t census and have survived the intervening year, and there are fish that hatched from eggs laid in year t and survived to become adults for year $t+1$. The addition of new fish through the process of birth and survival is called **recruitment**. We have

next year's population = survivors from this year's population+recruitment from this year's eggs.

Now let N_t be the population in year t. Counting year t as the current year, we have

$$N_{t+1} = \text{survivors from } N_t + \text{recruitment from eggs laid in year } t.$$

It remains to develop mathematical formulas that describe reasonable assumptions about how the numbers of survivors and recruits are related to the year t population. We want to make these formulas general enough to work for a variety of species that satisfy the assumptions we have made so far.

Let S be the fraction of adults that survive each year. Then the year $t+1$ census includes SN_t survivors from the year t census. The recruitment process has several stages, which we consider separately to allow for a flexible model. We assume that the year t adults lay an average of b eggs, for a total of bN_t eggs. Some of these eggs hatch, and some of the baby fish survive long enough to become mature adults in the next year. We want to be able to incorporate different assumptions about what happens during the short period right after spawning. Thus, we think of one year as consisting of two parts, a potentially complicated period of duration T, during which the eggs hatch and the larvae grow to become immature fish, followed by the remainder of the year, in which the rules governing the population dynamics of the immature fish are simple. Letting $p(N)$ be the probability that an egg yields an immature fish, the number of immature fish at the end of that period is bpN_t. With the assumption that a fraction S_I of these immature fish survive to the next census, we obtain the recruit population as S_IbpN_t. Note that we are allowing the possibility that the survival rate from egg to immature fish can depend on the total fish population. The result is the standard discrete fishery model

$$N_{t+1} = [S_Ibp(N_t) + S]N_t. \tag{1.1}$$

For a first approximation, we assume that p is constant. In Section 5, we will make the model more realistic by making p a function of the overall fish population. In this manner, we can build in assumptions about competition for resources or cannibalism by adult fish. Predation by other species is already built into the model insofar as predation is one of the factors that determine the survival probabilities S_I and S.

For reasons that will only become clear in hindsight, it is often better to think of the model as a formula for the change in the population rather than the population itself. The model in this form is

$$N_{t+1} - N_t = (S_I bp + S - 1)N_t.$$

For convenience, let $R = S_I bp + S - 1$. (Note the limiting value $R \geq -1$.) The population is viable only if it grows, so we assume $R > 0$. The significance of this condition is more clear when written as $S_I bp > 1 - S$. In this inequality, $S_I bp$ is the number of recruits per previous year's adult and $1 - S$ is the fraction of the previous year's adults that does not survive. The condition $R > 0$ means that the number of recruits exceeds the number of deaths in the adult population.

With the definition of R, we arrive at the simplest mathematical model for population growth,

$$N_{t+1} = (1 + R)N_t, \qquad R \geq -1. \tag{1.2}$$

If the initial population N_0 and the net relative growth rate R are known, we can use Equation 1.2 to determine each year's population from the previous year's population. For this particularly simple equation, we can do even better. Given N_0, we have $N_1 = (1 + R)N_0$, $N_2 = (1 + R)N_1 = (1 + R)^2 N_0$, $N_3 = \cdots = (1 + R)^3 N_0$, and so on. The pattern suggests the general formula

$$N_t = (1 + R)^t N_0, \tag{1.3}$$

a conjecture that is easily confirmed. The solution of the model is an exponential function of the independent variable t, and so the model is called the **discrete exponential growth model**.

We have two equations for the discrete exponential growth model. The original model (1.2) defines the sequence recursively, meaning that N_{t+1} is given in terms of N_t. The recursive definition is an example of a **difference equation**, and its solution (1.3) defines the sequence explicitly. The ready determination of an explicit formula for a discrete model is a luxury reserved for a few of the simplest models. Most of the models we study will be ones for which we have only the original recursive definition, and we will need methods for studying such equations without a solution formula.

The solution formula (1.3) discloses an unrealistic property of the discrete exponential growth model. Observe that

$$\lim_{t \to \infty} N_t = \infty.$$

Eventually, there will be so many fish that the model lake will have no room for water, but the model population will still be growing rapidly. Real populations do not behave this way, and we should certainly prefer models that don't do so either. The discrete exponential model can be used successfully for a short time only, during the period of growth when space and resources are plentiful. Eventually, however, the growth of the population will lead to crowding and limitation of resources. A better model should include a mechanism for slowing the net relative growth rate for larger populations.

Observe that the discrete exponential growth model can be written as

$$\frac{N_{t+1} - N_t}{N_t} = R. \tag{1.4}$$

The quantity $N_{t+1} - N_t$ is the change in population from time t to time $t + 1$. Since one time unit has elapsed, we can also think of $N_{t+1} - N_t$ as the rate of change of population per unit time. Dividing by N_t yields the **relative rate of change** of the population. It is often helpful to think of a discrete population model as a statement about the relative rate of change of the population rather than as a formula for computing the new population from the current population. In the case of the discrete exponential growth model, the resulting equation (1.4) provides a clear interpretation of the model, which is that the relative rate of change of the population is constant. Given $R > 0$, the model predicts that the population growth rate will be unabated as the population grows. This conclusion is, of course, confirmed by the solution formula (1.3).

Mathematical models in physics and chemistry are almost always derived from first principles. It is seldom possible to derive ecological models from first principles. We often settle for heuristic models instead. A **heuristic** model is one in which the specific details of the formulas that appear in the model are chosen because they have the right qualitative behavior. We can develop a heuristic fishery model that improves on the discrete exponential growth model by modifying Equation 1.4. We want the relative rate of growth to fall to 0 at some large value that represents the capacity of the environment. The easiest way to do that is to make the relative rate of growth linear with negative slope. Using the parameters specified in Figure 1.1, we have the **discrete logistic model**,

$$\frac{N_{t+1} - N_t}{N_t} = R\left(1 - \frac{N_t}{K}\right). \tag{1.5}$$

The relative rate of change in the logistic model is the same as in the exponential model for

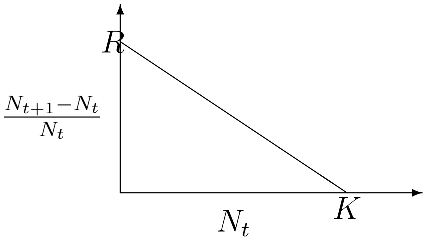

Figure 1.1: The relative rate of change for the discrete logistic model

$N_t \approx 0$, but it decreases as the population grows. Eventually, the relative rate of change becomes 0 when $N_t = K$. The discrete logistic model is the simplest population model that can account for the effect of a finite amount of space and resources. Two other models are the Beverton-Holt model and the Ricker model, which you will encounter in the exercises. These models can be derived from first principles (see Section 5).

For the purpose of simulations, we can rewrite the discrete logistic model in the form of a formula for N_{t+1} in terms of N_t:

$$N_{t+1} = N_t + RN_t\left(1 - \frac{N_t}{K}\right). \tag{1.6}$$

Example 1.1
Consider the model

$$N_{t+1} = N_t + 0.2N_t\left(1 - \frac{N_t}{1000}\right), \qquad N_0 = 1000.$$

This is the discrete logistic model with $R = 0.2$ and $K = 1000$. Using the model to determine population values for times greater than 0, we begin with $N_1 = 1000 + 200(1 - 1000/1000) = 1000$. Thus, $N_1 = N_0$. Similarly, the population in the model will be 1000 in all subsequent years. ◇

A value of N for which $N_{t+1} = N_t$ is called a **fixed point**. Fixed points play a special role in the study of discrete dynamic models, and so a key part of the analysis of any discrete dynamic model is the determination of fixed points. In general, fixed points can be determined by simple algebra. By definition, a **fixed point** P is a population value for which $N_{t+1} = P$ whenever $N_t = P$. The substitutions $N_{t+1} = P$ and $N_t = P$ into the discrete logistic model (1.5) yield the equation

$$P = P + RP\left(1 - \frac{P}{K}\right).$$

This equation defines the fixed points in terms of the model parameters r and K. After simplifying, we obtain

$$P\left(1 - \frac{P}{K}\right) = 0.$$

There are two fixed points, $P = K$ and $P = 0$. You can quickly check that these are fixed points by computing $N_1 = 0$ from $N_0 = 0$ and $N_1 = K$ from $N_0 = K$.

Example 1.2
Consider the model

$$N_{t+1} = \frac{rN_t^2}{A^2 + N_t^2},$$

where r and A are positive constants. To find the relative rate of change, we subtract N_t and then divide by N_t to get

$$N_{t+1} - N_t = \frac{rN_t^2}{A^2 + N_t^2} - N_t = N_t\left(\frac{rN_t}{A^2 + N_t^2} - 1\right) = N_t\frac{rN_t - A^2 - N_t^2}{A^2 + N_t^2},$$

and then

$$\frac{N_{t+1} - N_t}{N_t} = \frac{rN_t - A^2 - N_t^2}{A^2 + N_t^2}.$$

To find the fixed points of the model, we set $N_{t+1} = P$ and $N_t = P$ and obtain the equation

$$P = \frac{rP^2}{A^2 + P^2}$$

As is generally the case, $P = 0$ is a fixed point. If $P \neq 0$, the equation becomes

$$1 = \frac{rP}{A^2 + P^2},$$

which we can rewrite as

$$A^2 + P^2 = rP.$$

This is a quadratic equation for P. Applying the quadratic formula to the form $P^2 - rP + A^2$, we obtain

$$P = \frac{r \pm \sqrt{r^2 - 4A^2}}{2}.$$

These fixed points exist only if $r > 2A$, and this turns out to be a requirement for the model to be useful. With the assumption $r > 2A$, the model then has three fixed points.

$$P = 0, \qquad P = \frac{r - \sqrt{r^2 - 4A^2}}{2}, \qquad P = \frac{r + \sqrt{r^2 - 4A^2}}{2}.$$

◇

If the parameters in a model are fixed, we can run simulations with it by choosing different starting values and calculating the results.

Example 1.3

Consider the model

$$N_{t+1} = N_t + 0.2N_t\left(1 - \frac{N_t}{1000}\right), \qquad N_0 = 100.$$

This is the discrete logistic model with the same parameter values as Example 1.1. The initial population is only 100, which might be realistic for our fishery model. From Equation 1.5, we have the initial relative growth rate as $0.2(1-100/1000) = 0.18$. This is only slightly different from the growth rate in the discrete exponential model. We can use the model to obtain population figures for as many years as we like. For example,

$$N_1 = 100 + 20(1 - 100/1000) = 118, \qquad N_2 = 118 + 23.6(1 - 118/1000) = 138.8152 \approx 139.$$

The model generally yields fractional values, but this is not a problem. As a mathematical model, it only approximates reality anyway, and the error of predicting fractional fish is less serious than other errors, such as not using a theoretical argument to determine the details of the model. Figure 1.2 illustrates the population over a long period of time. For comparison, we also include the populations obtained with initial values of 0, 10, 500, and 1000. ◇

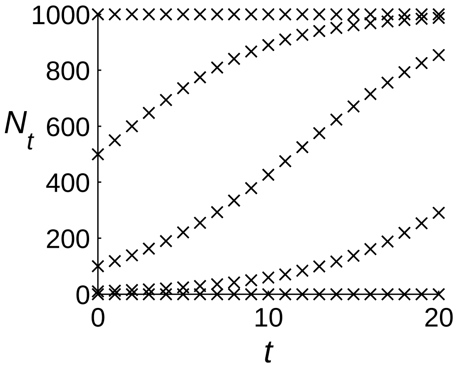

Figure 1.2: Population results for Example 1.3

Figure 1.2 illustrates the fact that there are different kinds of fixed points. The fixed point $P = 0$ is said to be **unstable** because sequences that start near it move away from it. The fixed point $P = K$ in the logistic growth model is said to be **asymptotically stable** because sequences that start near it move to it. (Graphs of N vs t have horizontal asymptotes at asymptotically stable fixed points.) It is a simple matter to find the fixed points of a discrete dynamic model, but it is more difficult to determine if a fixed point is stable or unstable. This issue will be addressed in the next two sections. Stability of fixed points is one of the most important properties of a discrete dynamic model, because the only values that a sequence can converge to are the stable fixed points.

2 Continuous Population Models

Consider a type of grass that spreads more by propagation than by seed production. Ignoring seasonal changes in climate, the growth of the grass occurs on a continuous basis, leading us to choose a continuous model. The simplest continuous model of population growth is similar to the simplest discrete model. The discrete exponential growth model had the property of a constant relative growth rate. This same property characterizes the **exponential growth model** for the continuous case. For a function $N(t)$ of continuous time, the derivative dN/dt indicates the rate of change. The **relative rate of change** for a function of continuous time is the ratio of the rate of change to the functional value. Thus, a constant relative rate of change corresponds to the equation

$$\frac{1}{N}\frac{dN}{dt} = R, \tag{2.1}$$

which compares directly to Equation 1.4. We can rewrite the equation in the standard form as

$$\frac{dN}{dt} = RN. \tag{2.2}$$

The exponential growth equation is so named because of its solution, $N = N_0 e^{Rt}$, where N_0 is the population at time 0. As in the discrete case, the exponential model is limited in its value to situations of short duration in cases where there is no significant limitation of resources. The unbounded solution of the equation makes the model unsuitable for any situations in which growth should be restricted.

A more realistic model is the **logistic growth model**, which we can define in a manner analogous to the discrete logistic model of Section 1. We again assume a relative rate of population change that is given by the linear relationship of Equation 1.5 and Figure 1.1, along with the continuous definition of relative rate of change, yielding the equation

$$\frac{dN}{dt} = RN\left(1 - \frac{N}{K}\right). \tag{2.3}$$

Example 2.1

Analogous to Example 1.3, consider the model

$$\frac{dN}{dt} = 0.2N\left(1 - \frac{N}{1000}\right), \qquad N(0) = 100.$$

It is possible to calculate a formula for $N(t)$ from these equations; however, it is not particularly advantageous to do so, as the result can be approximated to any degree of accuracy by numerical calculations. Numerical methods for differential equations work by computing the solutions to discrete approximations of the differential equations. Computer algebra systems such as Maple and mathematical software such as Matlab have excellent built-in routines for computing approximate solutions to differential equation models. Figure 2.1 shows the solution. The behavior is very similar to that of the corresponding discrete problem. ◇

Analogous to the fixed points of discrete models are **equilibrium solutions** of continuous models. These are values of N for which $dN/dt = 0$. Finding equilibrium solutions is a simple algebraic problem. Setting $dN/dt = 0$ in Equation 2.3 yields the equation

$$RN\left(1 - \frac{N}{K}\right) = 0;$$

the solutions $N = 0$ and $N = K$ are the equilibrium solutions for the logistic equation, the same as the fixed points for the discrete logistic model.

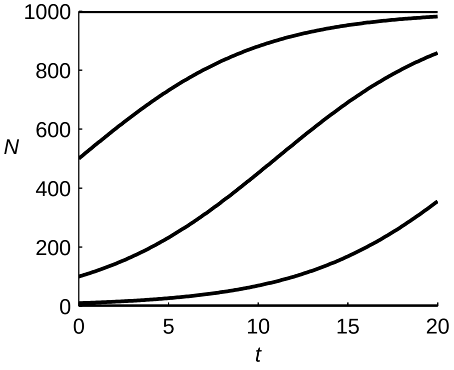

Figure 2.1: Population results for Example 2.1

A renewable resource model

So far, we have considered general models for growth in a continuous setting. Some modifications are needed to make a renewable resource model. First, we need to consider that it doesn't make much sense to measure a population of plant resources in terms of individuals. It makes more sense to think of the dependent variable as the total biomass of the plant resource. This does not change the model mathematically; it merely changes the interpretation of the model. Even so, the logistic equation is not quite suitable as a model for a renewable resource because it does not consider the utilization of the resource by some consumer. The simplest model for a renewable resource takes the form

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - Cq(V), \tag{2.4}$$

where V is the biomass of vegetation, C is the number of consumers, and $q(V)$ is the rate of consumption per consumer. The case $q = QV$ is the simplest reasonable case. This assumption will be considered in the exercises in the context of a continuous fishery model. For cows grazing on grass, a better model is

$$\frac{dV}{dt} = rV\left(1 - \frac{V}{K}\right) - C\frac{QV^2}{H^2 + V^2}, \tag{2.5}$$

where H is an additional parameter called the **semisaturation constant**. Figure 2.2 illustrates the function $q(V)$ for Equation 2.5. Note that the maximum value of q is Q, achieved in the limit $V \to \infty$. The significance of H is that $q = Q/2$ when $V = H$; thus, the semisaturation constant is the value of the resource corresponding to consumption that is half of the maximum (or saturation) level.

Equation 2.5 has five parameters, but the same model can be written with only two parameters. If we define the quantities v, τ, a, and c by

$$V = Kv, \qquad \tau = rt, \qquad a = \frac{H^2}{K^2}, \qquad c = \frac{CQ}{rK}, \tag{2.6}$$

we obtain the *dimensionless* form of the model:[1]

$$v' = v\left(1 - v - \frac{cv}{a + v^2}\right). \tag{2.7}$$

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[1] See the exercises for the derivation of this form of the model.

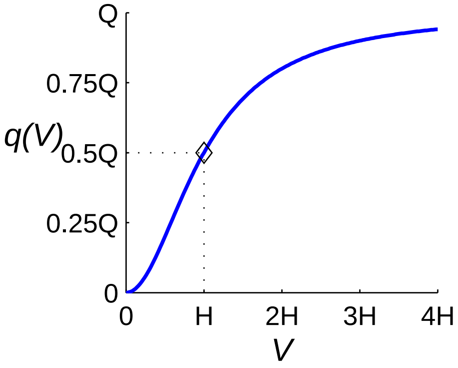

Figure 2.2: The consumption rate function $q = QV^2/(H^2 + V^2)$

Analysis of the renewable resource model of Equation 2.7 will be a recurring theme of this chapter. For now, we consider the problem of finding the equilibrium solutions. Setting $v' = 0$, we obtain the equation $1 - v - cv/(a + v^2) = 0$, which we can rewrite as

$$(1 - v)(a + v^2) = cv,$$

or

$$v^3 - v^2 + (c + a)v - a = 0. \tag{2.8}$$

There is a general formula for the solution of cubic equations, but it is too unwieldy to be of much value, particularly when the equation includes parameters. Here we see the advantage of the dimensionless version of the model. Equation 2.8 has only two parameters, while the corresponding equation, had we derived it from Equation 2.5, would have had four parameters (r, K, H, and CQ). The reduction from four parameters to two makes the analysis much more feasible.

There is a tendency among students of mathematics to immediately submit difficult algebra problems to a computer algebra system, such as Maple or Mathematica, rather than working on them by hand. This is often a mistake when a problem contains parameters. In our analysis, we should attempt to preserve as much generality and simplicity of form as possible. A focus on getting general information about the general problem is often much more useful than a focus on getting numerical solution values for specific choices of parameters.

How do we learn anything about the solutions of Equation 2.8 without solving the equation? By using a graphical approach rather than a symbolic approach. We first need to think about what information we want to obtain. The model is valid only for $0 \leq v \leq 1$; hence, the most important question to answer is,"How many roots does the equation have in the interval $0 \leq v \leq 1$?" To answer this question, we could think of Equation 2.8 as having the general form $f(v) = 0$. Solutions appear as the v intercepts on a graph of $f(v)$. If we can sketch the general 2-parameter family of cubic graphs, we can see the number of positive real roots. Unfortunately, this is too complicated to be practical.

A better approach is to split the terms in the equation, putting some on each side. Suppose we rewrite the equation as

$$v^2 - v^3 = (c + a)v - a. \tag{2.9}$$

The equation now has the form $f(v) = g(v)$. If we graph $f(v)$ and $g(v)$ together, solutions will consist of v values at which the graphs cross. Note that we could have split the terms in a variety of different ways. The choice of $v^2 - v^3$ on one side and $(c+a)v - a$ on the other side was quite deliberate. One side of Equation 2.9 contains the more complicated terms, but no parameters, while the other side contains the parameters in a very simple function. These functions are plotted together in Figure 2.3 with $a = 0.008$ and c=0.1, 0.2, and 0.3. Note that there are usually either one or three positive solutions.

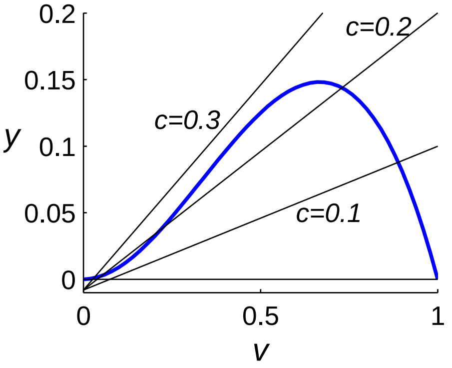

Figure 2.3: Graphs of $v^2 - v^3$ and $(c+a)v - a$, with $a = 0.008$

3 Graphical Analysis

Cobweb diagrams are graphical representations of discrete dynamic models. The *phase line* is a very simple graphical setting for representation of continuous dynamic models. Although the methods are very different, there are some unifying features. Both methods allow conclusions to be drawn regarding the long-term behavior of a univariate dynamic model. Both methods have the same two requirements that must be met by the model to which they are to be applied:

1. The formula that prescribes the model dynamics (by prescribing the population in the next time step for the discrete case or the rate of change of the population for the continuous case) must not refer directly to the time. In other words, the model must be **autonomous**, meaning that the evolution of the system is governed entirely by the current state of the system. This requirement rules out models that account for seasonal changes in the environment.

2. The formula that prescribes the model dynamics must be of **first order**. In the discrete case, this means that the formula for the population at time $t+1$ can only refer to the population at time t and not to earlier population data. This requirement rules out models for organisms with a life history that involves stages of comparable duration, as is common among insect species. Suppose it takes two time units for an individual to become an adult. Individuals that survive the first period are juveniles for the second period of their lives. In this scenario, the adult population at time $t+1$ depends on the juvenile population at time t, which in turn depends on the adult population at time $t-1$. This is an example of a *second order* model. We defer consideration of higher order models for a later chapter. In the continuous case, a first order model is one in which the differential equation contains no derivatives higher than first order.

Fortunately, there are a lot of useful models that are autonomous and first order. In particular, the Beverton-Holt and Ricker models introduced in the Section 1 exercises are autonomous first-order discrete models, and the logistic model and renewable resource models of Section 2 are autonomous first-order continuous models.

Cobweb diagrams

Figure 3.1 shows a cobweb diagram for the discrete exponential growth model

$$N_{t+1} = 1.5N_t.$$

At first glance, cobweb diagrams are a mass of lines going in different directions. The diagrams actually contain a lot of useful information. We focus first on the construction of the diagram and then fill in details that help in the interpretation of the diagram.

The standard form for an autonomous first-order discrete model is

$$N_{t+1} = g(N_t). \tag{3.1}$$

Thus, the model is specified by the choice of the function g. For example, the diagram in Figure 3.1 is for the function $g(N) = 1.5N$. The basis of a cobweb diagram is a graph that displays $y = g(N)$ and $y = N$ on the same set of axes. In Figure 3.1, the heavy line is $y = g(N) = 1.5N$ and the medium line is $y = N$. The light line with a stair-step shape is a graphical rendition of a simulation. The line was created by the following procedure.

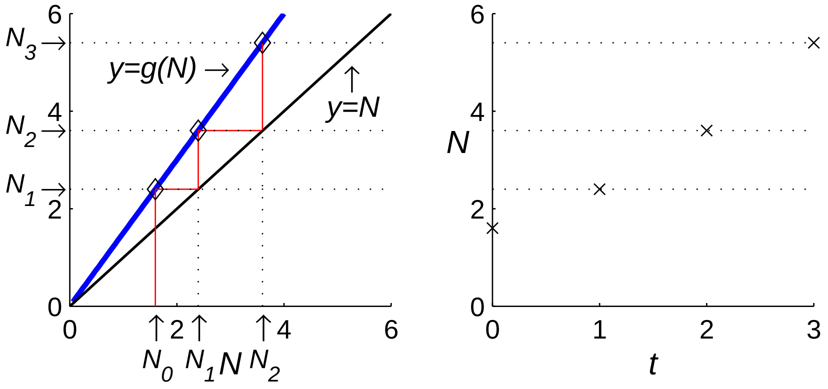

Figure 3.1: Cobweb diagram and time history for $N_{t+1} = 1.5N_t$

Algorithm 3.1 (Cobweb Diagram for $N_{t+1} = g(N_t)$)

1. *Choose a value for N_0. The starting point for the simulation is the point on the N axis corresponding to the chosen value of N_0.*
2. *Draw a vertical line segment from the starting point to the curve $y = g(N)$.*
3. *Draw a horizontal line segment from the (new) current point to the line $y = N$.*
4. *Continue extending the diagram by alternating vertical and horizontal line segments, always moving vertically to $y = g(N)$ and horizontally to $y = N$.*

Just as in a simulation by calculation, all of the parameters have to be chosen before constructing the cobweb diagram, including the initial value N_0. Once the parameters are chosen, the process of constructing the cobweb diagram is mechanical. Just plot the two functions and draw the line segments in the prescribed manner. Think of the construction and interpretation as separate steps, and the construction is easy.

We begin the interpretation of the cobweb diagram with the points marked by diamond symbols. These points are the endpoints of the vertical line segments of the diagram. The coordinates of the three marked points in the diagram of Figure 3.1 are (N_0, N_1), (N_1, N_2), and (N_2, N_3). Because the heavy curve is the equation $y = g(N)$ and the model is $N_{t+1} = g(N_t)$, it follows that any point on the curve that has N coordinate N_t for some t must have y coordinate N_{t+1}. The purpose of the vertical line segments is to compute new values of the population. This point is emphasized in the figure by the dotted horizontal lines that indicate the transfer of the y coordinate of each point to the corresponding point (t, N_t) on the time history plot.

At this point, the reader should be asking a key question: "How do we know that the horizontal coordinates of the marked points are N_0, N_1, and N_2?" We knew N_0 at the beginning of the process; however, the other points, N_1 and N_2, must have been determined by the process itself. This is where the horizontal line segments come in. The first marked point has coordinates (N_0, N_1), so the first horizontal line segment marks the line $y = N_1$. The segment ends on the line $y = N$. The intersection of the lines $y = N_1$ and $y = N$ is at $N = N_1$, and this is precisely the N value that we need to use to be able to draw a vertical line segment to the point (N_1, N_2). Thus, we can see the sequence of N values by looking at *either* the vertical or the horizontal coordinates of the marked points. The vertical coordinates are N_1, N_2, …, and the horizontal coordinates are N_0, N_1, ... You should now pause to review what has been said. Once you understand the reason for the alternating vertical and horizontal lines, the cobweb diagram loses its mystery and becomes a simple tool.

Up to this point, we have focused on explaining the process of the cobweb diagram and its interpretation as a simulation. Now we turn to the use of the diagram for analysis. What information does the diagram contain that is not contained in the corresponding time history? In a time history, we can see the current point and past points. In a cobweb diagram, we can see the future as well. For the model of Figure 3.1, the future is that the sequence will continue to increase as the diagram is extended to larger values of N and y. Every horizontal line segment will go to the right, so each value of N will be larger than the preceding value.

Figure 3.2 shows a cobweb diagram for

$$N_{t+1} = \frac{5N_t^2}{4 + N_t^2}.$$

The cobweb diagram for this model tells a different story. The graphs of $y = g(N)$ and $y = N$ cross at the fixed point $N = 4$, and the cobweb diagram indicates that the marked points will simply get closer to the fixed point. The cobweb diagram shows that the equilibrium solution $N = 4$ is asymptotically stable and that starting values between 1 and 4 cause the sequence to approach 4 as $t \to \infty$.

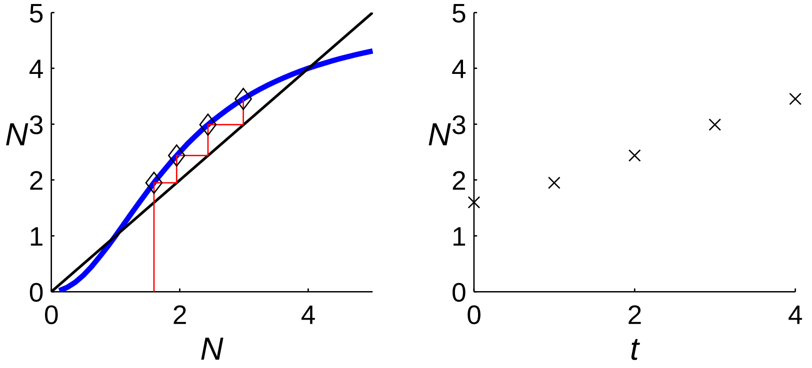

Figure 3.2: Cobweb diagram and time history for $N_{t+1} = \frac{5N_t^2}{4+N_t^2}$ with $1 < N_0 < 4$

Choosing other values of N_0 give a complete picture of the long-term behavior of the model. Any initial value greater than 1 leads to a cobweb diagram with the same general features as Figure 3.2. Initial values less than 1 lead to a qualitatively different picture, as shown in Figure 3.3. The horizontal line segments all move to the left, and the marked points approach the fixed point $N = 0$. Thus, $N = 0$ is a second asymptotically stable fixed point. The unstable fixed point $N = 1$ serves as a dividing point between solutions that go to 0 and solutions that go to 4.

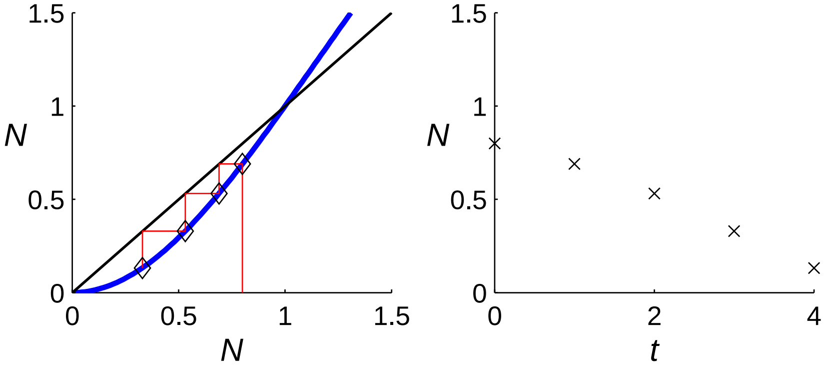

Figure 3.3: Cobweb diagram and time history for $N_{t+1} = \frac{5N_t^2}{4+N_t^2}$ with $0 < N_0 < 1$

Phase line analysis

Figure 3.4 shows the phase line representation of the logistic equation

$$\frac{dN}{dt} = N(1 - N)$$

along with the graph of $f(N) = N(1 - N)$.

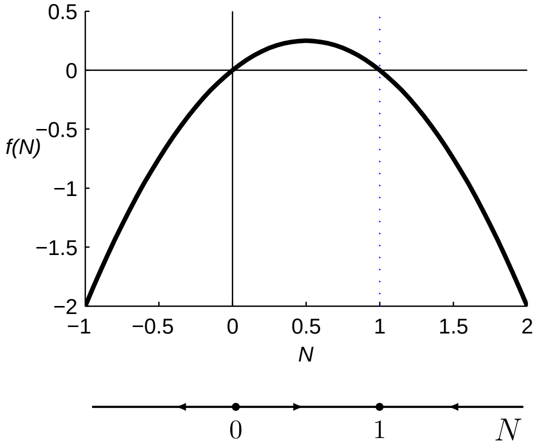

Figure 3.4: The function $f(N) = N(1 - N)$ and the phase line for $N' = N(1 - N)$

The phase line representation consists of a number line with some points and arrows. The points and arrows are easily obtained from the graph of $f(N)$.

Algorithm 3.2 (Phase Line Representation for $dN/dt = f(N)$)

1. *Find the equilibrium solutions* $(f(N) = 0)$ *and mark these points on the phase line.*
2. *The equilibrium solutions partition the interval* $[0, \infty)$ *into regions.*[2] *Each of these regions*

---

[2] This assumes that the dependent variable cannot be negative in the model, as is the case when the dependent variable represents a population. If the model makes sense for negative values of the dependent variable, then use the interval $(-\infty, \infty)$.

needs an arrow. The arrowhead points to the right for regions in which $f(N) > 0$ and to the left in regions where $f(N) < 0$.

This is pretty simple compared to the cobweb diagram. Nevertheless, the phase line is quite a powerful tool. The arrows in the phase line representation of Figure 3.4 indicate that the equilibrium solutions $P = 0$ and $P = 1$ are unstable and stable, respectively. One doesn't even need to think of initial conditions in using the phase line. Parameters can often be left unspecified simply by sketching the graph of f in a way that doesn't require values for the parameters. Figure 3.5 shows the phase line for the general logistic model

$$\frac{dN}{dt} = RN\left(1 - \frac{N}{K}\right).$$

With a small amount of effort, we have a rich analysis of the general model. The model predicts that K is a stable equilibrium value, and that all populations that are initially positive approach K in time.

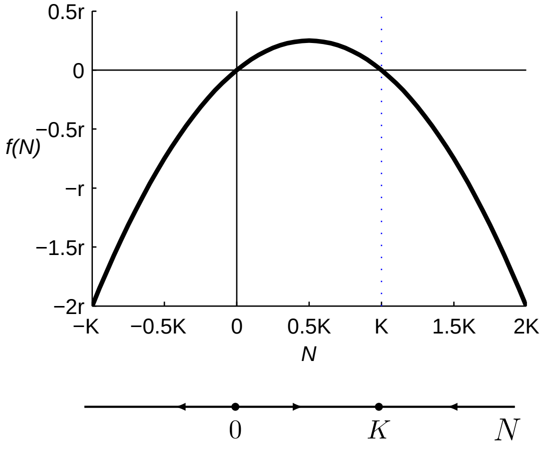

Figure 3.5: The function $f(N) = rN(1 - N/K)$ and the phase line for $N' = f(N)$

The phase line representation of a continuous population model can sometimes be obtained from graphs other than $f(N)$.

Example 3.1
Consider the renewable resource model from Section 2, given in dimensionless form as

$$v' = v\left(1 - v - \frac{cv}{a + v^2}\right). \tag{3.2}$$

The model can be rewritten as

$$v' = \frac{v}{a + v^2}[(1 - v)(a + v^2) - cv] = \frac{v}{a + v^2}[(v^2 - v^3) - (cv + av - a)],$$

which is of the general form

$$v' = s(v)[F(v) - G(v)], \qquad s > 0.$$

We (in essence) used this form in Section 2 to determine the equilibrium solutions, and it can also be used to determine stability. All we need for a phase line representation is information about which values of the dependent variable lead to an increase and which to a decrease. The points where F and G cross mark the equilibrium solutions, the region where $F > G$ indicates the values of v for which v is increasing, and the region where $F < G$ indicates the values of v for which v is decreasing. This information allows us to construct the phase line representations for the various cases, as displayed in Figure 3.6. For small values of c, there is one large equilibrium solution that is stable. For large values of c, there is one small equilibrium solution that is stable. Since c is proportional to the number of cows grazing on the land, these results indicate that there are two fundamentally different situations. The system evolves to one of two stable states, one with a large amount of vegetation and a small number of cows, and the other with a large number of cows and very little vegetation. For medium values of c, there are three equilibrium values; the largest and smallest are stable and the middle is unstable. With an intermediate number of cows, there can be a stable solution with a lot of vegetation and one with only a little. Which one is actually reached depends on the initial situation; if there is a lot of vegetation to begin with, then the system reaches the high-density stable equilibrium.

Suppose we start with a small number of cows and a large amount of vegetation, and we gradually add more cows. The picture will gradually change from the small c picture to the medium c picture to the large c picture. Initially, the change in the stable equilibrium solution will be small. As we move into the medium c regime, the change will continue to be small; the larger equilibrium solution will be the one achieved, since the amount of vegetation is initially, large. When the number of cows increases from medium to large, there will be enough cows so that only the low-density stable equilibrium exists. The system will at that point exhibit a drastic loss of vegetation due to overgrazing. ◇

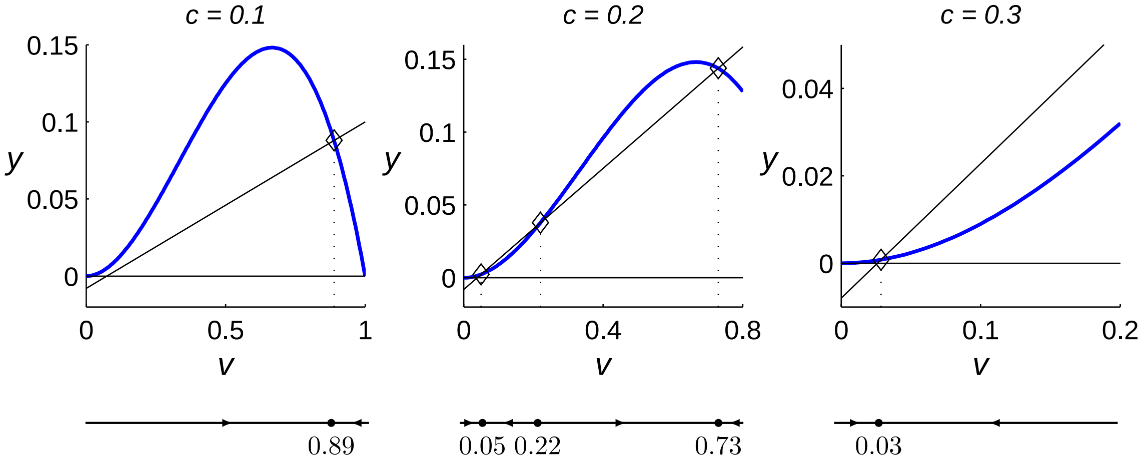

Figure 3.6: Phase line representations for the renewable resource model (3.2), with $a = 0.008$ and several values of c

Summary

Cobweb diagrams display a simulation graphically, allowing conclusions to be drawn about stability of fixed points and long-term behavior for solutions with all possible starting values. They do not give general information about the multi-parameter model, but they do give complete information about the model for any fixed set of parameter values.

Phase line representations do not display a simulation, but they focus directly on stability of equilibrium solutions and long-term behavior for solutions with all possible starting values. When the function $f(N)$ can be sketched for general parameter values, the corresponding phase line representation gives complete information about the multi-parameter model.

4 Linearized Stability Analysis

In Section 3, we learned how to analyze first-order autonomous population models graphically, with cobweb diagrams for discrete models $N_{t+1} = g(N_t)$ and phase line analysis for continuous models $N'(t) = f(N)$. Now we consider a method that is based on calculations. Asymptotic stability is a *local* property, which means that it depends only on the properties of the model very close to the point of interest. Local properties can be analyzed using calculus.

Stability analysis for discrete models

Figure 4.1 shows the graph of $g(N)$ for the model

$$N_{t+1} = \frac{5N_t^2}{4 + N_t^2}$$

in the vicinity of the fixed point $N = 4$, along with $y = N$ and $y = 4 + 0.4(N - 4)$.

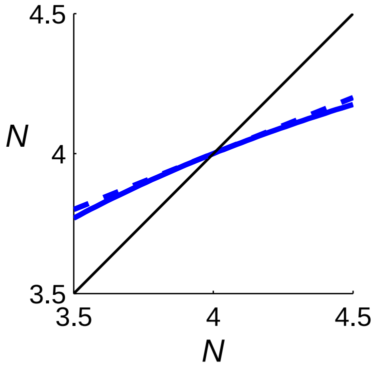

Figure 4.1: $y = g(N)$ (heavy), $y = N$ (medium), and $y = 4 + 0.4(N - 4)$ (dashed) for $N_{t+1} = \frac{5N_t^2}{4+N_t^2}$

The graph shows that

$$g(N) \approx 4 + 0.4(N - 4)$$

near the fixed point $N = 4$. Indeed, $y = 4 + 0.4(N - 4)$ is the equation of the line tangent to $y = g(N)$ at $N = 4$. Alternatively, we can say that the function $4 + 0.4(N - 4)$ is the **linear approximation** of the function g at $N = 4$. In the vicinity of $N = 4$, the original model is therefore approximated by the linear model

$$N_{t+1} = 4 + 0.4(N_t - 4).$$

We can simplify this model by defining the population perturbation x by $x_t = N_t - 4$. Replacing N by $4 + x$ yields the *linearized* model

$$x_{t+1} = 0.4x_t.$$

This is the exponential model, whose solution we can write as

$$x_t = 0.4^t x_0.$$

From this result, we can determine the long-time behavior of the model:

$$\lim_{t\to\infty} x_t = 0.$$

Since x_t is the approximate difference between N_t and 4, we also have

$$\lim_{t\to\infty} N_t = 4.$$

We must be careful not to read too much into this conclusion. The conclusion came from the linearized model, which is only valid if x_0 is "close enough" to 4. From our stability analysis alone, we can only conclude that the sequence N_t converges to 4 for starting populations N_0 that are close enough to 4 so that the linearized model has the same behavior as the nonlinear model.

The power of mathematics is in its use to obtain general results from motivating examples. For our current problem, the conclusion of asymptotic stability for $N = 4$ ultimately derived from the number 0.4 in the linearized model. That number is $g'(4)$, which is the slope of the linear approximation of $g(N)$ near 4. In general, if P is a fixed point for $N_{t+1} = g(N_t)$, then the **linearized model** at that fixed point is

$$x_{t+1} = g'(P)x_t.$$

The difference between N and P is approximately

$$x_t = [g'(P)]^t x_0.$$

This quantity vanishes if $|g'(P)| < 1$, and this serves as a sufficient condition for asymptotic stability.

The complete result of the linearization technique is summarized in Theorem 4.1.

Theorem 4.1 *Let P be a fixed point for the sequence defined by $N_{t+1} = g(N_t)$, with g a differentiable function. Let $x_t = N_t - P$ be a small perturbation from the fixed point. Then the linearized model near $N = P$ is*

$$x_{t+1} = g'(P)x_t.$$

Furthermore:

- *The fixed point P is asymptotically stable if $|g'(P)| < 1$ and unstable if $|g'(P)| > 1$;*
- *x_t alternates in sign whenever $g'(P) < 0$ and retains its sign whenever $g'(P) > 0$.*

Theorem 4.1 allows for a very efficient determination of stability, as long as $g'(P) \neq 1$. With a combination of linearized stability analysis and cobweb diagrams, we can often obtain a complete picture of long-term behavior for a discrete model with arbitrary initial point.

Example 4.1
Consider again the model

$$N_{t+1} = \frac{5N_t^2}{4 + N_t^2}.$$

The fixed points[3] are the solutions of

$$P = \frac{5P^2}{4 + P^2};$$

---

[3] See also Example 1.2.

either $P = 0$ or $1 = 5P/(4 + P^2)$, and the latter simplifies to the quadratic equation $P^2 - 5P + 4 = 0$. The fixed points are thus $N = 0$, $N = 1$, and $N = 4$. To determine the stability of all three fixed points, we first need to determine g'. From

$$g(N) = \frac{5N^2}{4 + N^2},$$

we have

$$g'(N) = \frac{(10N)(4 + N^2) - (5N^2)(2N)}{(4 + N^2)^2} = \frac{40N}{(4 + N^2)^2}.$$

Specifically, $g'(0) = 0$, $g'(1) = 1.6$, and $g'(4) = 0.4$. By Theorem 4.1, 0 and 4 are asymptotically stable and 1 is unstable. Combined with the cobweb diagram of Figure 3.2, we can conclude that the population approaches 4 if $N_0 > 1$ and approaches 0 if $N_0 < 1$. This is an example of a model in which extinction can occur when the population is below some threshold value, a phenomenon sometimes called the **Allee effect**. ◇

So far, we have used the linearization technique only for a model with fixed parameters. Linearization is capable of greater generality because it can be used without fixing the values of parameters.

Example 4.2
Consider the discrete logistic model

$$N_{t+1} = N_t + RN_t \left(1 - \frac{N_t}{K}\right), \qquad r > -1.$$

We found the fixed points to be $N = 0$ and $N = K$ in Section 1. For stability analysis, we have

$$g(N) = N + RN - \frac{RN^2}{K};$$

thus,

$$g'(N) = 1 + r - \frac{2RN}{K}.$$

At the fixed points, we have $g'(0) = 1 + R$ and $g'(K) = 1 - R$. The stability requirement for 0 is $-1 < 1+R < 1$, from which we have that 0 is asymptotically stable for $R < 0$ and unstable for $R > 0$. The stability requirement for K is $-1 < 1-R < 1$, which reduces to the inequalities $R < 2$ and $R > 0$. Our conclusions are as follows:

- For $-1 < R < 0$, 0 is asymptotically stable and K is unstable. The population will approach 0 from any starting value.
- For $0 < R < 2$, 0 is unstable and K is asymptotically stable. The population will approach K from any positive starting value. More specifically, the population will oscillate as it approaches K if $1 < R < 2$ and it will not oscillate in its approach if $0 < R < 1$.
- For $R > 2$, both 0 and K are asymptotically unstable. The long-term behavior is not clear from this analysis. There are a number of possibilities, including periodic behavior and chaotic behavior.

◇

Stability analysis for continuous models

Stability analysis for continuous models is also based on examination of a linearized model. The idea is exactly the same as for discrete models, but the result is different.

Let P be an equilibrium solution for the problem $dN/dt = f(N)$. As with the discrete case, we can replace f near $N = P$ by a linear approximation $f(N) \approx f(P) + f'(P)(N - P) = f'(P)(N - P)$, where we have used the fact that $f(P) = 0$ because P is an equilibrium solution. Thus, we have

$$\frac{dN}{dt} \approx f'(P)(N - P).$$

With $x(t) = N(t) - P$, we have the linearized model

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

This is the exponential equation, and it has the solution

$$x = x(0)e^{f'(P)t}.$$

Thus, $x \to 0$ whenever $f'(P) < 0$. We have a theorem analogous to Theorem 4.1.

Theorem 4.2 *Let P be an equilibrium solution for the differential equation $N' = f(N)$, with f a differentiable function. Let $x = N - P$ be a small perturbation from the fixed point. Then the linearized system near $N = P$ is*

$$x' = f'(P)x.$$

Furthermore:

- *The equilibrium solution P is asymptotically stable if $f'(P) < 0$ and unstable if $f'(P) > 0$.*

Example 4.3
Consider the renewable resource model

$$v' = v\left(1 - v - \frac{cv}{a + v^2}\right) = v - v^2 - \frac{cv^2}{a + v^2}.$$

Differentiating $f(v) = v - v^2 - cv^2/(a + v^2)$ yields

$$f'(v) = 1 - 2v - c\frac{(2v)(a + v^2) - (v^2)(2v)}{(a + v^2)^2} = 1 - 2v - \frac{2cav}{(a + v^2)^2}.$$

For the equilibrium solution $v = 0$, we have $f'(0) = 1 > 0$, so 0 is unstable. Now let P be a positive equilibrium solution. Then

$$1 - P - \frac{cP}{a + P^2} = 0,$$

or

$$\frac{cP}{a + P^2} = 1 - P. \tag{4.1}$$

By Theorem 4.2, we have asymptotic stability for any equilibrium solution P for which $f'(P) < 0$, that is,

$$1 - 2P < \frac{2caP}{(a + P^2)^2}.$$

This inequality can be simplified by substituting from Equation 4.1. We have

$$1 - 2P < \frac{2a}{a + P^2} \frac{cP}{a + P^2} = \frac{2a(1 - P)}{a + P^2}.$$

This simplifies to

$$(1 - 2P)(a + P^2) < 2a - 2aP,$$

or

$$P^2(1 - 2P) < a. \tag{4.2}$$

Given any pair of values for a and c, we can compute the equilibrium solutions and check them according to this simple inequality. Note that one fairly general result follows directly from the inequality. Any equilibrium solution greater than or equal to 1/2 is stable. $\diamond$

5 Connecting Discrete and Continuous Models

We have chosen to treat discrete and continuous models simultaneously to emphasize the similarities and differences between the two types of univariate dynamic models. In Section 4, we developed a linearization technique for stability analysis for each type. The results given in Theorems 4.1 and 4.2 seem very different, but the differences are largely due to differences in the standard notation for the models rather than the actual properties. In this section, we present the results of Section 4 again using a common notation for the two types of models. We also introduce the concept of *metered models*, which are discrete models based on continuous mathematics.

Similarities and differences

The standard forms for discrete and continuous models are $N_{t+1} = g(N_t)$ and $N' = f(N)$. The functions g and f do not represent corresponding quantities; one is the new population while the other is the rate of change. We could use a unifying notation by focusing on the rate of change in both types of models. In terms of the rate of change, discrete models have the form

$$N_{t+1} - N_t = F(N_t), \tag{5.1}$$

for some function F, which we can rewrite in standard form as

$$N_{t+1} = N_t + F(N_t).$$

The identification

$$g(N) = N + F(N)$$

allows us to recast Theorem 4.1 in terms of the rate of change. Differentiating, we have

$$g'(N) = 1 + F'(N).$$

The discrete stability requirement $|g'(P)| < 1$ becomes

$$-1 < 1 + F'(P) < 1,$$

which reduces to a pair of requirements:

$$F'(P) < 0, \qquad F'(P) > -2. \tag{5.2}$$

We therefore have a version of Theorem 4.1 in terms of F rather than g.

Theorem 5.1 *The fixed point P for the discrete model $N_{t+1} - N_t = F(N_t)$, with F continuous, is asymptotically stable if and only if $F'(P) < 0$ and $F'(P) > -2$.*

Compare Theorems 4.2 for the continuous case and 5.1 for the discrete case. The requirements $f'(P) < 0$ and $F'(P) < 0$ both say that the derivative of the rate of change must be negative at the point P. This is enough in the continuous case, but there is an extra requirement in the discrete case. While P is stable in the continuous case no matter how negative $f'(P)$ is, P loses stability in the discrete case if $F'(P)$ is too negative. This fact has two important consequences, one biological and one mathematical. Biologically, it means that populations whose dynamics are governed by synchronous processes are more likely to be unstable than those whose dynamics are governed by asynchronous processes.

Most continuous models can not be conveniently solved for an explicit solution formula. It is common in these cases to do a numerical simulation, which is actually done on a discretized version of the model. Since discrete models have an extra stability criterion that is not present for continuous models, there is a possibility that the discretized version used for simulation is unstable even though the original continuous model is stable. One must always be careful in applying numerical methods to continuous models because of this possibility of instability due to choice of method rather than model properties. Fortunately, this problem can be dealt with effectively. Numerical analysts use the term **stiff** to describe a differential equation that is prone to loss of stability when discretized. If you suspect that the problem you are working on is stiff, you can use special numerical methods designed to prevent the loss of stability. In practice, stiffness is seldom encountered in univariate models but is rather common in multivariate models in biology and chemistry.

Metered models

In Section 1, we derived a simple discrete fishery model,

$$N_{t+1} = [S_I b p(N_t) + S] N_t. \tag{5.3}$$

where S_I and S are constant survival probabilities for immature and mature fish, respectively, b is the number of eggs per adult fish, and p is the probability that an immature fish will develop out of an egg during the initial phase of duration T. We did not concern ourselves with the choice of the function p, somewhat arbitrarily taking it as constant for the exponential model and linear for the logistic model. A more sophisticated plan is to use a continuous model to determine a functional form for p that is based on assumptions about the life history of the type of fish. The idea is to write down a continuous model for the larva population $L(t)$, and then identify the desired survival probability $p(N_t)$ for Equation 5.3 as $L(T)/(bN_t)$.[4] Models created in this manner are called **metered models**.

Example 5.1
The Beverton-Holt model assumes that eggs and/or larvae die primarily from strong competition. This is a reasonable assumption if the main cause of death is lack of resources. The model has been successfully used with several fish populations, particularly some oceanic species. Suppose the per capita mortality rate of larvae is proportional to the larvae population. Then we have the continuous model

$$\frac{1}{L}\frac{dL}{dt} = -mL, \qquad L(0) = bN_t,$$

or

$$\frac{dL}{dt} = -mL^2, \qquad L(0) = bN_t.$$

Although we have not seen this kind of equation before, it is a simple matter to check that the function

$$L(t) = \frac{bN_t}{1 + mbN_t t}$$

is the solution. With $k = mbT$, we have

$$L(T) = \frac{bN_t}{1 + kN_t}.$$

---

[4] Recall that bN_t is the number of eggs.

Thus, the survival probability is

$$p(N_t) = \frac{L(T)}{bN_t} = \frac{1}{1 + kN_t},$$

and the Beverton-Holt model is

$$N_{t+1} = \left(S + \frac{r}{1 + kN_t} \right) N_t.$$

The substitution $y = kN$ yields the dimensionless model

$$y_{t+1} = \left(S + \frac{r}{1 + y_t} \right) y_t.$$

It is sometimes valid to assume that adult fish do not survive from one census to the next, in which case the model simplifies to

$$y_{t+1} = \frac{ry_t}{1 + y_t}.$$

◇