Understanding Nonlinear Dynamics

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Daniel Kaplan Leon Glass

Understanding Nonlinear Dynamics

With 294 Illustrations



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987654321

To Maya and Tamar. — DTK

To Kathy, Hannah, and Paul and in memory of Daniel. — LG

Series Preface

Mathematics is playing an ever more important role in the physical and biological sciences, provoking a blurring of boundaries between scientific disciplines and a resurgence of interest in the modern as well as the classical techniques of applied mathematics. This renewal of interest, both in research and teaching, has led to the establishment of the series: *Texts in Applied Mathematics* (*TAM*).

The development of new courses is a natural consequence of a high level of excitement on the research frontier as newer techniques, such as numerical and symbolic computer systems, dynamical systems, and chaos, mix with and reinforce the traditional methods of applied mathematics. Thus, the purpose of this textbook series is to meet the current and future needs of these advances and encourage the teaching of new courses.

TAM will publish textbooks suitable for use in advanced undergraduate and beginning graduate courses, and will complement the Applied Mathematical Sciences (AMS) series, which will focus on advanced textbooks and research level monographs.

About the Authors

Daniel Kaplan specializes in the analysis of data using techniques motivated by nonlinear dynamics. His primary interest is in the interpretation of irregular physiological rhythms, but the methods he has developed have been used in geophysics, economics, marine ecology, and other fields. He joined McGill in 1991, after receiving his Ph.D from Harvard University and working at MIT. His undergraduate studies were completed at Swarthmore College. He has worked with several instrumentation companies to develop novel types of medical monitors.

Leon Glass is one of the pioneers of what has come to be called chaos theory, specializing in applications to medicine and biology. He has worked in areas as diverse as physical chemistry, visual perception, and cardiology, and is one of the originators of the concept of "dynamical disease." He has been a professor at McGill University in Montreal since 1975, and has worked at the University of Rochester, the University of California in San Diego, and Harvard University. He earned his Ph.D. at the University of Chicago and did postdoctoral work at the University of Edinburgh and the University of Chicago.

Preface

This book is about *dynamics*—the mathematics of how things change in time. The universe around us presents a kaleidoscope of quantities that vary with time, ranging from the extragalactic pulsation of quasars to the fluctuations in sunspot activity on our sun; from the changing outdoor temperature associated with the four seasons to the daily temperature fluctuations in our bodies; from the incidence of infectious diseases such as measles to the tumultuous trend of stock prices.

Since 1984, some of the vocabulary of dynamics—such as *chaos*, *fractals*, and *nonlinear*—has evolved from abstruse terminology to a part of common language. In addition to a large technical scientific literature, the subjects these terms cover are the focus of many popular articles, books, and even novels. These popularizations have presented "chaos theory" as a scientific revolution. While this may be journalistic hyperbole, there is little question that many of the important concepts involved in modern dynamics—global multistability, local stability, sensitive dependence on initial conditions, attractors—are highly relevant to many areas of study including biology, engineering, medicine, ecology, economics, and astronomy.

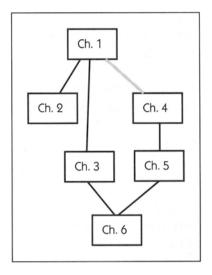
This book presents the main concepts and applications of nonlinear dynamics at an elementary level. The text is based on a one-semester undergraduate course that has been offered since 1975 at McGill University and that has been constantly updated to keep up with current developments. Most of the students enrolled in the course are studying biological sciences and have completed a year of calculus with no intention to study further mathematics. Since the main concepts of nonlinear dynamics are largely accessible using only elementary arguments, students are able to understand the mathematics and successfully carry out computations. The exciting nature and modernity of the concepts and the graphics are further stimuli that motivate students.

Mathematical developments since the mid 1970's have shown that many interesting phenomena can arise in simple finite-difference equations. These are introduced in Chapter 1, where the student is initiated into three important mathematical themes of the course: local stability analysis, global multistability, and problem solving using both an algebraic and a geometric approach. The graphical iteration of one-dimensional, finite-difference equations, combined with the analysis of the local stability of steady states, provides two complementary views of the same problem. The concept of chaos is introduced as soon as possible, after the student is able graphically to iterate a one-dimensional, finite-difference equation, and understands the concept of stability. For most students, this is the first exposure to mathematics from the twentieth century!

From the instructor's point of view, this topic offers the opportunity to refresh students' memory and skills in differential calculus. Since some students take this course several years after studying geometry and calculus, some skills have become rusty. Appendix A reviews important functions such as the Hill function, the Gaussian distribution, and the conic sections. Many exercises that can help in solidifying geometry and calculus skills are included in Appendix A.

Chapters 2 and 3 continue the study of discrete-time systems. Networks and cellular automata (Chapter 2) are important both from a conceptual and technical perspective, and because of their relevance to computers. The recent interest in neural and gene networks makes this an important area for applications and current research.

Many students are familiar with fractal images from the myriad popularizations of that topic. While the images provide a compelling motivation for studying nonlinear dynamics, the concepts of self-similarity and fractional dimension are important from a mathematical perspective. Chapter 3 discusses self-similarity and fractals in a way that is closely linked to the dynamics discussed in Chapter 1. Fractals arise from dynamics in many unexpected ways. The concept of a fractional dimension is unfamiliar initially but can be appreciated by those without advanced technical abilities. Recognizing the importance of computers in studying fractals, we use a computer-based notation in presenting some of the material.



Dependencies among the chapters.

The study of continuous-time systems forms much of the second half of the book. Chapter 4 deals with one-dimensional differential equations. Because of the importance of exponential growth and decay in applications, we believe that every science student should be exposed to the linear one-dimensional differential equation, learning what it means and how to solve it. In addition, it is essential that those interested in science appreciate the limitations that nonlinearities impose on exponential ("Malthusian") growth. In Chapter 4, algebraic analysis of the linear stability of steady states of nonlinear equations is combined with the graphical analysis of the asymptotic dynamics of nonlinear equations to provide another exposure to the complementary use of algebraic and geometric methods of analysis.

Chapter 5 deals with differential equations with two variables. Such equations often appear in the context of compartmental models, which have been proposed in diverse fields including ion channel kinetics, pharmacokinetics, and ecological systems. The analysis of the stability of steady states in two-dimensional nonlinear equations and the geometric sketching of the trajectories in the phase plane provide the most challenging aspect of the course. However, the same basic conceptual approach is used here as is used in the linear stability analyses in Chapter 1 and Chapter 4, and the material can be presented using elementary methods only.

In most students' mathematical education, a chasm exists between the concepts they learn and the applications in which they are interested. To help bridge this gap, Chapter 6 discusses methods of data analysis including classical methods (mean, standard deviation, the autocorrelation function) and modern methods derived from nonlinear dynamics (time-lag embeddings, dimension and related

topics). This chapter may be of particular interest to researchers interested in applying some of the concepts from nonlinear dynamics to their work.

In order to illustrate the practical use of concepts from dynamics in applications, we have punctuated the text with short essays called "Dynamics in Action." These cover a wide diversity of subjects, ranging from the random drift of molecules to the deterministic patterns underlying global climate changes.

Following each chapter is supplementary material. The notes and references provide a guide to additional references that may be fun to read and are accessible to beginning students. A set of exercises reviewing concepts and mathematical skills is also provided for each chapter. Solutions to selected exercises are provided at the end of the book. For each chapter, we also give a set of computer exercises. The computer exercises introduce students to some of the ways computers can be used in nonlinear dynamics. The computer exercises can provide many opportunities for a term project for students.

The appropriate use of this book in a course depends on the student clientele and the orientation of the instructors. In our instruction of biological science students at McGill, emphasis has been on developing analytical and geometrical skills to carry out stability analysis and analysis of asymptotic dynamics in one-dimensional finite-difference equations and in one- and two-dimensional differential equations. We also include several lectures on neural and gene networks, cellular automata, and fractals.

Although this text is written at a level appropriate to first- and second-year undergraduates, most of the material dealing with nonlinear finite-difference and differential equations and time-series analysis is not presented in standard undergraduate or graduate curricula in the physical sciences or mathematics. This book might well be used as a source for supplementary material for traditional courses in advanced calculus, differential equations, and mathematical methods in physical sciences. The link between dynamics and time series analysis can make this book useful to statisticians or signal processing engineers interested in a new perspective on their subject and in an introduction to the research literature.

Over the years, a number of teaching assistants have contributed to the development of this material and the education of the students. Particular thanks go to Carl Graves, David Larocque, Wanzhen Zeng, Marc Courtemanche, Hiroyuki Ito, and Gil Bub. We also thank Michael Broide, Scott Greenwald, Frank Witkowski, Bob Devaney, Michael Shlesinger, Jim Crutchfield, Melanie Mitchell, Michael Frame, Jerry Marsden, and the students of McGill University Biology 309 for their many corrections and suggestions. We thank André Duchastel for his careful redrawing of many of the figures reproduced from other sources. Finally, we thank Jerry Lyons, Liesl Gibson, Karen Kosztolnyik, and Kristen Cassereau for their excellent editorial assistance and help in the final stages of preparation of this book.

McGill University has provided an ideal environment to carry out research and to teach. Our colleagues and chairmen have provided encouragement in many ways. We would like to thank in particular, J. Milic-Emili, K. Krjnevic, D. Goltzman, A. Shrier, M. R. Guevara, and M. C. Mackey. The financial support of the Natural Sciences Engineering and Research Council (Canada), the Medical Research Council (Canada), the Canadian Heart and Stroke Association has enabled us to carry out research that is reflected in the text. Finally, Leon Glass thanks the John Simon Guggenheim Memorial Foundation for Fellowship support during the final stages of the preparation of this text.

We are making available various electronic extensions to this book, including additional exercises, solutions, and computer materials. For information, please contact understanding@cnd.mcgill.ca.

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February 1995

Daniel Kaplan Leon Glass

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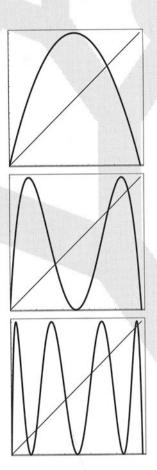
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CHAPTER 1



Finite-Difference Equations

1.1 A MYTHICAL FIELD

Imagine that a graduate student goes to a meadow on the first day of May, walks through the meadow waving a fly net, and counts the number of flies caught in the net. She repeats this ritual for several years, following up on the work of previous graduate students. The resulting measurements might look like the graph shown in Figure 1.1. The graduate student notes the variability in her measurements and wants to find out if they contain any important biological information.

Several different approaches could be taken to study the data. The student could do statistical analyses of the data to calculate the mean value or to detect long-term trends. She could also try to develop a detailed and realistic model of the ecosystem, taking into account such factors as weather, predators, and the fly populations in previous years. Or she could construct a simplified theoretical model for fly population density.

Sticking to what she knows, the student decides to model the population variability in terms of actual measurements. The number of flies in one summer

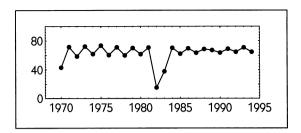


Figure 1.1 The number of flies caught during the annual fly survey.

depends on the number of eggs laid the previous year. The number of eggs laid depends on the number of flies alive during that summer. Thus, the number of flies in one summer depends on the number of flies in the previous summer. In mathematical terms, this is a relationship, or **function**,

$$N_{t+1} = f(N_t). (1.1)$$

This equation says simply that the number of flies in the t+1 summer is determined by (or is a function of) the number of flies in summer t, which is the previous summer. Equations of this form, which relate values at **discrete times** (e.g., each May), are called **finite-difference equations**. N_t is called the **state** of the system at time t. We are interested in how the state changes in time: the **dynamics** of the system.

Since the real-world ecosystem is complicated and since the measurements are imperfect, we do not expect a model like Eq. 1.1 to be able to duplicate exactly the actual fly population measurements. For example, birds eat flies, so the population of flies is influenced by the bird population, which itself depends on a complicated array of factors. The assumption behind Eq. 1.1 is that the number of flies in year t+1 depends solely on the number of flies in year t. While this is not strictly true, it may serve as a working approximation. The problem now is to figure out an appropriate form for this dependence that is consistent with the data and that encapsulates the important aspects of fly population biology.

1.2 THE LINEAR FINITE-DIFFERENCE EQUATION

Let us start by making a simple assumption about the propagation of flies: For each fly in generation t there will be R flies in generation t+1. The corresponding finite-difference equation is

$$N_{t+1} = RN_t. (1.2)$$

Equation 1.2 is called a **linear equation** because a graph of N_{t+1} versus N_t is a straight line, with a slope of R.

The **solution** to Eq. 1.2 is a sequence of states, N_1 , N_2 , N_3 , ..., that satisfy Eq. 1.2 for each value of t. That is, the solution satisfies $N_2 = RN_1$, and $N_3 = RN_2$, and $N_4 = RN_3$, and so on.

One way to find a solution to the equation is by the process of **iteration**. Given the number of flies N_0 in the initial generation, we can calculate the number of flies in the next generation, N_1 . Then, having calculated N_1 , we can apply Eq. 1.2 to find N_2 . We can repeat the process for as long as we care to. The state N_0 is called the **initial condition**.

For the linear equation, it is possible to carry out the iteration process using simple algebra. By iterating Eq. 1.2 we can find N_1 , N_2 , N_3 , and so forth.

$$N_1 = RN_0,$$

 $N_2 = RN_1 = R^2N_0,$
 $N_3 = RN_2 = R^2N_1 = R^3N_0,$
:

There is a simple pattern here: It suggests that the solution to the equation might be written as

$$N_t = R^t N_0. (1.3)$$

We can verify that Eq. 1.3 is indeed the solution to Eq. 1.2 by **substitution**. Since Eq. 1.3 is valid for all values of time t, it is also valid for time t + 1. By replacing the variable t in Eq. 1.3 with t + 1, we can see that $N_{t+1} = R^{t+1}N_0$. Expanding this, we get

$$N_{t+1} = R^{t+1}N_0 = RR^tN_0 = RN_t,$$

which shows that the solution implies the finite-difference equation in Eq. 1.2.

BEHAVIOR OF THE LINEAR EQUATION

Equation 1.3 can produce several different types of solution, depending on the value of the parameter R:

Decay When 0 < R < 1, the number of flies in each generation is smaller than that in the previous generation. Eventually, the number falls

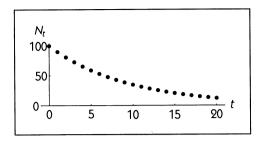


Figure 1.2 The solution to $N_{t+1} = 0.90 N_t$.

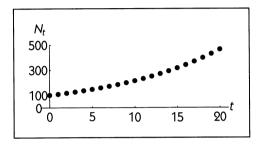


Figure 1.3 The solution to $N_{t+1} = 1.08N_t$.

to zero and the flies become extinct (see Figure 1.2). Since the solution is an exponential function of time (see Appendix A), this behavior is called exponential decay.

Growth When R > 1, the population of flies increases from generation to generation without bound. The solution is said to "explode" to ∞ (see Figure 1.3). Again the solution is an exponential function, and this behavior is thus called **exponential growth**.

Steady-state behavior When R is exactly 1, the population stays at the same level (see Figure 1.4). This is clearly an extraordinary solution, because it only happens for a single, exact value of R, whereas the other types of solutions occur for a range of R values.

The behaviors in the fly population study involve R>0. It doesn't make biological sense to consider cases where R<0 in Eq. 1.2. After all, how can flies

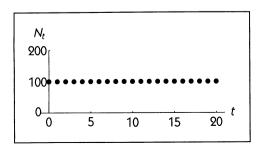


Figure 1.4 The solution to $N_{t+1} = 1.00N_t$.

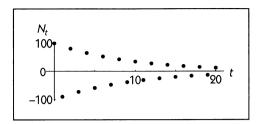


Figure 1.5 The solution to $N_{t+1} = -0.90N_t$.

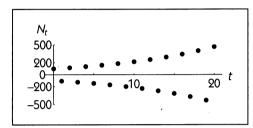


Figure 1.6 The solution to $N_{t+1} = -1.08N_t$.

lay negative eggs? Later, in Section 1.5, we shall see cases where it makes sense to talk about R < 0. Such cases produce different types of behavior:

Alternating decay When -1 < R < 0, the solution to Eq. 1.2 alternates between positive and negative values. At the same time, the amplitude of the solution decays to zero in the same exponential fashion seen for 0 < R < 1 (see Figure 1.5).

Alternating growth When R < -1, the solution still alternates between positive and negative values. However, the amplitude of the solution grows exponentially and explodes to $\pm \infty$ (see Figure 1.6).

Periodic cycle When R is exactly -1, the solution alternates between N_0 and $-N_0$ and neither grows nor decays in amplitude. A periodic cycle occurs when the solution repeats itself. In this case, the solution repeats every two time steps, ..., N_0 , $-N_0$, N_0 , $-N_0$, ..., and so the duration of the period is two time steps (see Figure 1.7).

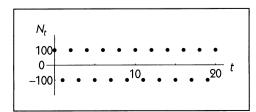


Figure 1.7 The solution to $N_{t+1} = -1.00N_t$.

1.3 METHODS OF ITERATION

We have seen how the solution to Eq. 1.2 could be found using algebra. Later we will encounter finite-difference equations in which an algebraic solution cannot be found. Here, we introduce two other methods for iterating finite-difference equations, the cobweb method and the method of numerical iteration.

THE COBWEB METHOD

The **cobweb method** is a graphical method for iterating a finite-difference equation like Eq. 1.1. No algebra is required in order to perform the iteration; one only needs to graph the function $f(N_t)$ on a piece of paper.

To illustrate the cobweb method, we will start with the linear system of Eq. 1.2. To perform the iteration using the cobweb method, we do the following:

1. Graph the function. In this case, $f(N_t) = RN_t$. In order to make a plot of the function RN_t , we need to pick a specific value for R. (Note that the algebraic method for finding solutions did not require this.) As an example, we will set R = 1.9 so that the finite-difference equation is $N_{t+1} = 1.9N_t$. The resulting function is shown by the dark line in Figure 1.8.

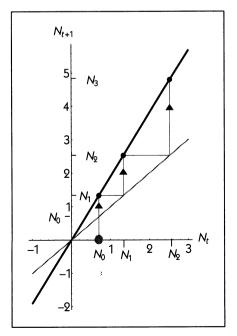


Figure 1.8 The cobweb method applied to the linear dynamical system $N_{t+1} = 1.9N_t$ with initial condition $N_0 = 0.7$.

- 2. Pick a numerical value for the initial condition. In this case, as an example, we will select $N_0 = 0.7$, shown as the gray dot on the x-axis in Figure 1.8. (In the algebraic method, we did not need to select a specific numerical value. Instead we were able to use the symbol N_0 to stand for any initial condition.)
- 3. Draw a vertical line from N_0 on the x-axis up to the function. The position where this vertical line hits the function (shown as a solid dot at the end of the arrow) tells us the value of N_1 .
- 4. Take this value of N_1 , plot it again on the x-axis, and again draw a vertical line to find the value of N_2 . There is a simple shortcut in order to avoid plotting N_1 on the x-axis: Draw a horizontal line to the $N_{t+1} = N_t$ line (shown in gray—it's the 45-degree line on the plot). The place where the horizontal line intersects the 45-degree line is the point from which to draw the next vertical line to find N_2 .
- 5. In order to find N_3 , N_4 , and so on, repeat the process of drawing vertical lines to the function and horizontal lines to the line of $N_{t+1} = N_t$.

As Figure 1.8 shows, the result of iterating $N_{t+1} = 1.9N_t$ is growth toward ∞ . This is consistent with the algebraic solution we found in Eq. 1.3 for R > 1.

NUMERICAL ITERATION

Since the cobweb method is a graphical method, it may not be very precise. In order to acheive more precision, we can use **numerical iteration**. This is a simple procedure, easily implemented on a computer or even a hand calculator. To illustrate, suppose we want to find a numerical solution to $N_{t+1} = RN_t$ with R = 0.9 and $N_0 = 100$.

$$N_0 = 100,$$

 $N_1 = f(N_0) = 0.9 \times 100 = 90,$
 $N_2 = f(N_1) = 0.9 \times 90 = 81,$
 $N_3 = f(N_2) = 0.9 \times 81 = 72.9,$
:

When applied to the linear finite-difference equation in Eq. 1.2, the cobweb method and the method of numerical iteration merely allow us to confirm the existence of the types of behavior we found algebraically. Since the cobweb and numerical iteration methods require that specific numerical values be specified for the parameter R and the initial condition N_0 , it might seem that they are inferior to

the algebraic method. However, when we consider nonlinear equations, algebraic methods are often impossible and numerical iteration and the cobweb method may provide the only means to find solutions.

1.4 NONLINEAR FINITE-DIFFERENCE EQUATIONS

The measurements of the fly population shown in Figure 1.1 don't suggest explosion or extinction, nor do they remain steady. This suggests that the model of Eq. 1.2 is not good. It does not take much of an ecologist to see where a mistake was made in formulating Eq. 1.2. Although it is all right to have rapid growth in populations for low densities, when the fly population is high, competition for food limits growth and starvation may cause a decrease in fertility. The larger population may also increase predation, as predators focus their attention on an abundant food supply.

A simple way to modify the model is to add a new term that lowers the number of surviving offspring when the population is large. In the linear equation, R was the number of offspring of each fly in generation t. In order to make the number of offspring per fly decrease as N_t gets larger, we can make the growth rate a function of N_t . For simplicity, we will chose the function $(R - bN_t)$. The positive number b governs how the growth rate decreases as the population gets bigger. R is the growth rate when the population is very, very small.

This assumption that the number of offspring per fly is $(R - bN_t)$ gives us a new finite-difference equation,

$$N_{t+1} = (R - bN_t)N_t = RN_t - bN_t^2.$$
 (1.5)

Equation 1.5 is a **nonlinear equation** since the rightmost side is *not* the equation of a straight line. Nonlinear equations arise commonly in mathematical models of biological systems, and the study of such equations is the focus of this book.

In Eq. 1.5 there are two parameters, R and b, that can vary independently. However, a simple change of variables shows that there is only one parameter that affects the dynamics. We define a new variable $x_t = \frac{bN_t}{R}$, which is just a way of scaling the number of flies by the number $\frac{b}{R}$. Substituting x_t and x_{t+1} in Eq. 1.5, we find the equation

$$x_{t+1} = Rx_t(1 - x_t). (1.6)$$

Although Eq. 1.6 (called the **quadratic map**) may not seem much more complicated than Eq. 1.2, the solution cannot generally be found using algebra. Numerical iteration and the cobweb method, however, can be used to find solutions. In order to apply the cobweb method to Eq. 1.6, we first must draw a

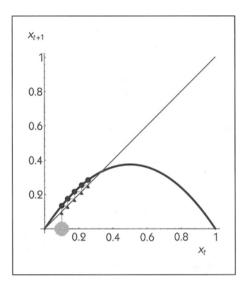


Figure 1.9 Cobweb iteration of $x_{t+1} = 1.5(1 - x_t)x_t$.

graph of the function. (Anyone who has not practiced calculus recently may find sketching the graph of an equation intimidating. If you are in this category, go over the material in Appendix A and pay particular attention to the section on quadratic functions since this is what we have here.) In this case, the graph is a parabola, with intercepts at $x_t = 0$ and $x_t = 1$, as Figure 1.9 shows.

Next, we need to pick specific values for the parameter R in Eq. 1.6. Since we don't yet know what the behavior of this equation will be, we will have to study a range of parameter values. Doing so reveals a number of different behaviors:

Steady state The nonlinear equation can have a solution that approaches a certain state and remains fixed there. This is shown in Figure 1.10 for R = 1.5, where the solution creeps up on the steady state from one side; this is called a **monotonic** approach.

As shown for R = 2.9 in Figure 1.11, the approach to a steady state can also **alternate** from one side to the other.

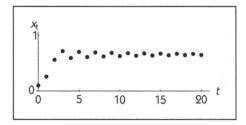


Figure 1.10 The solution to $x_{t+1} = 1.5(1 - x_t)x_t$.

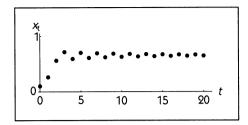


Figure 1.11 The solution to $x_{t+1} = 2.9(1 - x_t)x_t$.

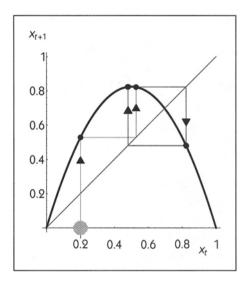


Figure 1.12 Cobweb iteration of $x_{t+1} = 3.3(1 - x_t)x_t$.

Periodic cycles The solution to the nonlinear equation can have cycles. This is shown for R=3.3 in Figures 1.12 and 1.13, where the cycle has duration 2. When carrying out the cobweb iteration, a cycle of period two looks like a square that is repeatedly traced out (see Figure 1.12). The cycle in this case follows the sequence $x_t=0.48$, $x_{t+1}=0.82$, $x_{t+2}=0.48$, and so on.

For R = b = 3.52 (see Figure 1.14), the cycle has duration 4 and follows the sequence $x_t = 0.88$, $x_{t+1} = 0.37$, $x_{t+2} = 0.82$, $x_{t+3} = 0.51$, $x_{t+4} = 0.88$, and so forth.

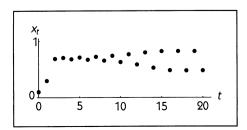


Figure 1.13 The solution to $x_{t+1} = 3.3(1 - x_t)x_t$.

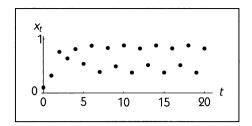


Figure 1.14 The solution to $x_{t+1} = 3.52(1 - x_t)x_t$.

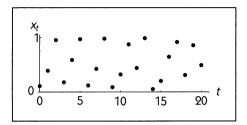


Figure 1.15 The solution to $x_{t+1} = 4(1 - x_t)x_t$.

Aperiodic behavior The solution to the nonlinear equation may oscillate, but not in a periodic manner. Setting R=4, we find the behavior shown in Figures 1.15 and 1.16—a kind of irregular oscillation that is neither exponential growth or decay, nor a steady state. The cobweb iteration shows how the irregular iteration arises from the shape of the function (see Figure 1.15). This behavior is called **chaos**, and we will investigate it in greater detail in later sections in the book.

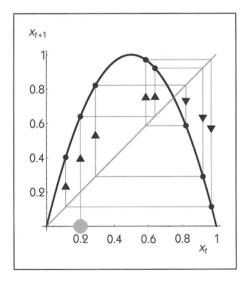


Figure 1.16 Cobweb iteration of $x_{t+1} = 4(1 - x_t)x_t$.

1.5 STEADY STATES AND THEIR STABILITY

A simple, but important, type of dynamical behavior is when the system stays at a **steady state**. A steady state is a state of the system that remains fixed, that is, where

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

Steady states in finite-difference equations are associated with the mathematical concept of a **fixed point**. A fixed point of a function $f(x_t)$ is a value x_t^* that satisfies $x_t^* = f(x_t^*)$. Later on, we shall see how fixed points can also be associated with periodic cycles.

There are three important questions to ask about fixed points in a finite-difference equation:

- Are there any fixed points—in other words, are there any values of x_t^* that satisfy $x_t^* = f(x_t^*)$?
- If the initial condition happens to be near a fixed point, will the subsequent iterates approach the fixed point? If subsequent iterates approach the fixed point, we say the fixed point is locally stable. (Mathematicians call this "locally asymptotic stability.")
- Will the system approach a given fixed point regardless of the initial condition? If the fixed point is approached for all initial conditions, we say that the fixed point is **globally stable**.

FINDING FIXED POINTS

From the graph of $x_{t+1} = f(x_t)$ it is easy to locate fixed points: They are simply those points where the graph intersects the line $x_{t+1} = x_t$. Or, we can use algebra to solve the equation $x_t = f(x_t)$.

For the linear finite-difference equation, x_t^* is a fixed point if it satisfies the equation $x_t^* = Rx_t^*$. One solution to this equation is always $x_t^* = 0$. This means that the origin is a fixed point for a linear system. This has an obvious biological interpretation: If there are no flies in one year, there can't be any the next year (unless, of course, they migrate from distant parts or evolve again, both of which are beyond the scope of our simple model).

The solution $x_t = 0$ is the only fixed point, unless R = 1. If R is exactly 1, then all points are fixed points. Clearly, this is an exceptional case, because any change in R, no matter how small, will eliminate all of the fixed points except the one at the origin.

Nonlinear finite-difference equations can have more than one fixed point. Figures 1.17 and 1.18 show the location of the fixed points for Eq. 1.6 for R=2.9

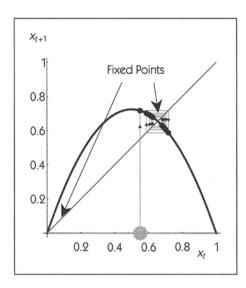


Figure 1.17 $x_{t+1} = 2.9(1 - x_t)x_t$

and R=3.52, respectively. For the quadratic map of Eq. 1.6, the fixed points can also be found using algebra from the **roots** of the quadratic equation

$$x_t = Rx_t(1 - x_t)$$
 or, $x_t(R - Rx_t - 1) = 0$.

The roots of this equation are

$$x_t = 0$$
 and $x_t = \frac{R-1}{R}$.

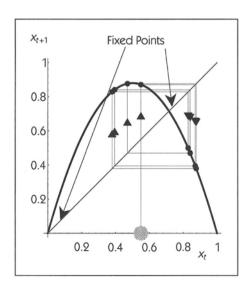


Figure 1.18 $x_{t+1} = 3.52(1 - x_t)x_t$

Again, in our model the biological meaning of the root $x_t = 0$ is that flies don't appear from nowhere. The biological interpretation of the fixed point at $x_t = \frac{R-1}{R}$ is that this is a self-sustaining level of the population, with neither a decrease nor an increase.

Clearly, it is impossible for the fly population to be at both these fixed points at the same time. So now we have to address the question of which of these fixed points will be reached by iterating from the initial condition, if indeed either of them will be.

LOCAL STABILITY OF FIXED POINTS

Figures 1.17 and 1.18 both have two fixed points, but in Figure 1.17 the iterates approach the nonzero fixed point while in Figure 1.18 the iterates do not. The difference between these cases is the *local stability* of the fixed points.

We say that a fixed point is **locally stable** if, given an initial condition sufficiently close to the fixed point, subsequent iterates eventually approach the fixed point.

How do we tell if a fixed point is locally stable? For a linear finite-difference equation, $x_{t+1} = Rx_t$, we already know the answer: The stability of the fixed point at the origin depends on the slope R of the line. If |R| < 1, future iterates are successively closer to the fixed point at the origin—this is exponential decay to zero. If |R| > 1, future iterates are successively farther away from the fixed point at the origin.

How does one determine the stability of a fixed point in a nonlinear finitedifference equation? In calculus classes, one discusses the notion that over limited regions a curve can be approximated by a straight line of the appropriate slope. In the neighborhood of the intersection of the straight line $x_{t+1} = x_t$ with the curve $x_{t+1} = f(x_t)$, it is therefore possible to approximate the curve by a straight line.

Figures 1.19 through 1.22 illustrate four separate cases that show the region of intersection. Let x^* be a fixed point of $f(\cdot)$, that is a state for which $x^* = f(x^*)$. The slope of the curve at the fixed point, $\frac{df}{dx_t}\Big|_{x^*}$, establishes the stability of the fixed point. We will designate this slope by m. Figures 1.19 through 1.22 plot y_{t+1} versus y_t , where $y_t = x_t - x^*$. This means that in the figures the fixed point appears at the origin, whereas in the original variable, x_t , the fixed point is at x^* . Observe that

- If |m| < 1, the fixed point is *stable* so that nearby points approach the fixed point under iteration.
- If |m| > 1, the fixed point is *unstable* and points leave the neighborhood of the fixed point.

Also, note that

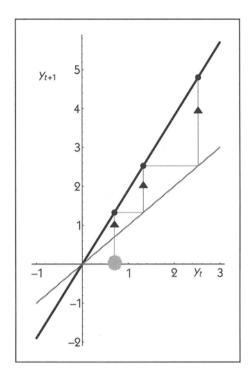


Figure 1.19 The dynamics of $y_{t+1} = my_t$. m > 1 produces monotonic growth as shown here with m = 1.9.

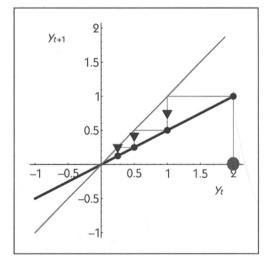


Figure 1.20 The dynamics of $y_{t+1} = my_t$. 0 < m < 1 produces monotonic decay to $y_t = 0$. Here, m = 0.5.

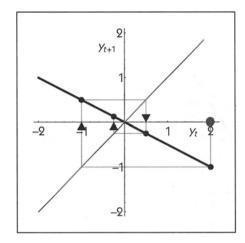


Figure 1.21 The dynamics of $y_{t+1} = my_t$. -1 < m < 0 produces alternating decay as shown here with m = -0.5.

- If m > 0, the points approach or leave the fixed point in a monotonic fashion.
- If m < 0, the points approach or leave the fixed point in an oscillatory fashion.

From the above considerations, a general method can be given for determining the stability of a fixed point in finite-difference equations with one variable. The steps are as follows:

1. Solve for the fixed points. This involves solving the equation

$$x_t = f(x_t).$$

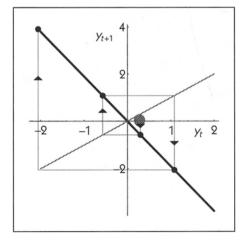


Figure 1.22 The dynamics of $y_{t+1} = my_t$. m < -1 produces alternating growth. Here, m = -1.9.

Linear equations always have only one fixed point—the one at $x_t = 0$. Nonlinear equations may have more than one fixed point. Steps 2 and 3 can be applied to each of the fixed points, one at a time. Call the fixed point we are studying x^* . Like all fixed points, this satisfies $x^* = f(x^*)$.

2. Calculate the slope m of $f(x_t)$, evaluating x_t at the fixed point x^* . That is, compute

$$m = \left. \frac{df}{dx_t} \right|_{x_t = x^*}.$$

3. The slope m at the fixed point determines its stability.

1 < m Unstable, exponential growth.

0 < m < 1 Stable, monotonic approach to $y_t = 0$ (i.e., approach to $x_t = x^*$).

-1 < m < 0 Stable, oscillatory approach to $y_t = 0$ (i.e., approach to $x_t = x^*$).

m < -1 Unstable, oscillatory exponential growth.

TRANSIENT AND ASYMPTOTIC BEHAVIOR

If a fixed point is locally stable, then once the state is very near to the fixed point, it will stay near throughout the future. Before the state reaches the fixed point, it may show different behavior. For example, in Figure 1.10, the state is far enough away from the fixed point for the first five or six iterations that we can see it change from iteration to iteration. After that, the state appears to have reached the fixed point. In Figure 1.11, the movement toward the fixed point is visible for approximately twenty iterations. The term **asymptotic dynamics** refers to the dynamics as time goes to infinity. Behavior before the asymptotic dynamics is called **transient**.

STABILITY AND NUMERICAL ITERATION

Suppose that we want to use numerical iteration to find fixed points. One strategy would be to pick a large number of initial conditions and iterate numerically each of these initial conditions. If the iterates converge to a fixed value; then we have identified a fixed point at that value. (Figure 1.10 shows an example of this.)

If a fixed point is locally stable, then this strategy may well succeed, since the fixed point will eventually be approached if any of the initial conditions is close to the fixed point. Once the state is close to the fixed point, it will remain near the fixed point. If a fixed point is unstable, however, then we will find it only if one of the iterates happens to land on the fixed point *exactly*, and this is extremely unlikely. In general, we can use numerical iteration only to find stable fixed points. If we want to find unstable fixed points, another approach is needed, namely solving the equation $x_t = f(x_t)$.

☐ EXAMPLE 1.1

Cells reproduce by division; the process by which the cell nucleus divides is called **mitosis**. One way to regulate the rate of reproduction of cells is by regulating mitosis. There is (controversial!) biochemical evidence that there are compounds, called **chalones**, that are tissue-specific inhibitors of mitosis (see Bullough and Laurence, 1968).

For simplicity, assume that the generations of cells are distinct and that the number of cells in each generation is given by N_t . Following the same logic as in Eq. 1.2, assume that for each cell in generation t, there are R cells in generation t+1. (If every cell divided in half every time step, then R would equal 2.) The finite-difference equation describing this situation is the linear equation $N_{t+1} = RN_t$, which leads either to exponential growth or to decay to zero.

A possible role of chalones is to make *R* depend on the number of cells. Assume that the amount of chalone produced is proportional to the number of cells. The more chalone there is, the greater the inhibitory effect on mitosis.

The biochemical action of chalones is to bind to a protein involved in mitosis, rendering the protein inactive. Binding of molecules to proteins is often modeled by a Hill function (see Section A.5), which suggests that an appropriate equation for the hypothetical chalone control mechanism is

$$N_{t+1} = f(N_t) = \frac{RN_t}{1 + \left(\frac{N_t}{\theta}\right)^n},$$

where θ and n are parameters. We will assume that $n \ge 2$. Figure 1.23 shows this finite difference equation when R = 2, $\theta = 5$, and n = 3.

Find the fixed points of this system and determine their stability.

1. To determine the fixed points we solve the equation

$$N^{\star} = \frac{RN^{\star}}{1 + \left(\frac{N^{\star}}{\theta}\right)^{n}}.$$

There are two real solutions: $N^* = 0$ and $N^* = \theta(R-1)^{\frac{1}{n}}$. These are the only fixed points. There are also imaginary solutions that can be ignored in this case because we are only concerned with biologically

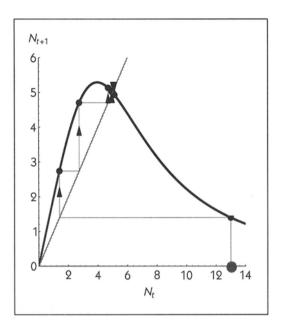


Figure 1.23 A cobweb analysis of chalone production for the parameters R = 2, $\theta = 5$, n = 3.

meaningful solutions, and the number of cells in each generation must be a real number.

To determine the stability of the fixed points it is necessary to compute the slope at the fixed points. Differentiating the right-hand side of the finite-difference equation, we find

$$\frac{df}{dN_t} = \frac{R + R\left(\frac{N_t}{\theta}\right)^n (1-n)}{\left(1 + \left(\frac{N_t}{\theta}\right)^n\right)^2}.$$

3. From the above equation we find that the slope at the fixed point $x_t = 0$ is just R. If R > 1, the fixed point at the origin is always unstable. (To be a plausible model of the regulation of cell reproduction, we must have R > 1. Otherwise, the population would always fall to zero even in the complete absence of the mitosis-inhibiting chalones.)

The slope at the fixed point $N^* = \theta(R-1)^{\frac{1}{n}}$ is

$$\left. \frac{df}{dN_t} \right|_{N^*} = 1 + n \left(\frac{1}{R} - 1 \right).$$

For R=2, the fixed point will be unstable when n>4 and stable otherwise.

GLOBAL STABILITY OF FIXED POINTS

In this section we've studied local stability. Local stability tells us whether the fixed point is approached if the initial condition is sufficiently close to the fixed point. The local stability can be assessed simply by looking at the slope of the function at the fixed point.

A slightly different—and often much more difficult—question is whether a locally stable fixed point is **globally stable**.

For linear finite-difference equations, the answer is straightforward. A locally stable fixed point is also globally stable: Regardless of the initial condition, the iterates will eventually reach the locally stable point (i.e., the origin) from any initial condition.

For nonlinear finite-difference equations, there can be more than one fixed point. When multiple fixed points are present, none of the fixed points can be globally stable.

The set of initial conditions that eventually leads to a fixed point is called the **basin of attraction** of the fixed point. Often, the basin of attraction for fixed points in nonlinear systems can have a very complicated geometry (see Chapter 3). If multiple fixed are locally stable we say there is **multistability**.

1.6 CYCLES AND THEIR STABILITY

In Figures 1.7, 1.13, and 1.14 we can see that periodic cycles are one form of behavior for finite-difference equations. In everyday language, a **cycle** is a pattern that repeats itself, and the **period** of the cycle is the length of time between repetitions. In finite-difference equations like Eq. 1.1, a cycle arises when

$$x_{t+n} = x_t$$
, but $x_{t+j} \neq x_t$ for $j = 1, 2, ..., n-1$. (1.7)

There is a useful correspondence between fixed points and periodic cycles which helps in understanding how to find cycles and assess their stability. A simple case is a cycle of period 2. Consider the finite-difference equation

$$x_{t+1} = f(x_t) = 3.3(1 - x_t)x_t.$$
 (1.8)

As shown in Figure 1.13, the solution is a cycle of period 2. The definition of a cycle of period 2 is that

$$x_{t+2} = x_t$$
 while $x_{t+1} \neq x_t$. (1.9)

By substitution into $x_{t+1} = f(x_t)$, we can write the value of x_{t+2} as

$$x_{t+2} = f(x_{t+1}) = f(f(x_t)).$$
 (1.10)

If there is a cycle of period 2, then $x_t = f(f(x_t))$. For the quadratic map (Eq. 1.6), we can find $f(f(x_t))$ with a bit of algebra:

$$f(f(x_t)) = f(x_{t+1}) = Rx_{t+1} - Rx_{t+1}^2$$

$$= R(Rx_t - Rx_t^2) - R(Rx_t - Rx_t^2)^2$$

$$= R^2x_t - (R^2 + R^3)x_t^2 + 2R^3x_t^2 - R^3x_t^4.$$
(1.11)

The equation may seem a little formidable, but the M-shaped graph, shown in the lower graph in Figure 1.24, is quite simple.

We can see from Eq. 1.10 that there is an analogy between fixed points and cycles: If a system $x_{t+1} = f(x_t)$ has a cycle of period 2, then the function $f(f(x_t))$ has at least two fixed points. Thus, we can find the cycles of period 2 by solving the equation $x_t = f(f(x_t))$. This can be done graphically, algebraically, or numerically.

One trivial type of solution to $x_t = f(f(x_t))$ is a solution to $x_t = f(x_t)$. These solutions correspond to the fixed points of $f(x_t)$ and hence are not cycles of period 2—they are "cycles of period 1," that is, steady states. In the graph of Eq. 1.11 shown in Figure 1.24, we can see four fixed points of $f(f(x_t))$: at $x_t = 0$, at $x_t = 0.479$, at $x_t = 0.697$, and at $x_t = 0.823$. Two of these values are also fixed points of $f(x_t)$ and therefore correspond to cycles of period 1.

Longer cycles can be found in the same way. A cycle of period n is found by solving the equation

$$x_t = \underbrace{f(f(\cdots f(x_t)))}_{n \text{ times}},$$

avoiding solutions that correspond to periods less than n. In practice, this problem can be very hard to solve algebraically.

STABILITY OF CYCLES

Just as a fixed point can be locally stable or unstable, a cycle can be stable or unstable. We say that a cycle is **locally stable** if, given that the initial condition is

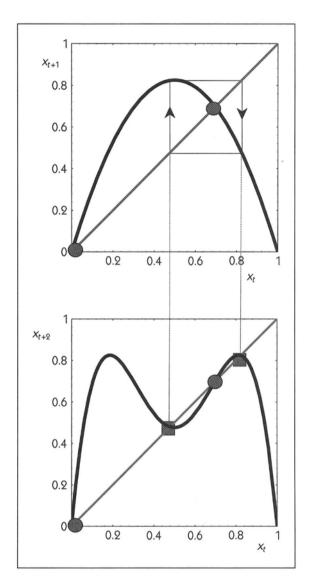


Figure 1.24 A cycle of period 2 in the system $x_{t+1} = R(1 - x_t)x_t = f(x_t)$ for R = 3.3. The graph of x_{t+1} versus x_t has two fixed points, marked as gray dots, but neither of them is stable. When plotted as x_{t+2} versus x_t , the cycle of period two looks like 2 fixed points in the finite-difference equation $x_{t+2} = f(f(x_t))$. Altogether, this system has four fixed points—the two corresponding to the cycle of period 2 (marked as small gray squares) and the two fixed points from the system $x_{t+1} = f(x_t)$.

close to a point on the cycle, subsequent iterates approach the cycle. (Again, this is what mathematicans call "local asymptotic stability").

We can now consider the computation of the stability of the fixed point of the finite-difference equation $x_{t+2} = f(f(x_t))$. We will use x^* to denote a solution to the equation $x_t = f(f(x_t))$ that is not also a fixed point of $x_t = f(x_t)$. Referring to Section 1.5, we can see that the stability of the fixed point of $x_{t+2} = f(f(x_t))$ depends on the value of

$$\frac{df(f(x_t))}{dx_t}\bigg|_{x^*}.$$

Using the chain rule for derivatives, we have

$$\left. \frac{df(f(x_t))}{dx_t} \right|_{x^*} = \left. \frac{df}{dx_t} \right|_{f(x^*)} \left. \frac{df}{dx_t} \right|_{x^*}.$$

Thus, the stability of a fixed point of period 2 depends on the slope of the function $f(x_t)$ at both of the two points x^* and $f(x^*)$.

A method for finding cycles by numerical iteration is quite easy in principle: Start at some initial condition and at each iteration, see if the value has been produced previously. Once the same value is encountered twice, the intervening values will cycle over and over again.

When cycles are found by numerical iteration, it is important to realize that unstable cycles will tend not to be found. This is exactly analogous to the situation when using numerical iteration to look for fixed points. When a cycle is stable, any initial condition in the cycle's basin of attraction will eventually lead to the cycle. For unstable cycles, the cycle will not be approached unless some iterate of the initial condition lands exactly on a point on the cycle.

EXAMPLE 1.2

Consider the finite-difference equation

$$x_{t+1} = \frac{1 - x_t}{3x_t + 1}.$$

- a. Sketch x_{t+1} as a function of x_t .
- b. Determine the fixed point(s), if any, and test algebraically for stability.
- c. Algebraically determine x_{t+2} as a function of x_t and determine if there are any cycles of period 2. If so, are they stable? Based on the analysis above, determine the dynamics starting from any initial condition.

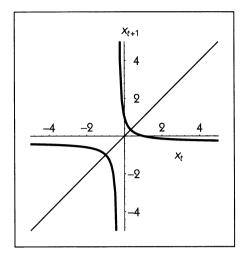


Figure 1.25 The graph of $x_{t+1} = \frac{1-x_t}{3x_t+1}$.

Solution:

- a. This is the graph of a hyperbola, see Figure 1.25. There are no local maxima or minima, but there are asymptotes at $x_t = -\frac{1}{3}$ and at $x_{t+1} = -\frac{1}{3}$.
- b. The fixed points are determined by setting $x_{t+1} = x_t$ to give the quadratic equation

$$3x_t^2 + 2x_t - 1 = 0.$$

This equation can be factored to yield two solutions, $x_t = \frac{1}{3}$ and $x_t = -1$. To determine stability, we compute

$$\frac{dx_{t+1}}{dx_t} = \frac{-4}{(3x_t+1)^2}.$$

When this is evaluated at the fixed points, the slope is -1. Note that a slope of -1 does not fall into the classification scheme presented in Section 1.5—if the slope were slightly steeper than -1, the fixed point would be unstable; if the slope were slightly less steep than -1, the fixed point would be stable. We cannot determine the stability of the steady states from this computation: The steady state is neither stable nor unstable.

c. Iterating directly we find that

$$x_{t+2} = \frac{1 - x_{t+1}}{3x_{t+1} + 1}$$

$$= \frac{1 - \left(\frac{1 - x_t}{3x_{t+1}}\right)}{3\left(\frac{1 - x_t}{3x_t + 1}\right) + 1}$$
$$= x_t.$$

Amazingly, all initial conditions are on a cycle of period 2. The cycles are neither locally stable nor unstable, since initial conditions neither approach nor diverge from any given cycle.

The preceding discussion shows that if there are stable cycles, then an examination of the graph of x_{t+n} as a function of x_t will show certain definite features. If there is a stable cycle of period n, there must be at least n fixed points associated with the stable cycle, where the slope at each of the fixed points is equal and the absolute value of the slope at each of the fixed points is less than 1.

Now let's consider a specific situation, the quadratic map

$$x_{t+1} = f(x_t) = 4(1 - x_t)x_t.$$
 (1.12)

This now-familiar parabola is plotted again in Figure 1.26. We can see that there are two fixed points, both of which are unstable because the slope of the function at these fixed points is steeper than 1.

To look for cycles of period 2, we can plot x_{t+2} versus x_t as shown in Figure 1.27. The four places where this graph intersects the line $x_{t+2} = x_t$ (i.e., the 45-degree line) are the possible points on the cycle of period 2—recall that two of the intersection points correspond to cycles of period 1. Since the slope of

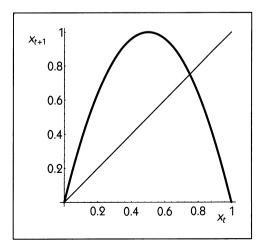


Figure 1.26 x_{t+1} versus x_t for Eq. 1.12.

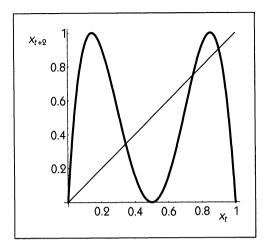


Figure 1.27 x_{t+2} versus x_t for Eq. 1.12.

the function at all these points is steeper than 1, we can conclude that there are no stable cycles of period 2 in Eq. 1.12.

We can continue looking for longer cycles. Figure 1.28 shows the graph of $x_{t+3} = f(f(f(x_t)))$. This graph intersects the line $x_{t+3} = x_t$ in eight places. (Of these, two correspond to cycles of period 1.) At all of these places the slope of the function is steeper than 1, so all of the possible cycles of period 3 are unstable. Similarly, Figure 1.29 shows that the cycles of period four are also unstable.

In fact, there are no stable cycles of *any* length, no matter how long, in Eq. 1.12, although we will not prove this here. What are the dynamics in Eq. 1.12? The next section will explore the answer to this question.

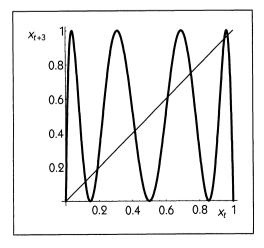


Figure 1.28 x_{t+3} versus x_t for Eq. 1.12.

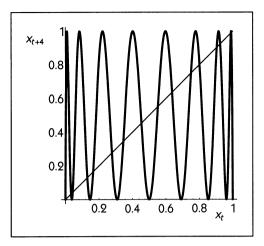


Figure 1.29 x_{t+4} versus x_t for Eq. 1.12.

1.7 CHAOS

DEFINITION OF CHAOS

Let's do a numerical experiment to investigate the properties of Eq. 1.12. Pick an initial condition, say $x_0 = 0.523423$, and iterate. Now start over, but change the initial condition by just a little bit, to $x_0 = 0.523424$. The results are shown in Figure 1.29.

There are several important features of the dynamics illustrated in Figure 1.29. In fact, based on the figure we have strong evidence that this equation displays **chaos**—which is defined to be aperiodic bounded dynamics in a deterministic system with sensitive dependence on initial conditions.

Each of these terms has a specific meaning. We define the terms and explain why each of these properties appears to be satisfied by the dynamics in Figure 1.29.

Aperiodic means that the same state is never repeated twice. Examination of the numerical values used in this graph shows this to be the case. However, in practice, by either graphically iterating or using a computer with finite precision, we eventually may return to the same value. Although a computer simulation or graphical iteration always leaves some doubt about whether behavior is periodic, the presence of very long cycles or of aperiodic dynamics in computer simulations is partial evidence for chaos.

Bounded means that on successive iterations the state stays in a finite range and does not approach $\pm \infty$. In the present case, as long as the initial condition x_0 is in the range $0 \le x_0 \le 1$, then all future iterates will also fall in this range. This is because for $0 \le x_t \le 1$, the minimum value of $4(1 - x_t)x_t$ is 0 and the maximum value is 1. Recall that in the linear

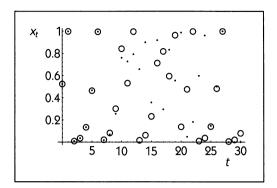


Figure 1.30 Two solutions to $x_{t+1} = (4 - 4x_t)x_t$. The solution marked with a dot has the initial condition $x_0 = 0.523423$, while the solution marked with a circle has $x_0 = 0.523424$. The solutions are almost exactly the same for the first seven iterations, and then move apart.

finite-difference equation, Eq. 1.2, we have already seen a system where the dynamics are not bounded and there is explosive growth.

Deterministic means that there is a definite rule with no random terms governing the dynamics. The finite-difference equation 1.12 is an example of a deterministic system. For one-dimensional, finite-difference equations, "deterministic" means that for each possible value of x_t , there is only a single possible value for $x_{t+1} = f(x_t)$. In principal, for a deterministic system x_0 can be used to calculate all future values of x_t .

Sensitive dependence on initial conditions means that two points that are initially close will drift apart as time proceeds. This is an essential aspect of chaos. It means that we may be able to predict what happens for short times, but that over long times prediction will be impossible since we can never be certain of the exact value of the initial condition in any realistic system. In contrast, for finite-difference equations with stable fixed points or cycles, two slightly different initial conditions may often lead to the same fixed point or cycle. (But this is not always the case; see Chapter 3.)

Although the possibility for chaos in dynamical systems was already known to the French mathematician Henri Poincaré in the nineteenth century, the concept did not gain broad recognition amongst scientists until T.-Y. Li and J. Yorke introduced the term "chaos" in 1975 in their analysis of the quadratic map, Eq. 1.12. The search for chaotic dynamics in diverse physical and biological fields, and the mathematical analysis of chaotic dynamics in nonlinear equations, have sparked research in recent years.

THE PERIOD-DOUBLING ROUTE TO CHAOS

We have seen that the simple finite-difference equation

$$x_{t+1} = R(1-x_t)x_t$$

can display various qualitative types of behavior for different values of R: steady states, periodic cycles of different lengths, and chaos. The change from one form of qualitative behavior to another as a parameter is changed is called a **bifurcation**. An important goal in studying nonlinear finite-difference equations is to understand the bifurcations that can occur as a parameter is changed.

There are many different types of bifurcations. For example, in the linear finite-difference equation $x_{t+1} = Rx_t$, there is decay to zero when -1 < R < 1. For R > 1, however, the behavior changes to exponential growth. The bifurcation point, or the point at which a change in R causes the behavior to change, is at R = 1. Nonlinear systems can show many other types of bifurcations. For example, changing a parameter can cause a stable fixed point to become unstable and can lead to a change of behavior from a steady state to a periodic cycle.

The finite-difference equation in Eq. 1.6 and many other nonlinear systems displays a sequence of bifurcations in which the period of the oscillation doubles as a parameter is changed slightly. This type of behavior is called a **period-doubling bifurcation**.

We can derive an algebraic criterion for a period-doubling bifurcation. In a nonlinear finite-difference equation there are n fixed points of the function

$$x_t = \underbrace{f(f(\cdots f(x_t)))}_{n \text{ times}}$$

that are associated with a period-n cycle. The slope at each of these fixed points is the same. As a parameter is changed in the system, the slope at each of these fixed points also changes. When the slope for some parameter value is equal to -1, it is typical to find that at that parameter value the periodic cycle of period n loses stability and a periodic cycle of period 2n gains stability. In other words, there is a period-doubling bifurcation. Unfortunately, application of this algebraic criterion can be very difficult in nonlinear equations since iteration of nonlinear equations such as Eq. 1.6 can lead to complex algebraic expressions that are not handled easily. Consequently, people have turned to numerical studies.

Using a programmable pocket calculator in a numerical investigation of period-doubling bifurcations in Eq. 1.6 led Mitchell J. Feigenbaum to one of the major discoveries in nonlinear dynamics. Feigenbaum observed that as the parameter R varies in Eq. 1.6, there are successive doublings of the period of

oscillation. Numerical estimation of the values of R at the successive bifurcations lead to the following approximate values:

- For 3.0000 < R < 3.4495, there is a stable cycle of period 2.
- For 3.4495 < R < 3.5441, there is a stable cycle of period 4.
- For 3.5441 < R < 3.5644, there is a stable cycle of period 8.
- For 3.5644 < R < 3.5688, there is a stable cycle of period 16.
- As R is increased closer to 3.570, there are stable cycles of period 2^n , where the period of the cycles increases as 3.570 is approached.
- For values of R > 3.570, there are narrow ranges of periodic solutions as well as aperiodic behavior.

These results illustrate a sequence of period-doubling bifurcations at R = 3.0000, R = 3.4495, R = 3.5441, R = 3.5644, with additional period-doubling bifurcations as R increases. This transition from the stable periodic cycles to the chaotic behavior at R = 3.570 is called the **period-doubling route to chaos**.

Notice that the range of values for each successive periodic cycle gets narrower and narrower. Call Δ_n the range of R values that give a period-n cycle. For example, since 3.4495 < R < 3.5441 gives a period-4 cycle, we have $\Delta_4 = 3.5441 - 3.4495 = 0.0946$. Similarly, $\Delta_8 = 3.5644 - 3.5441 = 0.0203$.

The ratio $\frac{\Delta_4}{\Delta_8}$ is $\frac{0.0946}{0.0203}=4.6601$. By considering successive period doublings, Feigenbaum discovered that

$$\lim_{n\to\infty}\frac{\Delta_n}{\Delta_{2n}}=4.6692\ldots.$$

The constant, 4.6692... is now called **Feigenbaum's number**. This number appears not only in the simple theoretical model that we have discussed here but also in other theoretical models and in experimental systems in which there is a period-doubling route to chaos.

One way to represent graphically complex bifurcations in finite-difference equations is to plot the asymptotic values of the variable as a function of a parameter that varies. This type of plot is called a **bifurcation diagram**. Figure 1.31 shows a bifurcation diagram of Eq. 1.6. This figure is constructed by scanning many values of R in the range $3 \le R \le 4$. For each value of R, 1.6 is iterated many times. After allowing enough time for transients to decay, several of the values x_t , x_{t+1} , x_{t+2} , and so on are plotted. For example, when R = 3.2, Eq. 1.6 approaches a cycle of period 2, so there are two values plotted. The period-doubling bifurcations appear as "forks" in this diagram.

A summary of the dynamic behaviors discussed in Eq. 1.6 is contained in Figure 1.32. As the parameter *R* changes, different behaviors are observed. If you

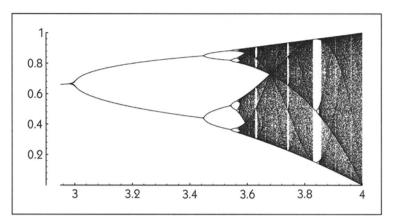


Figure 1.31 A bifurcation diagram of Eq. 1.6. The asymptotic values of x_t are plotted as a function of R using the method described in the text.

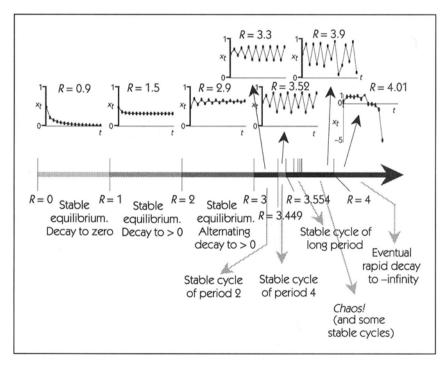


Figure 1.32 The various types of qualitative dynamics seen in $x_{t+1} = Rx_t(1 - x_t)$ for different values of the parameter R.

understand the origin of each of these behaviors, you have mastered the material in this chapter!

EXAMPLE 1.3

The following equation, called the **tent map**, is often used as a very simple equation that gives chaotic dynamics.

Consider the finite-difference equation

$$x_{t+1} = f(x_t), \qquad 0 \le x_t \le 1,$$

where $f(x_t)$ is given as

$$f(x_t) = \begin{cases} 2x_t & \text{for } 0 \le x_t \le \frac{1}{2}, \\ 2 - 2x_t & \text{for } \frac{1}{2} \le x_t \le 1. \end{cases}$$
 (1.13)

Draw a graph of x_{t+1} as a function of x_t . Graphically iterate this equation and determine if the dynamics are chaotic.

Solution: The graph of this equation looks like an old-fashioned pup tent (see Figure 1.33). Starting at two points chosen randomly near to each other we find that both points lead to aperiodic dynamics, where the distance between subsequent iterates of the points initially increases on subsequent iterations. Therefore, this system gives chaotic dynamics. This problem is tricky, however, since many people will start at a point such as 0.1, find that the subsequent iterates are 0.2, 0.4, 0.8, 0.4, 0.8, ..., and then conclude that since they have found a cycle

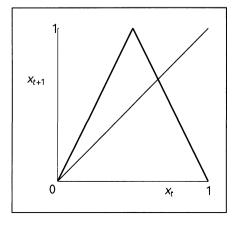


Figure 1.33
The graph of Eq. 1.13.

the dynamics in this equation are not chaotic. However, although there are many other such cycles in this equation, "almost all" values between 0 and 1 give rise to aperiodic chaotic dynamics. This is because the cycles are all unstable, as was defined in Section 1.6. Most equations that display chaotic dynamics also exhibit unstable cycles for some initial conditions, and thus this example is typical of what is found in other circumstances.

If you use a computer to iterate this map, watch out! You will probably find that the map rapidly converges to the fixed point at $x_t = 0$, even though this is an unstable fixed point. The reason involves the fact that numbers are represented in computers in base 2—all of the numbers that a computer can store in finite precision will be attracted to $x_t = 0$. To eliminate this problem, you can approximate the 2 in Eq. 1.13 by 1.99999999.

1.8 QUASIPERIODICITY

In chaotic dynamics there is an aperiodic behavior in which two points that are initially close will diverge over time. There is another type of aperiodic behavior in which two points that are initially close will remain close over time. This type of behavior is called **quasiperiodicity**. In quasiperiodic dynamics there are no fixed points, cycles, or chaos.

To see how this type of dynamics can arise, consider the equation

$$x_{t+1} = f(x_t) = x_t + b \pmod{1},$$
 (1.14)

where (mod 1) is the "modulus" operator that takes the fractional part of a number (e.g., 3.67 (mod 1) = 0.67). To iterate this equation, we calculate $x_t + b$ and then take the fractional remainder. For example, if $x_t = 0.9$ and the parameter b = 0.3, then $x_t + b = 1.2$ and $x_t + b \pmod{1} = 0.2$. Now consider the second iterate. We can do the iteration algebraically:

$$x_{t+2} = x_{t+1} + b \pmod{1} = (x_t + b \pmod{1} + b) \pmod{1}$$

= $x_t + 2b \pmod{1}$.

In similar fashion, we can find that

$$x_{t+n} = f^n(x_t) = x_t + nb \pmod{1}.$$

Consequently, if $nb \pmod{1} = 0$, then all values are on a cycle of period n; otherwise no values will be.

One way to think of this is by analogy to the odometer of a car, that shows the total mileage driven. Imagine that the odometer has a decimal point in front of it so that it shows a number between zero and one, for instance .07325. Every day the car goes b miles. After reaching .99999 the odometer resets to zero. x_t is the odometer value at the end of the trip on day t.

An example illustrates these ideas. In Figure 1.34 we show a graph of Eq. 1.14 for the particular case where $b = \frac{1}{\pi}$. This graph shows that the function has no fixed points, because there are no intersections of the function with the line $x_{t+1} = x_t$. The cobweb diagram for several iterations shows that there does not appear to be a cycle but that nearby points stay close together under subsequent iterations. Therefore, the dynamics appear to be quasiperiodic.

Can we know that there are never any periodic points no matter how many iterations we take? Here's where a bit of advanced mathematics can help. Recall the definition of a **rational number**: A number that can be written as the ratio of two integers $\frac{p}{q}$. **Irrational numbers** cannot be written as a ratio of two integers. π is an irrational number and $\frac{1}{\pi}$ is therefore also an irrational number. It follows immediately that $\frac{n}{\pi} \pmod{1}$ can never be equal to 0 for any integer n. Therefore, there can never be any periodic cycles for Eq. 1.14 with $b=\frac{1}{\pi}$. Also, from the algebraic iteration, we see that the iterates of two initial conditions that are very close will remain very close. Therefore, the dynamics are quasiperiodic.

Though the concept of quasiperiodicity depends on abstract concepts in number theory, quasiperiodic dynamics can be observed in a large number of different settings. Consider the following odd sleep habits exhibited by one of our colleagues when he was in graduate school. The first day of graduate school the graduate student fell asleep exactly at midnight. Each day thereafter, the graduate student got up, worked, and went to sleep. However, this graduate student did

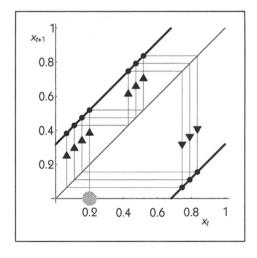


Figure 1.34 Iteration of $x_{t+1} = x_t + \frac{1}{\pi} \pmod{1}$. The dynamics are an example of quasiperiodicity.

not do this at the regular rhythms but rather with a rhythm of about 25 hours. The graduate student came into work about an hour later each day. Eventually, after 24 days, the graduate student goes to sleep again at about midnight. If the student's sleep cycle were exactly 25 hours, then there would be a cycle: 25 calendar days would equal 24 graduate student days exactly. However, it would be very unlikely that the graduate student's day would be exactly 25 hours. For example, suppose the graduate student days were $25 + 0.001\pi$ hours. Then, using the same arguments above, the graduate student would never again go to sleep exactly at midnight (independent of the length of time needed to complete graduate school!).

Another area in which quasiperiodic dynamics are often observed is in cardiology. There can be several different pacemakers in one heart. Normally one is in charge and sets the rhythm of the entire heart by interactions with other pacemakers (we will turn to this just ahead). However, in some pathological circumstances, pacemakers carry on their own rhythm—they are not directly coupled to each other. Typically one sees variable time intervals between the firing times of one pacemaker and the other. Cardiologists generally invent esoteric names to describe reasonably simple dynamic phenomena and have classification schemes for naming rhythms that are not based on nonlinear dynamics. Thus, two different rhythms that can be considered as quasiperiodic (to a first approximation) are parasystole and third-degree atrioventricular heart block. The analysis of these cardiac arrhythmias leads naturally into problems in number theory.

☐ EXAMPLE 1.4

The finite-difference equation, sometimes called the sine map,

$$x_{t+1} = f(x_t) = x_t + b \sin(2\pi x_t),$$

where $0 \le x_t \le 1$, has been considered as a mathematical model for the interaction of two nonlinear oscillators (Glass and Perez, 1982). See *Dynamics in Action* 1 for a typical experiment.

This system displays period-doubling bifurcations as the parameter b is varied.

- a. Find the fixed points of this equation.
- b. Algebraically determine the stability of all fixed points for $0 < b \le 1$. What are the dynamics in the neighborhood of each fixed point?

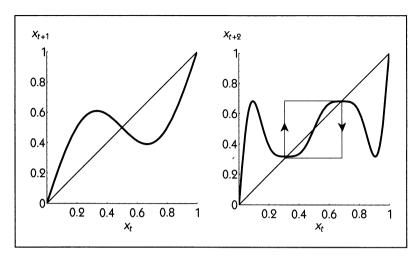


Figure 1.35 (left) The graph of $x_{t+1} = x_t + b \sin(2\pi x_t)$ for b = 0.4; (right) x_{t+2} versus x_t , showing the cycle of period 2 when b = 0.4.

Solution:

a. There are fixed points when

$$x_{t+1} = x_t + b \sin 2\pi x_t.$$

This will be true when $b \sin 2\pi x_t = 0$ which occurs when $x_t = 0, \frac{1}{2}, 1$.

b. To evaluate the stability we must first determine the slope at the steady states. The slope evaluated at the steady state is given by

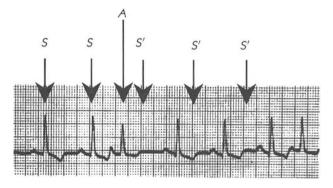
$$\frac{dx_{t+1}}{dx_t} = 1 + 2\pi b \cos 2\pi x_t.$$

Therefore, when $x_t = 0$ or $x_t = 1$, the slope at the steady state is $1 + 2\pi b > 1$, which indicates that the steady state is unstable. For $x_t = \frac{1}{2}$ the slope at the steady state is $1 - 2\pi b$. For $0 < b < \frac{1}{\pi}$ this is a stable steady state, which is approached in an oscillatory fashion; and for $b > \frac{1}{\pi}$ this is an unstable steady state, which is left in an oscillatory fashion (see Figure 1.35). The slope is -1 at $b = \frac{1}{\pi}$, so this value of b gives a period-doubling bifurcation.

DYNAMICS IN ACTION

1 CHAOS IN PERIODICALLY STIMULATED HEART CELLS

We are all familiar with bodily functions such as sleep, breathing, locomotion, heartbeat, and reproduction, which depend in a fundamental way on rhythmic behaviors. Such rhythmic behaviors occur throughout the animal kingdom, and a vast literature analyzes the mechanisms of the oscillations and how they interact with one another and the external environment. Anyone interested in obtaining an idea of the scope of the inquiry should consult the classic book by A. T. Winfree, The Geometry of Biological Time (1980).

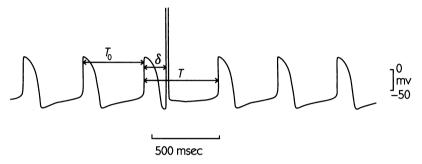


Phase resetting in the human heart. The wavey black line is an electrocardiogram—each sharp Λ -shaped spike corresponds to one beat. Those labeled S originate in the sinus node as normal. The beat labeled A originates elsewhere in the atria. In the absence of beat A, beats would have occurred at the times labeled S', however A resets the phase of the sinus node. Adapted from Chou (1991).

It turns out that the mathematical formulation of finite-difference equations has direct applications to the study of the effects of periodic stimulation on biological oscillators. The examination of periodic stimulation of biological oscillators involves many difficult issues, both in the biological and mathematical domains, and scientific investigation of these matters is still a research question under active investigation. However, compelling examples of chaotic dynamics in biological systems are found in the periodic stimulation of biological oscillations. Appreciation of the origin of the chaotic dynamics is possible using the material presented so far in this chapter.

Understanding the basics of the periodic stimulation of biological oscillators involves two related concepts: **phase** and **phase resetting**. The phase of an

oscillation is a measure of the stage of the oscillation cycle. Because of the cyclicity of oscillations, it is common to represent the phases of the cycle as a point on the circle. For example a phase of 120° can represent a time that is one third of the way through a cycle. Alternatively, we can also represent a phase of 120° as .333....

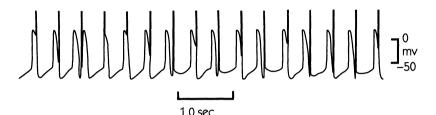


Recording of transmembrane voltage from spontaneously beating aggregates of embryonic chick heart cells. The intrinsic cycle length is T_0 . A stimulus delivered at a time δ following the start of the third action potential leads to a phase resetting so that the subsequent action potential occurs after time T. After this, the aggregate returns to its intrinsic cycle length. Adapted from Guevara et al. (1981). Copyright 1981 by the AAAS.

The term "phase resetting" refers to a change of phase that is induced by a stimulus. One example of phase resetting that many people experience is a consequence of jet travel. If you think about travel through different time zones, you will realize that the phenomenon of **jet lag** is associated with a discordance between the phase of your sleep—wake oscillator and the current local time. Staying in the new time zone for several days will lead to a phase resetting of your sleep—wake cycle. In this case the phase resetting takes place in a gradual fashion due to the different light—dark cycles and social stimuli in the new environment.

More abrupt phase resetting can be induced in many biological systems by appropriately chosen stimuli. For example, the rhythm of the human heart is normally set by a specialized region of the atria called the sinus node. However, in some people's hearts there are extra beats that can interfere with the normal sinus rhythm. Sometimes these extra beats can reset the rhythm. The figure on page 37 shows an example of an electrocardiographic (ECG) record. The normal sinus beats are labeled S and an atrial premature contraction is labeled A. If the atrial premature contraction had not occurred, the following sinus beat would have been expected at times labeled S'. However, the sinus firing is reset by the atrial premature stimulus,

leading to a sinus beat at a different time than would presumably have occurred without the atrial premature contraction.



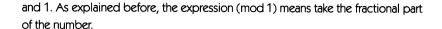
Periodic stimulation of spontaneously beating chick heart cell aggregates at a period slightly longer than the intrinsic period. The interaction of the intrinsic cycle and the periodic stimulation results in chaotic dynamics. Adapted from Guevara et al. (1981). Copyright 1981 by the AAAS.

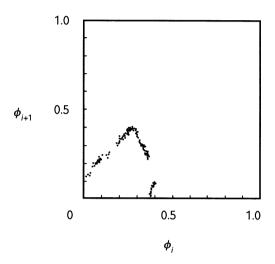
Since it is difficult to study the effects that electrical stimuli have on the heart, experimental preparations have been developed that enable detailed analysis (Guevara et al., 1981; Glass et al., 1984). The figure on page 38 shows phase resetting of spontaneously oscillating cardiac tissue derived from embryonic chick hearts. The upward deflections are called **action potentials** and are associated with the contraction cycle of the chick heart cells. The intrinsic length of the heart cycle is T_0 . The sharp spike delivered after a time interval of δ after the onset of an action potential is an electrical stimulus delivered to the aggregate. The stimulus phase resets the rhythm so that following the stimulus the new cycle length is T (rather than T_0). Experimental studies show that the magnitude of phase resetting depends on both the amplitude of the stimulus and the phase of the cycle at which the stimulus is delivered.

What happens when periodic stimulation is delivered to the oscillating heart cells? Each stimulus phase resets the rhythm. In fact, to a first approximation the amount of phase resetting during periodic stimulation depends on the phase of the stimulus in the cycle. The consequence of this is that the effects of periodic stimulation can be approximated by the finite-difference equation

$$\phi_{i+1} = g(\phi_i) + \tau \pmod{1},$$
 (1.15)

where ϕ_i is the phase of the oscillation when the *i*th stimulus is delivered, $g(\phi_i)$ is the new phase resulting from the *i*th stimulus, and τ is the time interval between stimuli (measured in units of the intrinsic cycle length). Here we take ϕ to lie between 0





Each stimulus in the preceding figure occurs at a specific phase of the intrinsic cycle. Here, we plot the phase of each stimulus as a function of the phase of the preceding stimulus, calculated for the experiment shown in the previous figure. The points suggest a function similar to the quadratic map. Adapted from Glass et al. (1984). Reprinted with permission from Glass (1984). Copyright 1984 by the American Physical Society.

Does the theory work? M. R. Guevara, L. Glass, and A. Shrier (1981) measured $g(\phi)$ by carrying out phase resetting experiments. They used the resulting finite-difference equation to predict the dynamics. For a moderate stimulation strength, they computed that chaotic dynamics should result, provided that the stimulation period was 15 percent larger ($\tau=1.15$) than the intrinsic cycle length. The effects of periodic stimulation with $\tau=1.15$ are shown in the figure on page 39. Note the irregular rhythm. On this record, the phase of each stimulus can be measured and successive phases can be plotted as a function of the preceding phase; see the figure on this page. The phases fall on a one-dimensional curve that is very similar to functions that give chaotic dynamics, as we have seen earlier. This observation, combined with the more extensive analyses of Glass et al. (1984), gives convincing evidence for chaotic dynamics in this experimental system.

SOURCES AND NOTES

There are now a number of elementary texts on chaos. A fine introduction to these topics from a noncalculus perspective is in Peak and Frame (1994). Those who have a good background in calculus and are interested in a presentation from a mathematical perspective should consult Devaney (1992). Elementary texts from the perspectives of physics (Baker and Gollub, 1990) and engineering (Moon, 1992) have also appeared. The application of chaos and nonlinear dynamics to physiology and human disease is discussed by Glass and Mackey (1988).

Edward N. Lorenz realized the practical implications of the sensitive dependence to initial conditions in his famous essay on deducing the climate from the governing fluid-dynamical equations (Lorenz, 1964a). Another influential paper (May, 1976) introduced many to the concept of chaos, with an ecological twist, and contained extensive references to early experimental and mathematical work. Descriptions of the occurrence of chaos in many different contexts can be found in assorted collections of papers (Hao, 1984; Holden, 1986; Cvitanovic, 1989). The popularization by James Gleick (1987) provides a enjoyable account of some of the recent discoveries concerning chaos and description of many of the scientists, such as Mitchell Feigenbaum, who have played a role. Another good read, by Thomas Bass, recounts how a group of physics graduate students in Santa Cruz (dubbed the "Santa Cruz collective" by Gleick) in the late 1970s tried to use their knowledge of nonlinear dynamics and physics to make a fortune playing roulette (Bass, 1985). Curiously, some of the same people are trying to predict the fluctuations of the currency market and have started a company, The Prediction Company in Santa Fe, New Mexico. The Santa Cruz collective presents a brief introduction to chaos in Crutchfield et al. (1986). Feigenbaum (1980) gives a memorable description of how he discovered his number.

Those scholars interested in the history of chaos will want to look through the many volumes of Poincaré's (1954) collected works trying to find the earliest reference to the concept of chaos—most cite "New Methods of Celestial Mechanics" as the earliest source, but we have not tried to check out if there are earlier citations. Li and Yorke (1975) first used "chaos" in its current meaning, but their paper is not for the faint-hearted.

EXERCISES

2.1 Assume that the density of flies in a swamp is described by the equation

$$x_{t+1} = Rx_t - \frac{R}{2000}x_t^2.$$

Consider three values of R, where one value of R comes from each of the following ranges:

a.
$$1 \le R < 3.00$$

b.
$$3.00 \le R \le 3.449$$

c.
$$3.570 \le R \le 4.00$$
.

For each value of R graph x_{t+1} as a function of x_t . Using the cobweb method follow x_t for several generations. Describe the qualitative behavior found for each case.

1.2 Not every finite-difference equation has fixed points that can be found algebraically. For example, the system

$$x_{t+1} = \cos(x_t)$$

involves a transcendental function and cannot be solved algebraically. Use a graph to find the approximate location and number of the fixed points. If you enter an initial condition into a pocket calculator and press the cosine key repeatedly, you are in effect iterating the finite-difference equation. Does the calculator approach a fixed point? Does the existence, location, or stability of the fixed point depend on whether x_t is measured in radians or in degrees?

■ 1.3 Find a function for a nonlinear finite-difference equation with four fixed points, all of which are unstable. Find a function with eleven fixed points, three of which are stable. Find a function with no fixed points, stable or unstable. (HINT: Just give a graph of the function without worrying about specifying the algebraic form.)

• 1.4 In a remote region in the Northwest Territories of Canada, the dynamics of fly populations have been studied. The population satisfies the finite-difference equation

$$x_{t+1} = 11 - 0.01x_t^2$$

where x_t is the population density (x_t must be positive).

- a. Sketch x_{t+1} as a function of x_t .
- b. Determine the fixed-point population densities and determine the stability of every fixed point algebraically.
- c. Assume that the initial density is less than $(1100)^{\frac{1}{2}}$. Discuss the dynamics as $t \to \infty$.

1.5 A population of flies in a mangrove swamp is described by the finitedifference equation

$$x_{t+1} = \begin{cases} 0.01x_t^2, & \text{for } x_t < K; \\ 0.01K^2 \exp[-r(x_t - K)], & \text{for } x_t \ge K. \end{cases}$$

Assume that $K = 10^3$ and $r = 1.75 \times 10^4$.

- a. Draw a graph of x_{t+1} as a function of x_t .
- b. From this graph determine the fixed points of the fly population.
- c. Determine the local stability of the fly population at each fixed point.
- d. Determine the dynamics for future times if the initial population of fly is (i) 60; (ii) 600; (iii) 6000; (iv) 60,000. For each case graphically iterate the equation for several generations and guess the dynamics as $t \to \infty$.

Ø 1.6 Consider the finite-difference equation

$$x_{t+1} = x_t^2 + c, \qquad -\infty < x_t < \infty,$$

where c is a real number that can be positive or negative.

- a. Sketch this function for c = 0. Be sure to show any maxima, minima, and inflection points (these should be determined algebraically). Show the location of all steady states.
- b. For what value(s) of c are there zero steady states? one steady state? two steady states?
- c. For what value of c is there a period-doubling bifurcation?
- d. Consider the sequence $x_0, x_1, x_2, \ldots, x_n$. For what range of c will x_n be finite given the initial condition $x_0 = 0$?

1.7 The following equation plays a role in the analysis of nonlinear models of gene and neural networks (Glass and Pasternack, 1978):

$$x_{t+1} = \frac{\alpha x_t}{1 + \beta x_t},$$

where α and β are positive numbers and $x_t \geq 0$.

a. Algebraically determine the fixed points. For each fixed point give the range of α and β for which it exists, indicate whether the fixed point is stable or unstable, and state whether the dynamics in the neighborhood of the fixed point are monotonic or oscillatory.

For parts b and c assume $\alpha = 1$, $\beta = 1$.

- b. Sketch the graph of x_{t+1} as a function of x_t . Graphically iterate the equation starting from the initial condition $x_0 = 10$. What happens as the number of iterates approaches ∞ ?
- c. Algebraically determine x_{t+2} as a function of x_t , and x_{t+3} as a function of x_t . Based on these computations what is the algebraic expression for x_{t+n} as a function of x_t ? What is the behavior of x_{t+n} as $n \to \infty$? This should agree with what you found in part b.
- 1.8 In cardiac electrophysiology, many phenomena occur in which two behaviors alternate on a beat-to-beat basis. For example, there may be an alternation in the conduction time of excitation from one region of the heart to another, or there may be an alternation of the morphology of the electrical complexes associated with each beat. A natural hypothesis is that these phenomena in electrophysiology are associated with period-doubling bifurcations in appropriate mathematical models of these phenomena. Both this problem and Problem 1.9 are motivated by possible connections between period-doubling bifurcations and cardiac electrophysiology.

During rapid electrical stimulation of cardiac tissues there is sometimes a beat-to-beat alternation of the action-potential duration.

Consider the equation

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

where x_t is the duration of the action potential of beat t and

$$f(x_t) = 200 - 20 \exp(x_t/62)$$
 for $0 \le x_t < 128$;
 $f(x_t) = 40$ for $128 < x_t \le 200$.

All quantities are measured in milliseconds (msec).

a. State the conditions (using calculus) for maxima, minima, and inflection points and say if any such points satisfy these conditions for the function defined above.

- b. Sketch $f(x_t)$ for $0 \le x_t \le 200$.
- c. Determine the fixed points (an approximation is adequate).
- d. In the neighborhood of each fixed point determine the stability of the dynamics and indicate if the dynamics are oscillatory or monotonic.
- e. Starting from a point near the fixed point, graphically iterate the equation and say what the behavior will be in the limit $t \to \infty$. A rough picture is adequate.

1.9 In the heart, excitation generated by the normal pacemaker in the atria travels to the ventricles, causing contraction of the heart and the pumping of blood to the body and the lungs. The excitation must pass through the atrioventricular node, which electrically connects the atria and the ventricles. The following problem is based on a mathematical model for atrioventricular (AV) conduction in mammals (Simson et al., 1981).

Assume that subsequent values of AV conduction time, designated x_t , are given by the finite-difference equation

$$x_{t+1} = \frac{375}{x_t - 90} + 100, \quad x_t \ge 90.$$

The units of all quantities are msec.

- a. Sketch x_{t+1} as a function of x_t . Indicate whether there are any maxima, minima, and inflection points.
- b. Determine the fixed point(s) of this equation in the range $x_t \ge 90$ msec.
- c. Determine the stability of the fixed point(s) found in part b.
- d. Based on your analysis, how will the dynamics evolve starting from an initial condition of $x_0 = 200$ msec?

1.10 The following equation was proposed as a model for population densities of insects in successive years:

$$x_{t+1} = \alpha x_t \exp(-\beta x_t^3),$$

where α and β are positive numbers and $x_t \geq 0$.

- a. Sketch the graph of x_{t+1} as a function of x_t . Determine any maxima or minima, but it is not necessary to compute the values of any inflection points.
- b. For $\alpha = 2.72$ and $\beta = 0.33$, determine the fixed point(s) and determine their stability. (HINT: The natural logarithm, designated as ln, is the

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logarithm to the base e. Since $e \approx 2.72$, you can assume that $\ln \alpha \approx 1$, to simplify the algebra.)

- c. Starting from an initial value of $x_0 = 137$, what are the possible dynamics in the limit $t \to \infty$?
- 1.11 The following equation has been proposed to describe the population dynamics of flies:

$$N_{t+1}=g(N_t), \qquad N_t\geq 0,$$

where the fly density in generation t is N_t and

$$g(N_t) = N_t \exp \left[r \left(1 - \frac{pN_t^2}{1 + N_t^2} \right) \right],$$

where r > 0 and p > 1.

a. For $0 < N_t \ll 1$, N_{t+1} is approximately given by

$$N_{t+1} = N_t e^r$$
.

In this case will N_1 be greater than, less than, or equal to N_0 ?

b. For $N_t \gg 1$ show that N_{t+1} can be approximately computed from the formula

$$N_{t+1} = KN_t,$$

where K does not depend on N_t . Compute K for $N_0 \gg 1$; will N_1 be greater than, less than, or equal to N_0 ?

- c. Determine all fixed-point values of N_t ($N_t \ge 0$). (HINT: If A = B, then $\log A = \log B$.)
- d. Compute $\frac{dg(N_t)}{dN_t}$.
- e. Assume that p = 2 and r = 1.2. Use the result from part d to compute all values of N_t , $N_t > 0$ for which $g(N_t)$ is either a maximum or minimum. (HINT: Let $z = N_t^2$.)
- f. Assume that p = 2 and r = 1.2. Use the result from part d to compute the stability of all fixed points found in part c.
- g. Sketch the graph of N_{t+1} versus N_t for p = 2, r = 1.2.

1.12 Assume an ecological system is described by the finite-difference equation

$$x_{t+1} = Cx_t^2(2 - x_t), \qquad 0 \le x_t \le 2,$$

where x_t is the population density in year t and C is a positive constant that we assume is equal to $\frac{25}{16}$.

- a. Sketch the graph of the right-hand side of this equation. Indicate the maxima, minima, and inflection points.
- b. Determine the fixed points of this system.
- c. Determine the stability at each fixed point and describe the dynamics in the neighborhood of the fixed points.
- d. In a brief sentence or two describe the expected dynamics starting from initial values of $x_0 = \frac{1}{3}$ and also $x_0 = 1$ in the limit as $t \to \infty$. In particular, comment on the possibility that the population may go to extinction or to chaotic dynamics in the limit $t \to \infty$.

1.13 In this problem P_t represents the fraction of neurons of a large neural network that fire at time t. As a simple model of epilepsy, the dynamics of the network can be described by the finite-difference equation

$$P_{t+1} = 4CP_t^3 - 6CP_t^2 + (1+2C)P_t,$$

where C is a positive number, and $0 \le P_t \le 1$.

- a. Compute the fixed points.
- b. Determine the stability at each fixed point and describe the dynamics in the neighborhood of the fixed points as a function of *C*.
- c. Sketch P_{t+1} as a function of P_t for C=4. Show all maxima, minima, and inflection points.
- d. On the basis of the preceding work discuss the dynamics as $t \to \infty$ starting from an initial condition of $P_0 = 0.45$ with C = 4. Try to do this graphically and, if possible, on a computer.
- 1.14 This problem deals with the equation

$$x_{t+1} = f(x_t) = 3.3x_t - 3.3x_t^2.$$

a. Determine the fixed points of $x_{t+2} = f(f(x_t))$. Which of these points are also fixed points of $x_{t+1} = f(x_t)$?

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- b. Are there any cycles of period 3?
- **1.15** Show that if there is one solution to $x_t = g(g(x_t))$, where $x_t \neq g(x_t)$, then there must also be another, different solution.
- 1.16 The dependence of the stability of a fixed point on the derivative can be shown algebraically using **Taylor series**. The Taylor series gives a polynomial expansion of a function in the neighborhood of a point. The Taylor series expansion of f(x) at a point a is

$$f(x) = f(a) + (x - a) \left. \frac{df}{dx} \right|_a + \frac{(x - a)^2}{2!} \left. \frac{d^2 f}{dx^2} \right|_a + \cdots$$
 (1.16)

This problem is aimed at using the Taylor series to derive analytically the local stability criteria for a fixed point in the finite-difference equation

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

Assume that there is a fixed point defined by $x_t = f(x_t) = x^*$. Define

$$m = \left. \frac{df}{dx} \right|_{x^*}$$

Derive the stability criteria for the fixed point at x^* using the Taylor series. (HINT: Define $y_t = x_t - x^*$ and consider the linear terms in the resulting equation.)

1.17 Periodically stimulated oscillators can often be described by one-dimensional finite-difference equations (see the *Dynamics in Action* 1 box). The variable ϕ_t refers to the phase of stimulus t during the cycle. The phase of the subsequent stimulus ϕ_{t+1} is a function of ϕ_t . The next three problems are all motivated by theoretical models that have been proposed for periodically stimulated oscillators.

The following finite-difference equation has been considered as a mathematical model for a periodically stimulated biological oscillator (Bélair and Glass, 1983):

$$\phi_{t+1} = \begin{cases} 6\phi_t - 12\phi_t^2, & 0 \le \phi_t < 0.5; \\ 12\phi_t^2 - 18\phi_t + 7, & 0.5 \le \phi_t \le 1. \end{cases}$$

a. Sketch ϕ_{t+1} as a function of ϕ_t for $0 \le \phi_t \le 1$. Be sure to show all maxima and minima and to compute the values of ϕ_{t+1} at these extremal points.

- b. Compute all fixed points. What are the qualitative dynamics in the neighborhood of each fixed point?
- c. If you have done part (a) correctly, you should be able to find a cycle of period 2. What is this cycle? Show it on your sketch.
- **7** 1.18 The finite-difference equation

$$\phi_{t+1} = 0.5 + \alpha \sin 2\pi \phi_t, \qquad 0 \le \phi_t < 1,$$

where $0 \le \alpha < 0.5$, has been used as a mathematical model for periodic stimulation of biological oscillators.

- a. There is one steady state. Determine this steady state and its stability as a function of α .
- b. For what value of α is there a period-doubling bifurcation?
- c. Sketch ϕ_{t+1} as a function of ϕ_t for $\alpha = 0.25$. Be sure to indicate all maxima, minima, and inflection points.
- d. For $\alpha = 0.25$ there is a stable period-2 orbit. What is it?

1.19 The following equation arose in the study of two independent oscillators competing for control of the heart. The resulting cardiac arrhythmia is called parasystole. Theoretical analysis of parasystole shows interesting rhythms obeying rules derived from number theory. The following example illustrates typical dynamics found when the ratio between the two frequencies is a rational number. For more details on the mathematical modeling of this cardiac arrhythmia, see Glass et al. (1986).

A mathematical model for a periodically forced biological oscillator can be written as

$$\phi_{t+1} = \begin{cases} \phi_t + 0.4, & \text{for } 0 \le \phi_i < 0.6; \\ \phi_t - 0.2, & \text{for } 0.6 \le \phi_i < 0.7; \\ \phi_t - 0.6, & \text{for } 0.7 \le \phi_t < 1.0, \end{cases}$$

where ϕ_t is the phase in the cycle of the forced oscillator at which the tth periodic stimulus falls, $0 < \phi_t < 1$.

- a. Accurately plot on graph paper ϕ_{t+1} as a function of ϕ_t .
- b. Determine the fixed points, if any, and determine their stability.
- c. Take an initial condition $\phi_0=0.65$ and determine the dynamics (both algebraically and graphically) until a periodic orbit is reached. Do the

same for an initial condition of $\phi_0 = 0.95$. An accurate graph is essential here.

d. Are the periodic orbits in part c stable?

$$x_{t+1} = ax_t \exp(-x_t), \qquad x_t \ge 0,$$

where a is a positive constant.

- a. Determine the fixed points.
- b. Evaluate the stability of the fixed points.
- c. For what value of a is there a period-doubling bifurcation?
- d. For what values of a will the population go extinct starting from any initial condition?
- e. On a computer, generate the bifurcation diagram as a function of a. Even though you might not be able to do this computation, do you expect that the bifurcation diagram will display the period-doubling route to chaos similar to that shown in Figure 1.31?
- 1.21 If you are tired about problems concerning flies, consider the following model about bird populations. Birds eat flies. Milton and Bélair (1990) proposed this equation as a model for bird densities in successive years:

$$x_{t+1} = \begin{cases} 3.22x_t & \text{for } 0 \le x_t \le 1\\ 0.5x_t & \text{for } 1 < x_t. \end{cases}$$
 (1.17)

Draw a graph of x_{t+1} as a function of x_t . Graphically iterate this equation and determine if the dynamics are chaotic.

1.22 Print your last name. Count the number of letters and multiply the number by 0.1. Your **magic number**, m, is 1 plus the number that you just computed. If your last name has nine or more letters, assume that m = 1.9.

Consider the finite-difference equation given by the following equations:

$$x_{t+1} = mx_t,$$
 for $0 \le x_t \le \frac{1}{m}$;

$$x_{t+1} = mx_t - 1$$
, for $\frac{1}{m} < x_t \le 1$.

a. Draw a graph of x_{t+1} as a function of x_t .

- b. Determine the fixed point(s) and determine their stability.
- c. Graphically iterate this equation.
- d. Are the dynamics chaotic?

1.23 In Example 1.4 in the text, we looked for period-doubling bifurcations in the finite-difference equation:

$$x_{t+1} = f(x_t) = x_t + b \sin(2\pi x_t).$$

We found that fixed points became unstable when $b=\frac{1}{\pi}$. At these bifurcation points, a stable period-2 cycle emerges. Here, we are interested in studying the stability of these cycles of period 2. In particular, we want to know when the cycles are "superstable," meaning that a nearby point is immediately moved onto the cycle rather than approaching it exponentially. Such superstability occurs when the graph has slope zero at the fixed points of the cycle, which will occur when the graph is at a maximum or a minimum on the cycle.

- a. Sketch the graph of the equation for $b = \frac{1}{\pi}$. Determine the values of all maxima, minima, and inflection points.
- b. For a particular value of b the maximum and minimum of $f(x_t)$ are on a cycle of period 2. Sketch the function for this case showing the cycle of period 2. It is not necessary to determine the value of b that leads to this behavior. However, will b be greater than or less than $\frac{1}{\pi}$?

COMPUTER PROJECTS

Consider the two following one-dimensional finite-difference equations.

$$x_{t+1} = 4\lambda x_t (1 - x_t),$$
 Equation A
 $x_{t+1} = \lambda \sin \pi x_t,$ Equation B

where $0 \le x_t \le 1, \ 0 \le \lambda \le 1$.

For both Equation A and Equation B carry out Projects 1-5.

Project 1 Write a computer program that can be used to iterate these equations.

Project 2 Compute a bifurcation diagram such as shown in Fig. 1.31. To compute this first set a value for λ . Then iterate the equation equation 200 times, but only save the values of the last 100 iterates. Plot these 100 values on a graph

above the corresponding value of λ . Increment λ in small steps. In doing this you may wish to experiment with the step size in λ , the length of the transient and the number of plotted points. Getting a nice looking picture depends on taking fine steps in λ , taking a sufficiently long transient, and plotting a sufficiently large number of points.

Project 3 Write a program that can determine if a sequence of values generated from iteration of the equations is periodic. If it is periodic, what is the period of the cycle? In doing this, it is best for you to set a specific value for convergence to a periodic orbit. This means that if the distance between 2 points is closer than some value, for example $\epsilon=10^{-5}$, you would declare that a periodic orbit had been found.

The next two projects make use of the techniques developed above. Carrying them out successfully requires some skill and careful numerical work. If you get stuck you might wish to look back at original sources. Project 4 is based on Metropolis et al. (1973), and Project 5 is based on Feigenbaum (1980).

Project 4 Determine the sequence of periodic orbits that are encountered as a function of λ . In doing this there are 3 parameters that you will have to adjust: the number of iterates, the increment in λ , and the convergence criterion. Although it probably seems like it should be trivial to decide what the period is for any value of λ you may surprised to find that different sets of the 3 parameters will give different answers. The situation can be particularly delicate when you are near values of λ that lead to bifurcations in the dynamics. The sequences of periodic orbits for the 2 different maps should be the same. Are they?

Project 5 Locate sequences of period doubling bifurcations. Write a program that can compute automatically the value of Feigenbaum's number for the two functions given above. Do you obtain the same value that has been found by Feigenbaum? Is the value the same for both of the functions? Is the value the same for the sequences of periodic orbits 2, 4, 8, . . . and 3, 6, 12, . . . ?

Project 6 Now that you have mastered functions with one parameter you are ready to explore functions with 2 parameters. Consider the function (often called the sine circle map)

$$x_{t+1} = x_t + a + b \sin(2\pi x_t) \pmod{1},$$

where $0 \le a \le 1$, $0 \le x_t \le 1$, and $b \ge 0$. Your task is to study the periodic orbits as a function of a and b. Since there are 2 parameters now, you will make a plot of the behavior with a on the horizontal axis and b on the vertical. At each value of a and b, plot a dot whose color depends on the length of the period

found. You will have to consider what to do if you do not find any period. An additional complication comes from the fact that the cycle that you find in some regions of parameter space will depend on the initial condition.