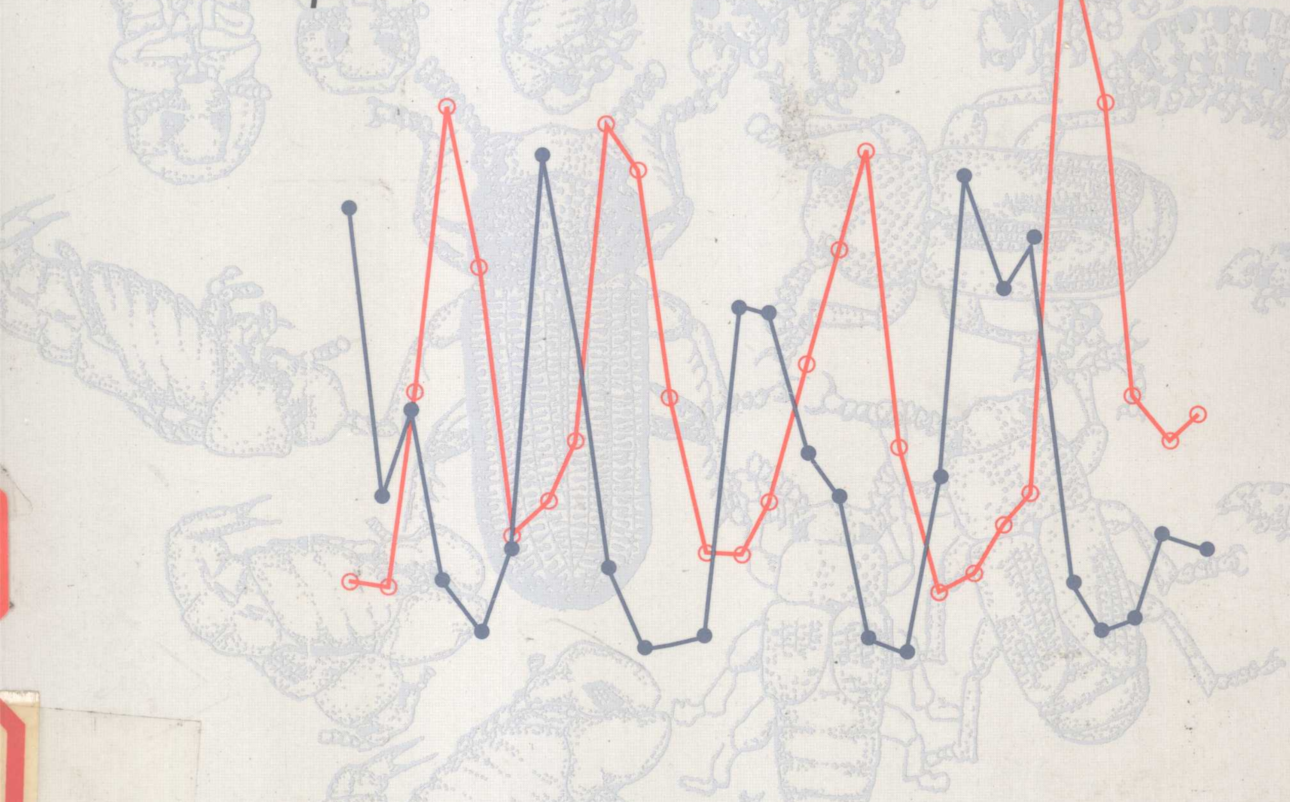
Alan Hastings

POPULATION BIOLOGY

Concepts and Models



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Concepts and Models

With 77 Illustrations

Springer

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To Elaine, Sara, and Toby

Preface

This book is based on a population ecology course I have taught for many years at the University of California, Davis, primarily to juniors and seniors majoring in Environmental Biology. The material is more than I have ever covered in a ten week quarter, and should be covered comfortably in a semester. This book will also be useful as a supplement to more general texts in population biology and ecology, which tend not to cover nearly enough theory.

The only mathematical prerequisite is one year of calculus (which I assume many students may not remember well). I assume that the student has had some previous exposure to ecological ideas, although this is not an absolute requirement. I believe that the material covered here is essential for any graduate student in ecology or population biology. One principle guiding this book is that students in population biology and ecology are shortchanged if they are not given the opportunity to work through and understand the mathematical models which have become a core part of our discipline. I have not overwhelmed the reader with an excessive number of biological examples in the text – when I teach the course I ask students to read a selection of recent experimental and observational studies to complement the material in the text.

If, after a glance at the table of contents and a look through the book, you begin to doubt that all students in ecology will really be able to do stability analyses, I assure you that students in my classes have had no difficulty rising to the challenge.

I have always tried for the simplest possible explanations of the underlying ideas. For example, I emphasize concepts of age structure in the context of just two age classes. I have also included detailed explanations of all the mathematical concepts and procedures which are likely to be new, at the point they are first used. These are set apart in boxes, so they are easier to find for future reference. Thus, boxes are more frequent in the earlier chapters. Also, since the mathematical development is essentially self-contained, there is more mathematics in the earlier chapters than in the later chapters.

Because the theoretical and mathematical development is such an integral part of the presentation, the book should really be covered in order, with one exception. The chapter on density dependence can be read before the chapter on population genetics. With some care, and review of the boxes in the chapter on population genetics, the chapter on population genetics could be skipped while still maintaining the logical flow of the book.

The extensive marginal notes serve several purposes. Steps that may be confusing for some readers, but clear to others, are explained in the notes. The notes point out connections among different topics. The notes are also used to suggest places where the reader should stop and think (and not just read!).

At the end of every chapter there are problems (some mathematical, some not). Almost all of these have been tested with students. These are an essential part of the text and need to be studied and pondered for a full understanding of the material.

I thank Bill Settle, who took the course many years ago and took careful notes which helped greatly in the preparation of this book. Other students since then have provided extensive feedback on preliminary versions of this text. Emilio Bruna read chapter three. Gary Huxel and Chris Ray have made numerous, helpful comments on the text. Rob Garber, the editor, provided extraordinary help in all phases, including extensive comments on earlier drafts. Finally, I thank Simon Levin, from whom I first learned ecological modeling.

Alan Hastings
Davis, California

Contents

List of Boxes

1
Introduction

1.1 What is population biology?

A *population* is a group of individuals of the same species that have a high probability of interacting with each other. A simple example would be trout in a lake, or moose on Isle Royale, although in many cases the boundaries delineating a population are not as clear cut. Population biology is simply the study of biological populations.

Population biology includes genetic and evolutionary questions; it is broader than population ecology.

Why study population biology? An understanding of complex ecological communities with numerous species interacting with each other and the environment requires an understanding of the simpler ecological systems of one or two species first. We will begin by focusing on the population biology of a single species for two reasons. First, an understanding of the dynamics of a single species leads to the primary questions of population ecology. Second, this is the simplest system that can be studied from a population approach.

Although population ecology might strictly refer to a single species, we use it in this text more broadly to refer to studies focusing on numbers within a species and explicitly consider one or two species at a time.

Why do we focus on numbers of individuals as the variable of interest, rather than a variable like energy flow? We do this because it is possible, even likely, that small numbers of individuals may have effects, especially on population stability, out of proportion to their numbers. For example, a small popuation of predators may play a major role in regulating a prey population with a large population size. Diseases, ranging from AIDS to the plague, may have extreme effects on the dynamics of the host populations.

Here 'regulating' means controlling the population growth.

Population biology is by its nature a science that focuses on numbers. Thus, we will be interested in understanding, explaining, and predicting changes in the size of populations. Several intriguing patterns of population change through time are illustrated in Figure 1.1. What causes these different patterns to appear? The answer to this question is a central theme of this book.

1.2 Role of models in population biology

Answering many important questions in conservation biology requires the use of models from population biology.

We do not address the important issues of population estimation or experimental design in this book.

The goals of population biology are to understand and predict the dynamics of populations. Understanding, explaining, and predicting dynamics of biological populations will require models, models that are expressed in the language of mathematics. In this book, we emphasize the role of models in understanding population biology. Mathematical models are essential in making precise theoretical arguments about the factors affecting the rate of change of population size.

A full appreciation of the role of models will come as you progress through the book, but a few preliminary observations on how models are employed are very useful. First, a model cannot be shown to be true by a single experiment. However, a model can be shown to be false by a single experiment that does not agree with the predictions of the model. What does it mean to say that a model is false? Assuming that no logical (or mathematical) mistakes have been made, it means that one of the assumptions of the model is not met by the natural system examined. This can be a very useful result, in that it indicates where empirical work should concentrate. In the next chapter we will see just this approach, in elucidating the central question in population biology: *What prevents uncontrolled population growth?*

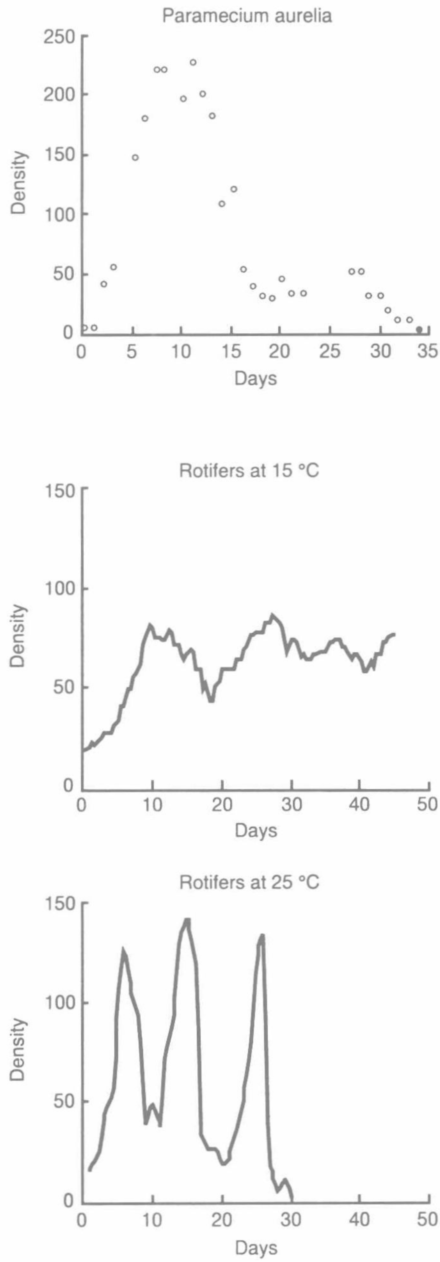

FIGURE 1.1. Three examples of population dynamics from the laboratory. The top example is from Gause (1935); the bottom two are dynamics of rotifers at two different temperatures from Halbach (1979).