

Population Harvesting

DEMOGRAPHIC MODELS OF FISH,
FOREST, AND ANIMAL RESOURCES

WAYNE M. GETZ AND
ROBERT G. HAIGHT

Population Harvesting

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WAYNE M. GETZ
AND
ROBERT G. HAIGHT

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To our wives
Jennifer and Georgiana

Contents

Preface	xiii
1. Introduction	3
1.1 Scope	3
1.1.1 Preview	3
1.1.2 Focus	9
1.1.3 Model Resolution	12
1.2 How to Read This Book	17
2. Linear Models	19
2.1 Life Tables	19
2.1.1 Scope	19
2.1.2 Mortality Column	20
2.1.3 Reproductive Cycle	22
2.2 Population Dynamics	26
2.2.1 Leslie Matrix Model	26
2.2.2 General Linear Model	27
2.2.3 Positive Linear Models	30
2.2.4 Stage-structured Populations	31
2.2.5 Age-structured Populations	40
2.3 Harvesting Theory	43
2.3.1 Formulation	43
2.3.2 Equilibrium Analysis	46
2.3.3 Linear Programming	50
2.3.4 Dynamic Analysis	51
2.4 Stochastic Theory	53
2.4.1 Introduction	53
2.4.2 Pollard's Stochastic Model	57
2.4.3 A Stochastic Environment	60
2.4.4 Harvesting Stochastic Populations	62

CONTENTS

2.5 Review	63
3. Nonlinear Models	66
3.1 Background	66
3.1.1 Scope	66
3.1.2 Linearization and Stability	67
3.2 Density-Dependent Recruitment	68
3.2.1 Density Dependence and Offspring	68
3.2.2 Equilibrium Solutions	73
3.2.3 Stability Properties	76
3.2.4 Sustainable Harvests	80
3.3 Nonlinear Stage-Class Models	83
3.3.1 Model Structure	83
3.3.2 Equilibrium Theory	85
3.3.3 Linearization and Stability	87
3.4 General Harvesting Theory	89
3.4.1 Sustainable Yields	89
3.4.2 Dynamic Yield Problem	92
3.4.3 Discounted Rent and a Maximum Principle	96
3.4.4 Planning Horizons	99
3.5 Stochastic Theory	103
3.5.1 Introduction	103
3.5.2 Stochastic Recruitment—Small Noise	103
3.5.3 Stochastic Recruitment—Large Noise	108
3.5.4 Stochastic Harvesting	110
3.5.5 Level of Complexity	111
3.5.6 Monte Carlo Methods	113
3.6 Aggregated Age Structure	119
3.6.1 Model	119
3.6.2 Stability	125
3.7 Review	130
4. Fisheries Management	136

CONTENTS

4.1 Background	136
4.2 Deterministic Models	137
4.2.1 Cohort Model	137
4.2.2 Seasonal Harvesting with Nonlinear Recruitment	141
4.3 Equilibrium Yield Analyses	146
4.3.1 Yield Effort Curves	146
4.3.2 Optimal Yields	148
4.3.3 Ultimate Sustainable Yield	150
4.3.4 Anchovy and Cod Fisheries	152
4.4 Deterministic Dynamic Harvesting	155
4.4.1 Maximum Yield	155
4.4.2 Suboptimal Policies	156
4.4.3 Anchovy Fishery	158
4.4.4 Rehabilitation of Fisheries	161
4.5 Stochastic Harvesting	165
4.5.1 A Stochastic Cohort Model	165
4.5.2 A Nonlinear Stochastic Recruitment Model	167
4.5.3 Constant Harvesting Policies	169
4.5.4 Escapement-Related Policies	173
4.5.5 Allocation of Variability	177
4.5.6 Optimal Harvesting of Widow Rockfish	185
4.5.7 Rational Harvesting of Anchovy	188
4.6 Aggregated Catch-Effort Analysis	192
4.7 Multispecies Multiparticipant Fisheries	196
4.7.1 Introduction	196
4.7.2 Technological Links	199
4.7.3 Sustainable Yields, Quotas, and Discarding	201
4.7.4 U.S. West Coast Groundfish Resource	204
4.7.5 U.S. Canadian Pacific Whiting Fishery	210
4.8 Review	220

CONTENTS

5. Forest Management	225
5.1 Background	225
5.2 Models for Predicting Stand Growth	227
5.2.1 Stand Management Systems	227
5.2.2 Univariate Models for Even-aged Stands	228
5.2.3 Linear Stage-Class Models	230
5.2.4 Nonlinear Stage-Class Models	237
5.2.5 Single-Tree Simulators	239
5.2.6 A Stage-Class Model for True Fir	242
5.2.7 Comparison of Model Projections	250
5.3 Evaluating Harvest Systems	259
5.3.1 Silvicultural Policy	259
5.3.2 Investment Model	261
5.3.3 Even-aged Management	263
5.3.4 Uneven-aged Management	267
5.3.5 Measuring Economic Efficiency	272
5.4 Nonlinear Optimization	275
5.5 Application to True Fir	285
5.5.1 Case Background	285
5.5.2 Fixed- and Equilibrium-Endpoint Problems	287
5.5.3 Case Summary	295
5.5.4 A Comparison of Harvest System Efficiency	297
5.6 Forest-Level Management	308
5.7 Review	315
6. Other Resources and Overview	320
6.1 Harvesting and Culling Large Mammals	320
6.1.1 Introduction	320
6.1.2 Environmental Variability and Elephant Dynamics	321
6.1.3 Stability and Resilience of Harvested Grey Seal Populations	332

CONTENTS

6.2 Mass Rearing Insects	337
6.2.1 Introduction	337
6.2.2 Fruit Fly Demography	339
6.2.3 Mass Rearing Fruit Fly	342
6.2.4 An Age-Stage Model	346
6.2.5 Mass Rearing the Potato Tuberworm	349
6.3 Overview	351
6.3.1 Importance of Theory	351
6.3.2 Applying the Theory	354
6.3.3 Future Directions	356
6.4 Conclusion	359
References	361
Index	381

Preface

Although the theory of harvesting populations has a number of different traditions drawn from fisheries, forest, and wildlife management, a common demographic thread runs through these various applications. Trees and many vertebrates reproduce on a seasonal basis so that their populations consist of cohorts of similarly aged individuals (age classes). Thus discrete age- and, more generally, stage-structured (e.g., size classes) population equations are appropriate for modeling the dynamical aspects of both animal and plant populations.

One of the aims of this book is to draw together the theory of discrete stage-structured population models as developed in the fisheries, forestry, population harvesting and general demography literature. We do this in the specific context of biological resource management. The disciplines of fisheries, forest-stand, pest, and wildlife management have their own unique problems, but common economic and demographic notions pervade the mathematical analyses of these problems. We hope, by unifying some of these notions across the various areas of application, that this book will encourage a cross-fertilization of ideas between professional fisheries, forest, pest, and wildlife management scientists, as well as population biologists and demographers.

A second aim of this book is to present a comprehensive account of our recent investigations into the theory of nonlinear stage-structured population harvesting models and its application to fisheries and forest-stand management problems. The linear theory of age-structured population growth is embodied in life-table analysis (static viewpoint) and Leslie matrix theory (dynamic viewpoint). Nonlinearities, however, are an essential aspect of biolog-

PREFACE

ical systems, the most obvious being increases in mortality and reduction in fecundity rates as population density increases in a resource-limited environment. Because a general linear theory is sufficiently extensive to warrant a book on its own, we only summarize this theory in Chapter 2 and provide the material necessary to achieve continuity with the applications presented in Chapters 4 to 6 and the nonlinear theory presented in Chapter 3.

Most of the advanced material presented here appears or will appear in the recent literature and references are provided, although a small percentage of the material is not published elsewhere. Our treatment assumes that the reader is comfortable with basic notions in calculus, matrix algebra, and complex number theory. Discrete models allow us to avoid some of the more difficult aspects of mathematical analysis associated with systems of differential and integro-differential equations. As this is an advanced rather than an introductory text, we assume that the reader is familiar with the basic elements of matrix algebra and complex numbers. We do lead the reader through a cursory treatment of matrix diagonalization (eigenvectors and eigenvalues) and the solution to linear matrix equations, but expect those readers who have difficulty with the concepts to supplement their reading using the references provided. We cover some aspects of linear and nonlinear programming, including a discrete version of Pontryagin's Maximum Principle, but only the minimum necessary to provide a self-contained presentation of the material in this book.

The material in this book should be accessible to those forest and fisheries economists and modelers who have read such books as Clark (1976) or Johansson and Löfgren (1985). We hope, however, that this book will be of value to population and wildlife biologists who only have an elementary background in calculus and matrix algebra, but are motivated to work hard and insert supplementary

PREFACE

readings when the going gets rough. In particular, these readers can omit the more difficult sections, 2.4 and 3.3 to 3.6, and still follow and appreciate much of the material presented in Chapters 4 to 6. We also hope that this work motivates applied mathematicians interested in resource management and/or population harvesting to study some of the more general properties of discrete nonlinear stage-structured models.

The ideas in this book draw strongly from our collaborations with colleagues. In particular, W.M.G. is indebted to R. C. Francis and G. L. Swartzman for many stimulating discussions over the past eight years while working on joint fisheries projects supported by the Northwest and Alaska Fisheries Center of the National Marine Fisheries Service. R.G.H. is indebted to D. Brodie and D. W. Hann for supervising his dissertation research which led directly to the forest management studies described in Chapter 5.

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Population Harvesting

CHAPTER ONE

Introduction

1.1 SCOPE

1.1.1 Preview

This book is about resources that are managed by harvesting cohort-structured biological populations. This includes fisheries, forest-stand, and wildlife management problems, as well as mass rearing of insects for biological control. Our aim in writing this book is to present a unified approach to modeling and managing such resource systems.

In this age of environmental crises we need to meet the challenge of managing biological resources in an efficient and minimally disruptive manner. This requires that we be precise about what we are doing; and to be precise we need to model the management process. In mathematical terms, efficient management typically translates into maximizing some suitably defined performance index, often net revenue. Precision requires that we model the dynamic response of the underlying population to management actions.

Population modeling is an inexact science. Populations are part of complex systems that defy the taming tethers of “physical laws.” Thus there is little to prevent a piecemeal approach to cohort-structured resource management, with each subdiscipline developing its own methods. To a large extent this has happened, and communication among scientists working on conceptually similar problems in different areas of applications has been hindered. Communication among scientists working on managing cohort-structured populations, albeit as different as trees, fish, mammals, and insects, can only be beneficial.

CHAPTER ONE

We hope this book will encourage communication among scientists working in different areas of application.

The first requirement in solving the communication problem is to develop a common language, especially in the context of population modeling, where the greatest barrier exists. We do this by adopting a neutral mathematical notation: the notation of mathematical systems theory. This has the added advantage of using a notation that is more suitable for the mathematical analysis of management problems than notations that are currently often used in the applied fields.

The second requirement in solving the communication problem is to develop a modeling framework that can be applied to any cohort-structured resource management problem. This facilitates comparative analyses of conceptually similar problems in the different areas of application, preventing duplication of effort and enhancing our general understanding of resource management issues. In the theory sections of this book, we develop an approach that allows us to incorporate such nonlinearities as density-dependent reproduction and survival, while retaining most of the clarity associated with linear population models. Such clarity is not apparent in current nonlinear approaches.

The various areas of resource management remain distinct not only because of differences in the biological species comprising the resource, but because each area of application poses a different set of problems. A major emphasis in fisheries science has been on the problem of estimating current and past population levels (i.e., stock abundance) using catch levels and fishing effort data (see Cushing, 1981; Gulland, 1983; Schnute, 1985). Many fish populations, especially those in which individuals live no more than several years, exhibit wide and largely unpredictable fluctuations in the number of young fish (i.e., recruits) joining that part of the stock that is vulnera-

INTRODUCTION

ble to fishing each year. Thus stochasticity is a critical aspect of analyzing the stock dynamics in most fisheries. This stochasticity, primarily due to environmental changes and the problems associated with estimating population abundance and age structure, poses severe constraints on our ability to develop appropriate management policies. These difficulties have led to a dichotomy in methodology, namely "cohort" and "surplus production" approaches to yield or catch analysis.

Origination of the "cohort" approach is largely due to Beverton and Holt (1957), who developed a method of analysis in which the age of the fish play a central role. Beverton and Holt's approach was essentially a deterministic equilibrium analysis which assumed constant recruitment. This approach has been extended to include nonlinear recruitment (Getz, 1980a,b; Reed, 1980), and dynamic (Getz, 1985, 1988) and stochastic (Reed, 1983; Getz, 1984a) analyses, but the multidimensional character of the models (model variables are age classes) makes the analysis complicated.

The "surplus production" approach typically ignores age by focusing on a single harvestable stock biomass variable (single variable models are sometimes referred to as "lumped-variable" models). The analysis leads to the derivation of a scalar catch equation (Baranov, 1925) that is more readily embedded into a nonlinear stochastic setting (Schnute, 1985). Although cohort structure is essentially ignored, the value of this approach lies in being able to analyze highly stochastic management situations (see Walters, 1986). There are some important drawbacks, however, to ignoring cohort structure when undertaking a detailed stochastic analysis. The market value of individual fish and our ability to catch them may vary quite considerably with age (or its correlate, size). Although we take a cohort approach throughout this book, in the fisheries chapter (Chapter 4) we

CHAPTER ONE

will demonstrate a link between cohort-structured and lumped-variable models.

In contrast to fisheries, individuals in a forest stand can be seen and counted, and tree attributes such as stem diameter, height, and volume are readily measured. In addition, the time units associated with birth, growth, and death processes for trees are at least an order of magnitude larger than for fish populations. Thus, density-dependent models for projecting stands of trees are based on short-term growth observations in a cross section of stands with a wide range of ages, densities, and environmental conditions.

The relative ease of measuring and harvesting trees has resulted in a variety of stand management systems and associated models for predicting growth and determining harvest policy. Models for projecting stand growth span the range from single-variable models for single-species even-aged stands to single-tree simulators for mixed-species uneven-aged stands. The stage-class model that we apply to forest stand projection has an intermediate level of biological detail and complexity. The stage-class model includes the important demographic processes such as species- and size-dependent birth, growth, and death processes. As a result, the same stage-class model can be used to project the effects of harvesting in either even-aged or uneven-aged stands with one or many species. Equally important, the stage-class model is simple enough for mathematical analysis and numerical optimization. Thus, the economic efficiencies of different timber harvesting systems can be evaluated and compared.

The utility of the stage-class model in forestry research is illustrated by the development of the theory associated with uneven-aged stand management. Prior to the application of stage-class models in forestry, uneven-aged management problems were formulated only in a steady-state framework because of the limitations of growth and yield

INTRODUCTION

models in use. Univariate models did not give realistic portrayals of stand dynamics in uneven-aged stands, and single-tree simulators were too complicated to analyze in a dynamic framework. The steady-state analyses often concluded that clearcutting and plantation management were the most efficient management system. In contrast to univariate models and single-tree simulators, the stage-class model provided a means to formulate and solve a dynamic harvesting problem. Results from the application of the dynamic model, as discussed in Chapter 5, show that clearcutting and even-aged management are just a special case of the more generally formulated uneven-aged management problem and are less efficient in the long term.

The problem of counting and measuring large-mammal populations (both terrestrial and marine¹) lies somewhere between fish and tree populations. One can more easily count mammals than fish and one can more easily estimate the size of individual mammals than trees. Of course, different mammal populations present different problems. Pinnipeds (seals, sea lions, walruses), for example, are easily observed only during their breeding season when they congregate in specific areas.

Insects present an altogether different challenge. Many species have multiple generations per year, where the length of each generation is strongly linked to the ambient temperature of its habitat. Survival rates fluctuate dramatically with environmental conditions so that populations in the field can exhibit dramatic changes from week to week. The methods of analysis described in this book are largely unsuitable for addressing insect pest management problems, although we illustrate how they can be applied to insect populations reared under controlled laboratory conditions.

¹ Exploitation of a marine mammal population is traditionally referred to as a fishery, although we treat the problem separately in this book.

CHAPTER ONE

As previously stated, the common thread running through managing fisheries and forest stands, exploiting large mammals, and mass rearing insects is the harvesting of populations that have a cohort structure. In analyzing the growth of these fish, tree, mammal, and insect populations, we usually categorize individuals by age or size and collect data to construct an age- or size-specific life table. One limitation with the age-specific approach, however, is that it is not always possible to determine the correct age of an individual. Thus size may often be a more appropriate variable.

In forest-stand management, in particular, individuals are assigned to size or "stage classes" rather than age classes. A size-specific analogue of a life table can be constructed for such populations, but this introduces other complications such as assessing the rate at which individuals move from one size class to the next. The application of age-specific life tables to certain insect populations also presents special problems. Holometabolous insects, such as flies, moths, butterflies, beetles, bees, ants, and wasps, have distinct life stages (egg, larval, pupal, adult) with, for example, very different feeding behaviors in each life stage. Because not all individuals spend the same period of time in each life stage, a more general age-stage life table is required.

In this book we focus on age- and stage-structured approaches to modeling populations and their application to problems in fisheries and forest-stand management, in harvesting large mammals, and in mass rearing insects. Although we do not deal with lumped population models (i.e., models in which all age classes are lumped together), we show how to collapse age-structured models to lumped-variable stock-biomass models that relate stock levels at several points in the past to current stock levels. These models are so-called discrete-delay difference equations. Since they capture certain essential features

INTRODUCTION

of age-structured models, some of their theoretical properties and their application to fisheries problems are discussed in this book.

Most resources are derived from populations that exhibit cyclic reproduction. For these populations, systems of discrete-time difference equations provide a more appropriate model of the resource than systems of continuous time differential equations. Compared with differential equations, difference equations are easier for the nonmathematician to construct and simulate on the computer. Thus we will not attempt to extend any of the theory presented here to continuous system models.

1.1.2 Focus

The field of biological resource management draws its tools of analysis from mathematics, statistics, computer science, and engineering. Thinking in this field is influenced by economists and other social scientists. Economically important resource systems include both plants and animals, in both marine and terrestrial environments.

The various resource management professions (fisheries, forestry, and wildlife management) are distinct from one another. Resource economists and modelers, however, provide a bridge between these professions (see Clark, 1976). The same mathematical and statistical techniques are often employed in different areas of applications (e.g., mathematical programming), although each area has its own distinct flavor. For example, multidimensional models and linear and nonlinear programming techniques are used extensively in forest management, while dynamic scalar models and statistical estimation theory are important tools in fisheries management. Thus resource managers in different areas of application have a different quantitative training; and this tends to keep managers, and even scientists, working in these different areas further apart than they should be. Additionally, even

CHAPTER ONE

within specific areas of application, some researchers are concerned primarily with the statistical problems associated with estimating model parameters, while other researchers are concerned with determining harvest rates and the dynamic response of the population to management.

The material in most resource management books is a vertical slice through the field in that it deals with a single area of application such as fisheries (e.g., Cushing, 1981; Gulland, 1983; Rothschild, 1986) or forests (e.g., Husch *et al.*, 1982; Johansson and Löfgren, 1985). Examples of books taking a horizontal slice are Clark's development of bioeconomic principles (Clark, 1976), Mangel's synthesis of uncertain resource systems management (Mangel, 1985), and Walters' exposition on the adaptive management of resource systems (Walters, 1986). This book is horizontal since its general theme is harvesting of age- and stage-structured populations. Our models are nonlinear extensions of discrete-time, age- or stage-class matrix models that can be traced back to Lewis (1942) and Leslie (1945, 1948). In Chapters 2 and 3 respectively we develop linear and nonlinear mathematical techniques of analysis and derive a small number of theoretical results. In Chapters 4 and 5 respectively we develop models for application in fisheries and forest-stand management, and include a number of literature case studies to illustrate how various types of resource management problems are approached. In Chapter 6 we illustrate how age- and stage-structured models have been applied to a few selected animal resource and pest management problems.

We have limited the scope of the book to dealing with questions that relate only to harvesting, and then only in populations where age or stage structure is regarded as an essential component of the management problem. This was done to keep the book a manageable size, but as a result we do not present any of the theory relating to re-

INTRODUCTION

source models in which populations are represented by a scalar population-biomass or population-numbers variable (i.e., lumped-variable models). For a treatment of this theory the reader is referred to Clark (1976, 1985). We also do not deal with the extremely important issue of how to estimate model parameters. Such questions rely heavily on both statistical analyses and the biology of the populations involved. Many of these questions are more appropriately dealt with in an application-specific vertical text. Further, the difficult statistical questions are best treated in a book that includes sufficient statistical background material to assist the reader with the development of the more sophisticated techniques. Here we only provide background material in discrete dynamic systems and age- and stage-structured models. We do include techniques for modeling and analyzing stochastic problems, but our stochastic treatment is limited to modeling questions. Stochastic analyses of structured systems present a major challenge, although some progress has been made (for example, see Horwood, 1983; Horwood and Shepherd, 1981; Reed, 1983; Nisbet and Gurney, 1982). A deep understanding of the influence of stochastic processes on harvesting is difficult to obtain in multidimensional models. Most of our understanding stems from simulation studies. The influence of stochastic processes is better understood in the framework of scalar or lumped-variable models (for example, see Beddington and May, 1977; May *et al.*, 1978; Ludwig and Walters, 1981; Walters and Ludwig, 1981), although this material is not presented here because the corresponding deterministic models are outside the scope of this book.

A central issue in applying models to particular problems is deciding how much biological detail should be included in a model. The models presented in this book include age or stage structure in the population, but ignore specific characterization of interactions between the

CHAPTER ONE

population and its predators, competitors, prey, or physical environment. Is this a reasonable approach? This is a difficult question to answer. We address this question below, in a discussion that is intended for readers that already have some modeling experience. Other readers should move on to Section 1.2.

1.1.3 Model Resolution

There are two fundamentally different sets of paradigms associated with modeling the dynamics of biological populations: the *top-down* and *bottom-up* approaches. In our discussion of these modeling paradigms we refer to *precision* and *accuracy*, where a lack of precision implies a large variance associated with model predictions and a lack of accuracy implies a bias in model predictions. A key question in modeling is when does increased biological detail lead to improved precision and/or improved accuracy? Intuitively it would seem that by incorporating additional biological mechanisms we can account for a greater variance in the population's behavior and, hence, construct more precise models. On the other hand, if some details are incorporated but a major component of the model is missing, a detailed model may be quite inaccurate when compared with a less detailed but intrinsically correct model.

To be more specific, suppose $x(t)$ represents the number of individuals in a population at time t , and let $b(t)$ and $d(t)$ respectively denote the number of births and deaths in the population over the time period $[t, t + 1]$. Then the number of individuals at time $t + 1$ is given by the equation

$$x(t + 1) = x(t) + b(t) - d(t). \quad (1.1)$$

The top-down approach assigns some functional form to the birth and death processes $b(t)$ and $d(t)$, such as

$$d(t) = \bar{d}x(t), \quad (1.2)$$

INTRODUCTION

where $\bar{d}$ is a constant per capita death rate. The bottom-up approach, on the other hand, identifies $d(t)$ as the sum of all deaths stemming from a number of different sources, including losses to possibly a number of different predators, for example, as well as death from a number of different diseases, etc. If an important source of mortality is omitted in the latter approach, however, then the best holistic estimate of the overall death rate $\bar{d}$ in relationship (1.2)² may provide a more accurate model than the bottom-up approach.

In general, the bottom-up modeling paradigm focuses on detail, is problem specific, and, in a sense, is an empirical approach; that is, modeling progresses by using biomass or energy flow equations to link those and only those components that are observed to be part of the system (Forrester, 1961; Odum, 1983; Swartzman and Kaluzny, 1987). In the bottom-up approach we explicitly recognize that populations are part of a complex ecosystem and we incorporate underlying ecosystem processes into a dynamic model of one or more populations of interacting individuals. Models are developed much in the same way as one develops computer software to solve specific problems. So-called ecosystem compartmental simulation models are an example of this approach (for specific examples, see Patten, 1971, 1972). In bottom-up modeling one generally opts for realism through detail, but at the same time one endeavors to simplify a model without sacrificing accuracy or substantially affecting precision.

In the top-down modeling paradigm we tend to ignore detail. This approach is more applicable than the bottom-up approach to addressing a general class of problems and, in a sense, is a phenomenological approach; that is, modeling begins by postulating a fundamental growth

² This estimate is obtained by counting the number of dead in each time period, or inferring the number that died from past and present population levels.

CHAPTER ONE

law for the population. (Equation (1.2) is a poor example of such a law. For better examples see Getz, 1984b, and Ginzburg, 1986.) In the top-down approach we recognize that populations are part of a hierarchical system with ever-increasing levels of complexity. We begin modeling at the simplest of these levels, and usually do not move beyond one or two additional levels of complexity. Models are holistic: model building begins by postulating a basic growth law (Getz, 1984b), employing a conservation equation (Schnute, 1985, 1987), or describing the demographic processes of mortality and natality in terms of average rates that summarize the cumulative effects of underlying but unspecified ecological factors. In top-down modeling one typically explores that trade-off between increased detail (which often results in a loss of comprehension) and development of principles (which we hope enhances our understanding). Certainly, one should not add details that do not increase the accuracy or precision of the model.

In population modeling, there is a place for both paradigms. The particular approach taken depends on the objectives of the modeling study. The bottom-up approach provides a method for structuring and coordinating ecosystem studies. The top-down approach provides a method for exploring theoretical questions, for example, relating to the effects of intra- and interspecific competition on population growth and stability (Getz, 1984b). It is one thing to simulate the response of a population to a number of environmental inputs and another to solve for optimal harvesting or management strategies. The latter requires extensive numerical work that is facilitated by simple models described by mathematical functions that are, for example, differentiable. Thus top-down models are going to be more easily applied to resource management problems. If we are able to show, as we do in the forestry chapter (Chapter 5), that a top-down model has

INTRODUCTION

essentially the same precision as a bottom-up model in predicting management-related variables, such as biomass yield, then the top-down model is preferable for the management study.

Because of the management orientation of this book, we take a top-down approach throughout. In addition to the greater generality and ease of implementation of top-down models, the amount of work required to fill in the biological details of a bottom-up approach would detract from research on management-oriented questions. Age and/or stage progression of individuals is included in our population models because such progression is a general phenomenon that has economic and logistical (implementation of strategies) implications for management. Details of ecological interactions tend to be case specific. Thus in the top-down approach it is appropriate to subsume these interactions in the form of density-dependent relationships and stochastic inputs, and retain some generality.

This is especially true of resource management studies where we focus on finding harvesting strategies that satisfy certain performance criteria rather than on explaining basic biological processes. In forest-stand management, for example, the models are not constructed to investigate the physiology of tree growth for which a bottom-up approach may be necessary. Rather, they are designed to assess the response of a stand of trees to various harvesting practices, and provide a tool for finding "optimal" harvesting strategies. Suppose a detailed physiological model were available that could accurately predict the growth of a tree as a function of its environment. Since every tree grows under a different set of local conditions ranging from soil type and water runoff rates to level of competition from immediate neighbors, a model that includes nutrient uptake and competition at the individual-tree level is impossible to implement at the stand level without investing a

CHAPTER ONE

great deal of time and money just to set up the initial conditions to begin the simulation. Thus some compromises are required, such as using data that reflect average growth and survival rates for classes of trees. The accuracy involved in estimating these averages depends on both the quantity and quality of data. There is an obvious marginal value associated with the collection of such data. Certainly, a manager would not want to invest the value of the stand in collecting data to determine the optimal harvesting regime. Our experience suggests that there is a negative marginal utility to assessing more than an average age- or stage-specific growth and survival parameter plus a couple of regeneration or reproductive parameters. The reason for this, as we discuss in Chapter 5, is that the relatively simple stage-structured models presented in this book seem to be indistinguishable from more detailed single-tree stand-growth simulators in predicting stand yield, at least at the level of accuracy determined by the quality of the data used to verify these models.

In fisheries, the limitations on biological detail are even more severe. The high degree of variability associated with survival of youngest age class (that is, individuals in the egg and larval stages) plus the difficulties associated with estimating the size of a population or even the age of individuals taken from the population limit the extent to which detailed age structure can be included in models. Nevertheless, as previously mentioned, the size of harvested individuals often has economic ramifications that cannot be ignored. For this reason, models that have age structure may prove to be more valuable than lumped models for making certain types of management decisions. It should be pointed out, however, that fisheries models which directly use time series of catch-effort data, say, to predict future population or yield levels without independently assessing model parameter values from biological

INTRODUCTION

data (e.g., Walters, 1986) are often more robust if age or stage structure is ignored. Time-series models are central to the analysis of many resource problems (Schnute, 1985, 1987), but are beyond the scope of this book.

1.2 HOW TO READ THIS BOOK

Since readers of this book will range from quantitative problem solvers (mathematicians, physicists, engineers) interested in resource management problems to population biologists interested in a particular resource application, we feel that it would be useful to have a guide to reading this book. A number of sections were not written for the general reader. In particular, Section 3.4 is only included for the more quantitatively oriented reader, especially those interested in dynamic optimization. Also, most of the material in Section 3.5 can be skipped over by those readers interested in Monte Carlo techniques for simulating stochastic phenomena, rather than directly modeling the time evolution of the population distribution or its first two moments.

The following is a list of selected sections that should be read by those with one of the identified interests. The reader interested in fisheries or forest-stand management should begin, respectively, with a preliminary reading of Chapter 4 or 5 before earnestly tackling the theory presented in Chapters 2 and 3. This will give that reader a feel for where the theory is heading in terms of particular applications.

- **Deterministic harvesting theory:** Sections 2.1–2.3; 3.1, 3.2, 3.3*, 3.6; 4.1–4.4, 4.6; (5.1–5.3)* (sections with an asterisk may be omitted by those readers not interested in stage-class models).
- **Stochastic harvesting theory:** To the above sections add Sections 2.4; 3.5; 4.5.

CHAPTER ONE

- **Fisheries management:** Skim Chapter 4 and then read Sections 2.1, 2.2.1–2.2.2; 3.1, 3.2, 3.5.6, 3.6. Reread Chapter 4.
- **Forest-stand management:** Skim Chapter 5 and then read Sections 2.1–2.3; 3.1, 3.3. Reread Chapter 5.
- **Animal demography:** Chapter 2; Sections 3.1, 3.2; 4.1–4.3; 6.1, 6.2.

The reader should note that theorems, lemmas, and results are numbered sequentially in the chapter in which they appear, with reference given to chapter number (e.g., Theorem 2.1, Lemma 2.2, Result 2.3). We also present five problems that are numbered sequentially throughout the book without reference to the chapter number in which they appear (e.g., Problem 1, Problem 2, etc.).

CHAPTER TWO

Linear Models

2.1 LIFE TABLES

2.1.1 *Scope*

Life-table analysis uses the average fecundity and mortality schedule of individuals within a population to study the growth and cohort or age-structure dynamics of that population. Classical life tables are constructed under a number of severe assumptions. Fecundity and mortality processes are assumed to be unaffected by population density and to be time invariant (stationary with respect to time). The reproductive success of females is assumed to be unaffected by the number of males in the population, and all individuals are subjected to the same fecundity and mortality schedules. Let the continuous variable a be used to denote age. All females in the population are assumed to be subject to the same

- birth processes, characterized by an age-dependent female fecundity (natality) rate or *force of maternity* function ϕ_a ;
- death processes, characterized by an age-dependent female mortality rate or *force of mortality* function μ_a .

These assumptions can be used to construct a life table for the female component of the population, or for the population as a whole if a constant sex ratio is assumed.

In real populations we know that mortality and fecundity rates change with time, depending on environmental conditions, population density, and the sex ratio in the population. Insofar as population density and sex ratio can be assumed to play a minor role in determining mortality and fecundity schedules, and as time or seasonally related

CHAPTER TWO

variations in parameter values around average values can be ignored, a deterministic theory of population growth and age structure can be developed using the functions ϕ_a and μ_a defined above. Since we focus on populations that live for at least several years and exhibit an annual breeding cycle, it is convenient to select one year (for animals which live on the order of tens of years) or five years (for trees which live on the order of hundreds of years) as an appropriate unit of time, and to discretize the analysis using an integer index $i = 1, \dots, n$, where n is the oldest cohort (age category) considered in the analysis. Of course, other time units have been used, including 2 years for such long-lived animals as elephants and whales. In the case of insects, 1 or 2 days is the time unit commonly used.

In this chapter, it is our intention to review only that part of life-table analysis that relates to the development in Chapter 3 of a nonlinear demographic theory for the management of animals and timber. Other texts are available that treat life-table analysis in the context of classical (human) demography (Henry, 1976; Keyfitz, 1968; Pollard, 1973), and evolutionary biology (Charlesworth, 1980).

2.1.2 Mortality Column

Suppose that l_0 individuals are born at time $t = 0$ (typically l_0 is taken as 1000 for the presentation of life table mortality data). Then, since the force of mortality is assumed to be dependent on an individual's age but is independent of population density and time—that is, $\mu_a(t) = \mu_a$ is the per capita mortality rate for all values of t —the number of individuals l_a in this cohort that live to time (age) a by definition satisfies the differential equation

$$\frac{dl_a}{dt} = -\mu_a l_a,$$

which can be solved to yield at the integer time $t = i$

$$l_i = l_0 e^{-\int_0^i \mu_a da}.$$

LINEAR MODELS

Since the age-specific mortality rates are assumed to be stationary with respect to time, it follows that l_i/l_0 is the proportion of individuals that survives up to *exact* age i , irrespective of whether these individuals were born at time 0 or some arbitrary time t . To simplify notation, we will assume throughout that the mortality schedule l_i has been normalized to directly represent proportions; that is, $l_0 = 1$. It also follows that s_i , the proportion of individuals (alive at age i) that survives from exact age i to exact age $i + 1$ is independent of time t and is given by

$$s_i = \frac{l_{i+1}}{l_i}, \quad i = 0, 1, 2, \dots \quad (2.1)$$

Note that the positivity and monotonicity of l_i imply that $0 < s_i \leq 1$, for all i except the oldest age group. For the latter, by definition, we have $s_n = 0$. Also, equation (2.1) leads to the relationship (recalling that $l_0 = 1$)

$$l_{i+1} = \prod_{j=0}^i s_j. \quad (2.2)$$

The values $l_0, l_1, \dots, l_n$ listed vertically in a life table are referred to as the *survivorship* column. (For an example see Table 6.1). From this column a number of other life-table entries are generated, including

$$q_i = (l_i - l_{i+1})/l_i,$$

the proportion of individuals that die between exact age i and exact age $i + 1$, and (see Emlen 1984 for a derivation)

$$e_i = \left(\sum_{j=i+1}^n l_j \right) / l_i,$$

the life expectancy of an individual at exact age i (note that in the formula for e_i , n must be the oldest age beyond which no individuals are known to survive). In continuous time, the values of $\log l_a$ plotted as a function of

CHAPTER TWO

a are referred to as the survivorship curve for the population in question. Three classes of survivorship curves are distinguished (Figure 2.1), respectively typified by very low infant and juvenile mortality rates (e.g., man), constant mortality rates with respect to age (e.g., some birds), and very high infant mortality rates (marine invertebrates, many species of fish).

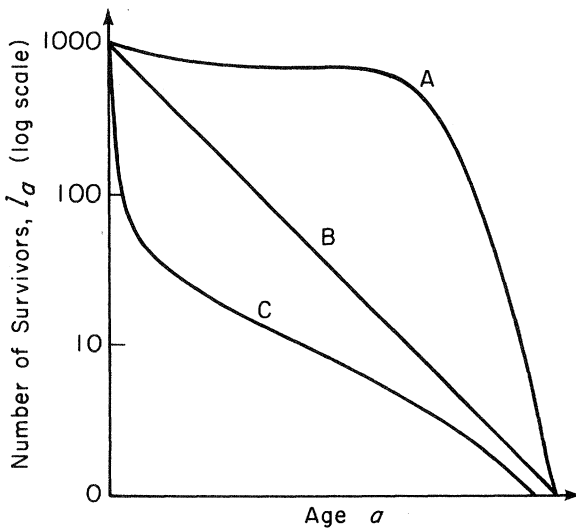


FIGURE 2.1. The logarithm of survivorship curves l_a for three contrasting life histories: A, low infant and juvenile mortality rate; B, constant mortality rate with age; C, high infant mortality rate.

2.1.3 Reproductive Cycle

Subject to the biological problem of determining the age of each individual in a population, the population can be divided into age classes. If populations have a regular reproductive cycle (usually annual), we can count the population immediately after births have taken place and

LINEAR MODELS

set the time axis so that births occur at integer values of t (or integer multiples for long-lived species). If this occurs at time t , then the variable $x_i(t)$ can be used to denote the number in the i th class, $i = 0, \dots, n$, at time t , where $x_0(t)$ is the number of newborns. Note that n is either the maximum age to which any individual can live or, more generally, n represents all the individuals that have just turned n years and older.

It now follows from our definition of the survival parameters s_i in equation (2.1) that, over the reproductive cycle $[t, t + 1]$, $t = 0, 1, 2, \dots$, variables x_i will satisfy the relationship

$$x_{i+1}(t+1) = s_i x_i(t), \quad i = 0, \dots, n-2, \quad (2.3)$$

with this same equation holding for $i = n-1$ if $s_n = 0$, that is, if no individuals survive beyond age n . If $s_n > 0$, and it is assumed that s_n applies to all individuals older than n , then the equation for x_n becomes

$$x_n(t+1) = s_n x_n(t) + s_{n-1} x_{n-1}(t). \quad (2.4)$$

To complete our description of the population projection process from time t to $t + 1$, we need to consider the production of newborns x_0 at time $t + 1$. In a continuous model, we would need to integrate the natality function ϕ_a with respect to the female age distribution to obtain the actual rate of births at time t . However, if we assume that females only reproduce on their birthdays, so to speak (which is a good approximation if the breeding season is short with respect to the breeding cycle), then the natality function ϕ_a is replaced by a set of constants b_i denoting the expected number of females per aged i female (recall that we are either modeling a population with a constant sex ratio or we are modeling the female portion of the population under the assumption that there

CHAPTER TWO

are always sufficient males to allow normal levels of reproduction). In this case, the number of newborns is given by the following sum:

$$x_0(t+1) = \sum_{i=1}^n b_i x_i(t+1). \quad (2.5)$$

The system of equations (2.3)–(2.5) thus allows us to calculate the number of newborns $x_0(t+1)$ and the population vector $\mathbf{x}(t+1) = (x_1(t+1), \dots, x_n(t+1))'$ (that is, the number of individuals in each cohort) at time $t+1$, if we are given the survivorship and fecundity parameters s_i and b_i for all ages i and the population vector $\mathbf{x}(t)$ at time t . (Note throughout the text that $'$ is used to denote the transpose of a vector, since the standard representation of a vector is a column rather than a row of elements.) Alternatively, if the number of individuals x_0 born at times $t, t-1, \dots, t-n+1$ is known, then it follows from the iterative application of equation (2.3) and relationship (2.2) that (recalling $l_0 = 1$)

$$x_{i+1}(t+1) = l_{i+1} x_0(t-i), \quad i = 0, \dots, n-2, \quad (2.6)$$

which is another way of projecting $x_0(t+1)$ and $\mathbf{x}(t+1)$. Note that if equation (2.4) holds with $s_n > 0$, it is not possible to express $x_n(t+1)$ in terms of $x_0(t-i)$ (unless $x_0(t)$ is assumed to be constant as in the case of some fisheries models), since $x_n(t+1)$ in fact depends on $x_0(t-i-1), x_0(t-i-2), \dots$, etc. On the other hand, if $s_n = 0$ in (2.4) then equation (2.4) can be written as

$$x_0(t+1) = \sum_{i=1}^n b_i l_i x_0(t-i+1), \quad (2.7)$$

which is an n th order difference equation in the number-of-births variable x_0 . Since, for all populations, there exists some age beyond which no individuals are known to