Population Harvesting

Demographic Models of Fish, Forest, and Animal Resources

WAYNE M. GETZ

AND

ROBERT G. HAIGHT

PRINCETON UNIVERSITY PRESS

PRINCETON, NEW JERSEY

1989

Population Harvesting

Demographic Models of Fish, Forest, and Animal Resources

WAYNE M. GETZ

AND

ROBERT G. HAIGHT

PRINCETON UNIVERSITY PRESS

PRINCETON, NEW JERSEY

1989

Published by Princeton University Press,
41 William Street, Princeton, New Jersey 08540
In the United Kingdom: Princeton University Press, Guildford, Surrey

Library of Congress Cataloging-in-Publication Data

Getz, Wayne M., 1950–
Population harvesting: demographic models of fish, forest, and animal resources.
Wayne M. Getz and Robert G. Haight.

p. cm.—(Monographs in population biology; 27)
Bibliography: p.
Includes index.
ISBN 0-691-08515-3 (alk. paper)
ISBN 0-691-08516-1 (pbk.)
1. Population biology—Mathematical models. 2. Wildlife management—Mathematical models. 3. Forest management—Mathematical models.
I. Haight, Robert G., 1955– . II. Title. III. Series.
QH352.G47 1989
574.5′248—dc19 88-19950

This book has been composed with the TEX system in Autologic Baskerville II by Zoological Data Processing, Socorro, New Mexico, and set at TEXSource, Houston, Texas

Clothbound editions of Princeton University Press books are printed on acid-free paper, and binding materials are chosen for strength and durability. Paperbacks, although satisfactory for personal collections, are not usually suitable for library rebinding.

Printed in the United States of America by Princeton University Press, Princeton, New Jersey

To our wives

Jennifer and Georgiana

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 biological 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 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.

We typed this manuscript using LaTeX, a macro package written by L. Lamport for the TeX typesetting system developed by D. E. Knuth. To these two people, we are indeed grateful. We are also indebted to M. E. Bergh, L. W. Botsford, D. Goodman, J. E. Hightower, J. Schnute, B. Solberg, G. L. Swartzman, and D. Wear for critically reviewing drafts or portions of this manuscript. Of course all errors and omissions remain our own responsibility. We thank Nancy Munro for drafting the figures.

We would like to thank Judith and Robert May, our editors at Princeton, for their support and help in getting this book published.

W.M.G. would like to acknowledge the National Science Foundation (Grant DMS-8511717) and the Alfred P. Sloan Foundation (Grant No. 86-6-18) for support towards the research and writing of this book. R.G.H. would like to acknowledge support of an S. V. Ciriacy-Wantrup Postdoctoral Fellowship administered by the Graduate Division at the University of California, Berkeley.

Contents

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.

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 vulnerable 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