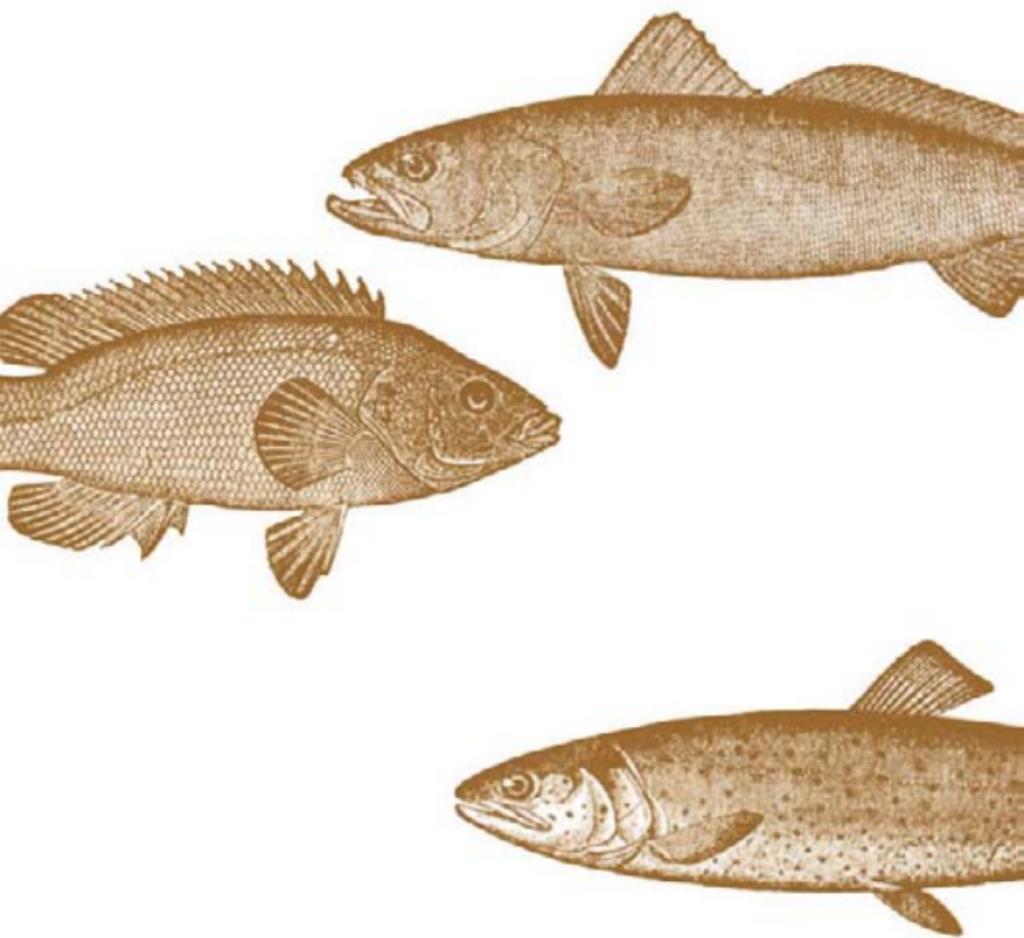


Quantitative Fish Dynamics



Terrance J. Quinn II and Richard B. Deriso

QUANTITATIVE FISH DYNAMICS

BIOLOGICAL RESOURCE MANAGEMENT SERIES

A Series of Primers on the Conservation and Exploitation
of Natural and Cultivated Ecosystems

Wayne M. Getz, Series Editor
University of California, Berkeley

Agricultural and Environmental Resource Economics

Edited by Gerald A. Carlson, David Zilberman,
and John A. Miranowski

Coastally Restricted Forests

Edited by Aimlee D. Laderman

Quantitative Fish Dynamics

Terrance J. Quinn II and Richard B. Deriso

QUANTITATIVE FISH DYNAMICS

Terrance J. Quinn II

Richard B. Deriso

New York • Oxford

Oxford University Press

1999

Oxford University Press

Oxford New York

Athens Auckland Bangkok Bogotá Buenos Aires Calcutta
Cape Town Chennai Dar es Salaam Delhi Florence Hong Kong Istanbul
Karachi Kuala Lumpur Madrid Melbourne Mexico City Mumbai
Nairobi Paris São Paulo Singapore Taipei Tokyo Toronto Warsaw

and associated companies in
Berlin Ibadan

Copyright © 1999 by Oxford University Press, Inc.

Published by Oxford University Press, Inc.
198 Madison Avenue, New York, New York 10016

Oxford is a registered trademark of Oxford University Press

All rights reserved. No part of this publication may be reproduced,
stored in a retrieval system, or transmitted, in any form or by any means,
electronic, mechanical, photocopying, recording, or otherwise,
without the prior permission of Oxford University Press.

Library of Congress Cataloging-in-Publication Data
Quinn, Terrance J., II, 1952-

Quantitative fish dynamics / Terrance J. Quinn II
and Richard B. Deriso.

p. cm. — (Biological resource management series)
Includes bibliographical references and index.

ISBN 0-19-507631-1

1. Fish populations—Mathematical models. I. Deriso, R. B.

(Richard B.) II. Title. III. Series.

QL618.3.Q5 1998

597.17'88'011—dc21 97-35538

1 3 5 7 9 8 6 4 2

Printed in the United States of America
on acid-free paper

We dedicate this book to the memory of R. Ian Fletcher, who taught us quantitative fish population dynamics, conceived of the idea of this book, and cajoled, criticized, and encouraged us repeatedly during our careers.

This page intentionally left blank

Preface

This book is a synthesis of quantitative models of fish population dynamics and methods for fisheries stock assessment. We emphasize rigorous development of models and methods and the use of statistical procedures for linking fisheries data to differential and difference equations of population dynamics. The last 20 years have seen major advances in the analysis of fish population data, and the 1980s and 1990s have been a particularly energetic time period of creative developments. We foresee that further methodological advances are likely to occur, particularly in the treatment of complexity in data and models and of uncertainty and risk in fisheries management decisions. Nevertheless, we believe that it is timely to attempt to unify what has already been accomplished.

This book is directed toward upper-division and graduate-level courses in fish population dynamics and stock assessment. We have used the material in this book for short-, one-, and two-semester courses. We require that our students have at least one year of calculus, one year of applied statistics, and familiarity with personal computers and spreadsheets, including macro writing. We also recommend that they have additional coursework in differential equations, statistical methodology (including non-linear regression, likelihood estimation, and basic probability and statistics concepts and operators), and experience with fisheries issues, management, and biological principles. We recommend that instructors supplement material in this book with subject matter related to the direct estimation of animal abundance, including mark-recapture, line-transect, and removal methods using catch-per-unit-effort. Seber's text (1982) contains much of the historical development of this material, which can be supplemented with more recent literature.

We were motivated to write this book more than a decade ago when we were teaching fish population dynamics and there were no up-to-date texts available. The classic work by Beverton and Holt (1957) was out of print (but it was republished in 1993), and Ricker's (1975) handbook did not cover recent developments. In addition, an integration of statistical methods and population models was sorely needed. During the course of our work, several good books on aspects of fish population dynamics and fisheries stock assessment have appeared, the most notable of which is that by Hilborn

and Walters (1992). We have gone into greater depth into the development of models than they do and provided a broader coverage of the field; however, we have not gone into as much detail into nonquantitative aspects of stock assessment. Other notable books the reader should consult include those by Pauly and Morgan (1987), Getz and Haight (1989), Caswell (1989), Gunderson (1995), and Gallucci et al. (1996).

We have modeled our book after Seber's (1982) book on the estimation of animal abundance. Our approach is similarly inclusive: to present all rigorous methods and models found in the literature and to include a large number of references, many of which cite other important work. We attempt to list assumptions and present a rigorous development for each approach, to illustrate the approach with an example, and to discuss limitations and advantages. We introduce the appropriate modern statistical concepts as needed for model development. We attempt to synthesize methodology and point toward future developments.

The organization of the book is in order of increasing complexity in models and/or data requirements. We present simple population growth and mortality models in chapter 1. The population growth models for abundance (in numbers of fish) are parameterized in terms of an intrinsic rate of increase and a carrying capacity, which subsumes the complicated processes of recruitment, mortality, and aging. The fundamental concept of density dependence is introduced and recurs throughout the book. We develop the complementary mortality models for a single year-class of individuals, leading to fundamental relationships for abundance, mortality, survival, death, and catch. Models for the fishing process are then described to show how fishery performance data can be used to understand trends in abundance and other population parameters. In particular, we derive the requirements for catch-per-unit-effort (CPUE) to be an index of abundance.

In chapter 2, we extend the simple population growth model to population biomass (in weight of fish). Fundamental concepts of surplus production and equilibrium yield (catch in weight) lead to the traditional concept of maximum sustainable yield and related parameters. Estimation procedures are developed and compared, and the relationship of surplus production to the processes of recruitment, growth, and mortality is described.

In chapters 3 and 4, we turn our attention to elemental processes affecting population dynamics. Chapter 3 focuses on the relationship of recruitment to spawning stock, egg production, and other variables. Spawner-recruit models are developed from fundamental assumptions affecting early life history, and concepts of compensation and depensation related to density dependence are introduced. Estimation methods account variously for error structure, measurement error, process error, and autocorrelation. The theory of population growth and harvesting for semelparous (once-spawning) populations naturally develops from these considerations. Chaotic behavior of populations occurs for certain models. We introduce the Bayesian paradigm in conjunction with spawner-recruit models, in which model parameters are treated as random variables and updated by analysis of data.

Chapter 4 presents models of processes affecting individuals in a population, including growth, maturity, and fecundity. The major models proposed for individual growth are described, along with estimation procedures and application to mark-recapture data. A compendium of procedures for comparing growth parameters and models is given. We develop models to describe variation in growth, including sea-

sonal, individual-variation, and stochastic. Some important considerations are given for analysis of the growth of an individual's scales, otoliths, or other hard parts. The types of models used for maturity and fecundity and population variables drawn from these processes are summarized. The egg production method of estimating spawning biomass derives from these considerations.

We develop difference equations for population abundance and biomass in chapter 5 that combine the concepts of age structure, mortality, individual growth, and recruitment. The most notable feature of these models is the direct incorporation of a lag between spawning and recruitment. For many of these models, the equations for abundance and biomass for the total population summed across ages are closed-form solutions that are not explicitly a function of age other than the lag term. This feature allows such models to be applied to data such as commercial fishery CPUE or a survey index where age-specific information is not available.

In chapters 6 and 7, age-structured models of population abundance are developed. Proceeding from the basic theory of mortality from chapter 1, chapter 6 elaborates on models for year-classes by combining mortality and growth processes. Explicit incorporation of harvesting parameters, such as gear selectivity and fishing mortality and effort, is featured. Expression of fundamental population statistics such as yield and spawning biomass on a "per-recruit" basis leads to fishery management strategies described in chapter 11. Chapter 7 connects year-class models with the population renewal process (in the form of early life survival and spawner-recruit relationships) to form a general theory of age-structured models, most commonly referred to as Leslie matrix models. We give stationarity and stability properties and describe situations where behavior is similar to simpler population models. Extensions of the Leslie matrix model include stochastic and continuous models.

In chapter 8, we return to estimation of population parameters, this time for age-structured data. Estimators of age composition from length data and from sampling catches are derived. A theory of catch-age relationships leads to analytical methods well used in stock assessment, including catch-curve, cohort analysis, and catch-age (or age-structured) analysis. These methods are the primary ones used in stock assessment for populations with age-specific data. Included in this chapter is the estimation of natural mortality, a fundamental parameter in many population models in previous and later chapters. We present it here because some of the techniques use methods in this chapter.

For many fish populations, age information is not available, but length information is. In chapter 9, we review length-based methods for modeling and estimation of population parameters. These models require specification of the conversion from length to age to follow year-classes throughout their lifetime. Two approaches are described: use of the growth transition matrix and incorporation of a stochastic growth model.

Spatial structure is the focus of chapter 10. As many fishes exhibit movement or migration at some stage of their lives, methods for estimating such movement and incorporating into population models are developed. A specific application of movement models to salmonlike populations where fish return during a season, called run reconstruction, allows estimation of abundance and related parameters. An alternative method of apportionment to geographic areas is described based on surveys of relative abundance. The extension of per-recruit methods from chapter 6 to migratory populations is also presented.

Finally, we summarize approaches for determining optimal harvesting strategies in chapter 11. We review approaches that have been used to quantitatively describe and evaluate such policies and describe optimization methods in terms of biology and harvest control. We summarize various biological reference points derived from population parameters that have been and can be used to determine biological limits on harvesting. We introduce the quantification of risk and uncertainty, a major research forefront at this time, and describe the concept of adaptive management as a paradigm for optimal harvesting. Necessarily, our coverage of optimal harvesting is limited to an overview. Much research has been devoted to this topic and many books have been and probably will be written on the subject.

Several people reviewed portions of this book, and we are grateful for their constructive and helpful remarks. First, we thank our students who were subjected to this material in various forms and stages. Second, we thank our colleagues Alejandro Anganuzzi, Milo Adkison, Bill Bayliff, Nic Bax, Jeremy Collie, David Evans, Steve Fleischman, Ian Fletcher, Chris Francis, Caihong Fu, Michio Fukushima, Vince Gallucci, Hal Geiger, Wayne Getz, Geoff Gordon, Jim Joseph, Peter Hagen, Jon Heifetz, Ray Hilborn, Larry Jacobsen, Roger Knight, Don MacCaughran, Bob Marshall, Ole Mathisen, Jim Nance, Ana Parma, Gregg Rosenkranz, Keith Sainsbury, Alastair Scott, George Seber, Jeff Short, Mike Sigler, Tony Smith, Pat Sullivan, Clive Turnbull, Carl Walters, and Ralf Yorque. These people reviewed drafts, provided logistic support, gave us insight, and/or offered encouragement and sympathy as we struggled to complete this book. Third, we acknowledge the support of our institutions, the School of Fisheries and Ocean Sciences of the University of Alaska Fairbanks and the Inter-American Tropical Tuna Commission. Finally, we thank Kirk Jensen, Lisa Stallings, Don Jackson, and their colleagues at Oxford for carefully shepherding this book to completion.

Juneau, Alaska
La Jolla, California
November, 1997

T.J.Q. II
R.B.D.

Contents

1. Population Growth, Mortality, and the Fishing Process 1
 - 1.1 Simple Population Growth Models 1
 - 1.1.1. *The Geometric and Exponential Growth Laws* 1
 - 1.1.2. *The Logistic Model* 4
 - 1.1.3. *Time-Varying Parameters* 6
 - 1.1.4. *Multispecies Extensions* 9
 - 1.2 Theory of Mortality 10
 - 1.2.1. *Deterministic Theory of Fishing* 11
 - 1.2.2. *Stochastic Theory of Fishing* 13
 - 1.3. Catch-per-unit-effort and the Fishing Process 15
 - 1.3.1. *Regional Considerations* 17
 - 1.3.2. *Standardization and Gear Selectivity* 18
 - 1.3.3. *Sampling for Catch and Effort* 25
 - 1.3.4. *More Complex Models* 28
 - 1.3.5. *Schooling and Search* 36
 - 1.3.6. *Effects of Catchability Differing Between Individuals* 40
 - 1.3.7. *Stochastic Fishing Models* 42
2. Stock Productivity and Surplus Production 50
 - 2.1. Theory of Stock Productivity 50
 - 2.1.1. *Graham-Schaefer Model* 52
 - 2.1.2. *Pella-Tomlinson Model* 56
 - 2.1.3. *Gompertz-Fox Model* 61
 - 2.1.4. *Fletcher Quadratic Model* 62
 - 2.1.5. *Threshold Models* 64
 - 2.1.6. *Models with Environmental Variables* 66
 - 2.2. Parameter Estimation 66
 - 2.2.1. *Annual Surplus Production* 67
 - 2.2.2. *Surplus Production–Biomass Relationship* 68
 - 2.2.3. *Recruitment Adjustment* 71
 - 2.2.4. *Surplus Production–Fishing Effort Relationship* 72
 - 2.2.5. *Equilibrium Approximation* 73
 - 2.2.6. *Schnute’s Nonequilibrium Method* 74
 - 2.2.7. *Difference Equations for Surplus Production* 75
 - 2.2.8. *Prager’s Nonequilibrium Method* 77

2.2.9. <i>Example</i>	78
2.3. Relation of Surplus Production to Recruitment, Growth, and Natural Mortality	82
3. Stock and Recruitment	86
3.1. Spawner-Recruit Models	86
3.1.1. <i>Beverton-Holt</i>	87
3.1.2. <i>Ricker</i>	89
3.1.3. <i>Cushing</i>	93
3.1.4. <i>Deriso-Schnute</i>	93
3.1.5. <i>Shepherd</i>	96
3.1.6. <i>Gamma</i>	97
3.1.7. <i>Miscellany</i>	98
3.2. Parameter Estimation	100
3.2.1. <i>Linear Regression Approach</i>	100
3.2.2. <i>Nonlinear Regression Approach</i>	103
3.2.3. <i>Measurement Error Approach</i>	108
3.2.4. <i>Autocorrelated Errors</i>	117
3.3. Dynamics for Semelparous Populations	117
3.4. Bayesian Considerations	124
4. Growth and Fecundity	128
4.1. Weight-Length Models	129
4.2. LVB Growth Model	132
4.2.1. <i>Length-Age</i>	132
4.2.2. <i>Difference Equation for Weight-Age</i>	139
4.2.3. <i>Combining Weight-Length and Length-Age Models</i>	139
4.3. Size-Age Models	143
4.3.1. <i>Allometric Model</i>	143
4.3.2. <i>Ad hoc Models</i>	143
4.3.3. <i>Gompertz Growth Model</i>	145
4.3.4. <i>Verhulst and Richards Growth Models</i>	147
4.3.5. <i>Schnute Growth Model</i>	148
4.3.6. <i>Schnute-Richards Growth Model</i>	154
4.4. Mark-Recapture Data	155
4.4.1. <i>Elapsed Time Models</i>	155
4.4.2. <i>Models with Aging Data</i>	162
4.5. Comparison of Growth Models	164
4.5.1. <i>Choosing the Best Model</i>	164
4.5.2. <i>Comparing Different Data Sets</i>	165
4.6. Scale and Otolith Measurements	180
4.7. Variation in Growth	182
4.7.1. <i>Seasonal Growth</i>	183
4.7.2. <i>Individual Variation in Growth</i>	184
4.7.3. <i>Stochastic Growth</i>	191
4.7.4. <i>Comparison</i>	197
4.8. Fecundity and Maturity	200

4.8.1. <i>Maturity</i>	200
4.8.2. <i>Fecundity</i>	202
4.8.3. <i>Population Statistics and the Egg Production Method</i>	204
5. Delay-Difference Models	208
5.1. Allen-Clark Abundance Models	208
5.2. Deriso-Schnute Biomass Models	212
5.2.1. <i>Deriso's Model</i>	212
5.2.2. <i>Schnute's Extension</i>	215
5.2.3. <i>Moments of the Weight Distribution of Adults</i>	216
5.3. Alternative Models and Representations	218
5.3.1. <i>Use of a Net Growth Parameter</i>	218
5.3.2. <i>Horbory's Approach</i>	218
5.3.3. <i>Some Generalizations</i>	220
5.3.4. <i>Mortality Models</i>	220
5.3.5. <i>Stock Reduction Analysis</i>	223
5.4. Parameter Estimation	224
5.4.1. <i>Measurement Error Model</i>	224
5.4.2. <i>Process Error Model</i>	226
5.4.3. <i>Combined Measurement and Process Error Model</i>	231
5.4.4. <i>Kalman Filters</i>	235
6. Age-structured Models: Per-Recruit and Year-Class Models	239
6.1. Beverton-Holt Models	241
6.1.1. <i>LVB Isometric Weight-Age Model</i>	244
6.1.2. <i>LVB Allometric Weight-Age Model</i>	248
6.1.3. <i>Brody-LVB Weight-Age Model</i>	248
6.2. Stochastic Model with Recruitment by Size Group	249
6.3. Generic Per-Recruit Models	255
6.4. Spawning Stock and Egg Production per Recruit	258
6.4.1. <i>Beverton-Holt Approach</i>	259
6.4.2. <i>Generic Approach</i>	260
6.4.3. <i>Effects of Harvesting</i>	261
6.5. Model Variations	263
6.5.1. <i>Discard Mortality</i>	263
6.5.2. <i>Trophy Fish and Slot Limits</i>	264
6.5.3. <i>Per-Recruit Models by Sex</i>	265
6.5.4. <i>Per-Recruit Models by Multispecies and Multiple Fisheries</i>	266
7. Age-structured Models: Renewal Theory	268
7.1. Leslie Matrix Discrete Model	268
7.2. Time-varying Linear Matrix Models	278
7.3. Stochastic Linear Matrix Models	279
7.4. Nonlinear Discrete Leslie-type Models	284
7.5. Forecasting	290
7.6. Continuous Linear Models	292

8. Catch-age and Age-structured Assessment Methods 295
 - 8.1. Estimation of Age Composition 295
 - 8.1.1. *Length Frequency Analysis* 295
 - 8.1.2. *Simple Random Sampling* 301
 - 8.1.3. *Estimating the Catch* 302
 - 8.1.4. *Two-Stage Random Sampling* 303
 - 8.1.5. *Sample Size Considerations* 306
 - 8.1.6. *Separate Length and Age Samples and Other Approaches* 311
 - 8.2. Estimation of Abundance and Population Parameters 317
 - 8.2.1. *General Catch-Age Relationship* 317
 - 8.2.2. *Catch Curve Analysis* 319
 - 8.2.3. *Virtual Population Analysis and Cohort Analysis* 323
 - 8.2.4. *Relative Abundance Analysis* 330
 - 8.2.5. *Catch-Age Analysis with Auxiliary Information* 333
 - 8.2.6. *Stratified Catch-Age Analysis* 349
 - 8.2.7. *Miscellaneous Alternative Approaches* 350
 - 8.2.8. *Computer Programs* 355
 - 8.3. Estimation of Natural Mortality 355
 - 8.3.1. *Catch Curve Analysis* 357
 - 8.3.2. *LFA and Related Analyses* 357
 - 8.3.3. *Mark-recapture Experiments* 358
 - 8.3.4. *Collection of Dead Organisms* 360
 - 8.3.5. *Use of Population Models; Multispecies VPA* 360
 - 8.3.6. *Life-History or Meta-analysis* 360
9. Size-structured Models and Assessment Methods 363
 - 9.1. Basic Models 364
 - 9.1.1. *Beverton-Holt Approach* 364
 - 9.1.2. *Basic Size-based Models* 368
 - 9.2. Stage-structured Matrix Models 369
 - 9.3. Stochastic Models 372
 - 9.4. Length-based Assessment Methods 380
 - 9.4.1. *Length Cohort Analysis* 380
 - 9.4.2. *Catch-Length Analysis and Length-Based Stock Synthesis Analysis* 382
10. Migration, Movement, and Other Spatiotemporal Considerations 398
 - 10.1. Population Models 399
 - 10.1.1. *Deterministic Model, Non-Age-structured Populations* 399
 - 10.1.2. *Stochastic Model, Non-Age-structured Populations* 404
 - 10.1.3. *Age-structured Populations* 407
 - 10.2. Estimation of Migration 412
 - 10.2.1. *Darroch's Method and Extensions* 412
 - 10.2.2. *Hilborn's Method and Extensions* 414
 - 10.2.3. *Miscellaneous Methods* 419
 - 10.3. Migratory Cohort and Catch-Age Analyses 421
 - 10.3.1. *Migratory Cohort Analysis* 421

10.3.2. <i>Migratory Catch-Age Analysis</i>	423
10.4. Run Reconstruction	428
10.5. Geographic Apportionment	432
10.6. Migratory Per-Recruit Analyses	434
11. Optimal Harvesting	437
11.1. Harvest Policies and Equilibrium Concepts	438
11.2. Goals, Objectives, and Constraints	442
11.2.1. <i>Stochasticity</i>	446
11.2.2. <i>Bioeconomic Objectives</i>	446
11.3. Optimization Methods	447
11.3.1. <i>Biological Models</i>	448
11.3.2. <i>Fixed-Parameter Harvest Control</i>	449
11.3.3. <i>Time-varying Harvest Control</i>	454
11.4. Biological Reference Points	459
11.4.1. <i>Yield-Effort Parameters</i> F_m and F_{ey}	459
11.4.2. <i>Natural Mortality Parameter</i> M	460
11.4.3. <i>Yield-per-Recruit Parameter</i> F_{\max}	462
11.4.4. <i>Relationships among</i> F_m , F_{\max} , and F_p	464
11.4.5. <i>Yield-per-Recruit Parameter</i> $F_{0.1}$	468
11.4.6. <i>Spawning Population per Recruit Parameters</i> $F_{x\%}$	472
11.4.7. <i>Spawning Population Parameters</i> F_{rep} , F_{med} , F_{low} , F_{high}	474
11.4.8. <i>Age-structured Population Parameter</i> F_{st}	479
11.4.9. <i>Threshold Reference Points</i>	480
11.5. Risk, Uncertainty, and Decision Analysis	482
References	486
Index	517

This page intentionally left blank

QUANTITATIVE FISH DYNAMICS

This page intentionally left blank

Population Growth, Mortality, and the Fishing Process

1.1. SIMPLE POPULATION GROWTH MODELS

Population dynamics is the study of how and why a population changes. Quantitative population dynamics is the mathematical and statistical representation of a population and its changes. To understand the dynamics of a population, principles of biological life history need to be represented by coherent mathematical and statistical expressions.

We use two common mathematical principles to represent change of a population: difference equations (Goldberg 1958) and differential equations (Braun 1983). In a difference equation, time is viewed as an ordinal index at discrete points. In a differential equation, time is used as a continuous variable. In this section, we consider simple models for population size based on minimal biological complexity.

1.1.1. The Geometric and Exponential Growth Laws

Difference equation setting

The simplest model for population growth (or decline) is based on the assumption that a population has a constant ratio of change from one point of time to the next, which can be written

$$\frac{N_{t+1}}{N_t} = R,$$

where R is the constant ratio of change ($R > 0$); t is the discrete time index ($t = 0, 1, 2, \dots$); and N_t is the population abundance at time t . Thus, the population size at any arbitrary time $t + 1$ is a constant multiple (or ratio) of the population at time t , or

$$N_{t+1} = N_t R. \quad (1.1)$$

The population declines geometrically over time to a limiting value of 0 if $R < 1$, remains the same if $R = 1$, and increases geometrically without bound if $R > 1$. For this reason, this model is referred to as the *geometric growth law* (Goldberg 1958).

2 QUANTITATIVE FISH DYNAMICS

Given an initial population size N_0 at $t = 0$, the difference equation (1.1) can be resolved in terms of N_0 , R , and t in the following manner:

$$\begin{aligned} N_1 &= N_0 R \\ N_2 &= N_1 R = N_0 R^2 \\ N_3 &= N_2 R = N_1 R^2 = N_0 R^3 \\ \text{or, in general, } N_t &= N_0 R^t. \end{aligned} \quad (1.2)$$

In this model, the change over any single time period from (1.1) is

$$\Delta N_t = N_{t+1} - N_t = (R - 1)N_t, \quad (1.3)$$

showing that the change in a population is a function of population size itself, a concept used throughout this book. It is convenient to express change in a population on a per capita basis. For the geometric law, the constant per capita change from (1.3) is

$$\Delta N_t / N_t = R - 1.$$

Example 1.1. Cell division

Cell division can be represented with this model with $N_0 = 1$ and $R = 2$, producing the sequence 1, 2, 4, 8, The per capita change is 1 (100%) for each time interval.

■

Example 1.2. Rockfish population decline

Suppose a population of 1024 rockfish loses half its population each year. Then $N_0 = 1024$, $R = \frac{1}{2}$, and the population sequence is 1024, 512, 256, 128, The per capita change is $-\frac{1}{2}$ (-50%) for each year. ■

Example 1.3. English “souls” in North America

Benjamin Franklin (1760, London Chronicle, “Observations concerning the increase of mankind”) supposed that there were a million English “souls” in North America and that the population would double in about 25 years. Setting $N_t = 2N_0$ and $t = 25$ in (1.2), the ratio R is $2^{1/25} = 1.0281$. The per capita change is 0.0281 (2.81%) for each year. The sequence of population sizes over the 25 years can be found by applying (1.2) directly. ■

Thomas Robert Malthus (1798, *Mathematics of Population and Food*) discussed the philosophical implications of geometric growth:

Plants and irrational animals are all impelled by a powerful instinct to the increase of their species and this instinct is interrupted by no doubts about providing for their offspring. Wherever therefore there is liberty, the power of increase is exerted; and the superabundant effects are repressed afterwards by want of room and nourishment.

The growth parameter R is often called the Malthusian parameter (Pollard 1973) due to the impact of his essay.

Differential equation setting

Alternatively, a differential equation setting can be used to model population change. In contrast to the difference equation approach, the focus is on instantaneous change

rather than on interval change, and on the calculus of differentials rather than on the calculus of finite differences. The analogous differential equation can be derived from the difference equation (1.1). From (1.2), population size N_{t+h} for an arbitrary increment, h , as a function of N_t is

$$N_{t+h} = N_0 R^{t+h} = N_0 R^t R^h = N_t R^h. \quad (1.4)$$

Expressing (1.4) as a rate of change yields

$$\frac{\Delta N_t}{\Delta t} \equiv \frac{N_{t+h} - N_t}{(t+h) - t} = N_t \frac{R^h - 1}{h}. \quad (1.5)$$

Using the substitution $R = e^r$, the limit as $h \rightarrow 0$ of (1.5) is

$$\begin{aligned} \frac{dN}{dt} &\equiv \lim_{h \rightarrow 0} \frac{\Delta N_t}{\Delta t} \\ &= \lim_{h \rightarrow 0} \frac{R^h - 1}{h} N_t \\ &= \lim_{h \rightarrow 0} \frac{\frac{d}{dh}(e^{rh} - 1)}{\frac{d}{dh}h} N_t \text{ (using l'Hôpital's Rule)} \\ &= \lim_{h \rightarrow 0} \frac{re^{rh}}{1} N_t \\ \text{or } \frac{dN(t)}{dt} &= rN(t), \end{aligned} \quad (1.6)$$

where the population size $N(t)$ is now a continuous function of a continuous time variable t . In analogy to (1.3), the simplest differential equation is thus based on the assumption that the instantaneous rate of change is proportional to abundance. Parameter r is the instantaneous growth parameter with units of t^{-1} . This equation is a first-order, linear, autonomous, homogenous differential equation. Writing (1.6) as

$$\frac{1}{N} \frac{dN}{dt} = r,$$

the per capita rate of change in the population is constant, equivalent to instantaneous growth parameter r . Given initial condition $N(0) = N_0$, the solution to (1.6) is

$$\begin{aligned} \int_{N_0}^N \frac{dN}{N} &= \int_0^t r dt \\ \ln N - \ln N_0 &= rt \\ N &\equiv N(t) = N_0 e^{rt} = N_0 (e^r)^t. \end{aligned} \quad (1.7)$$

Essentially the difference equation (1.1) and differential equation (1.6) show the same behavior with the conversion between the magnitudes of the parameters accomplished

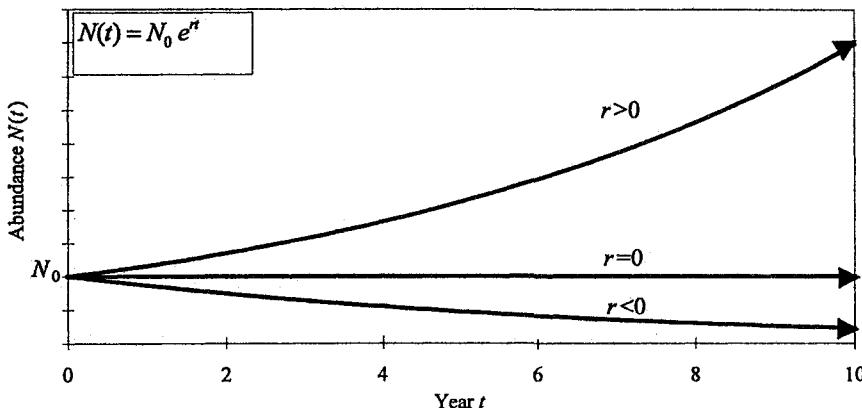


Figure 1.1. Time trajectories of the exponential growth law for population abundance when $r < 0$, $r = 0$, and $r > 0$.

by $R = e^r$. Ricker (1975a, pp. 8–9) gives an intuitive explanation of the meaning of an instantaneous parameter.

The behavior of the solution (1.7) as a function of time is dependent on the magnitude of r . The population decreases exponentially when $r < 0$, stays the same when $r = 0$, and increases exponentially when $r > 0$ (figure 1.1). For this reason, this model is called the *exponential law of population growth (or decline)*.

Example 1.4. Cell division

For example 1.1 with $N_0 = 1$ and $R = 2$, the corresponding magnitude of r in a continuous setting is $\ln(2) = 0.693$. The calculated population size at time $t = 4.5$, say, from (1.7) is $1 \times \exp(0.693 \times 4.5) = 23$ (rounded). However, the actual population size at time 4 is 16 and does not change to 32 until time 5. This example shows the danger of using a continuous model to calculate population size for a model with a discrete time index. ■

Example 1.5. Rockfish population decline

For example 1.2 with $R = \frac{1}{2}$, the corresponding magnitude of r is $\ln\left(\frac{1}{2}\right) = -0.693$. The population size at time $t = 4.5$ is $1024 \times \exp(-0.693 \times 4.5) = 45$ (rounded). ■

Example 1.6. English “souls” in North America

For example 1.3 with $R = 1.0281$, the corresponding magnitude of r is 0.0277. Under the law of exponential growth, the population of English “souls” would reach 250 million when $250 = 1 \times \exp(0.0277t)$ or after $t = 199$ years (rounded). Given initial year 1760, this would have occurred in 1959. An example in Braun (1983, pp. 32–34) modeled the entire U.S. population from 1790 to 1950. The magnitude of r was a similar 0.03134. Starting with a population of 3.929 million in 1790, the population in 1950 would be 592 million. The actual population in 1950 was 151 million, illustrating the deficiency of the exponential model to represent population growth. ■

1.1.2. The Logistic Model

No population can realistically grow without bound to an infinite population size. According to Malthus (1798):

Through the animal and vegetable kingdoms nature has scattered the seeds of life abroad with the most profuse and liberal hand, but has been comparatively sparing in the room and the nourishment necessary to rear them. . . . The race of plants and the race of animals shrink under this great restrictive law; and man cannot by any efforts of reason escape from it.

Malthus further speculated that food growth could increase at most according to an arithmetic progression despite the propensity of species to increase according to a geometric progression.

Food limitations, patterns of disease, space limitations, and inter- and intraspecific competition are some reasons for an upper limit K , called the carrying capacity, to the population. As a population gets closer to K , the slower its growth should be, until at K the growth rate should be 0. The easiest way to incorporate a decrease in growth rate is to include a linear modifying factor $(1 - N/K)$ in (1.6), or

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) = rN - \frac{r}{K}N^2, \quad (1.8)$$

which results in a first-order, quadratic, autonomous, homogeneous differential equation, which is solved in most differential equation texts (e.g., Braun 1983). It was first introduced by Verhulst in 1837. At a population size near 0, the per capita instantaneous rate of change, $r(1 - N/K)$, is approximately equal to r , diminishing to 0 at $N = K$. Its solution is obtained by the method of partial fractions. Note that (1.8) can be resolved as

$$\int_{N_0}^{N(t)} \frac{dN}{N} + \int_{N_0}^{N(t)} \frac{dN}{K - N} = \int_0^t r dt,$$

which results in the final solution, termed the *logistic law of population growth*:

$$N(t) = \frac{N_0 e^{rt}}{1 - \frac{N_0}{K} + \frac{N_0}{K} e^{rt}}. \quad (1.9)$$

The numerator is the same as the exponential law described earlier; the denominator acts as a damping term to regulate the population. Note that at $t = 0$, $N(0) = N_0$, and as $t \rightarrow \infty$, $N(t) \rightarrow K$. The behavior of the logistic curve is sigmoidal for values of $N < K$, constant for $N = K$, and exponentially decreasing for $N > K$ (figure 1.2). The logistic law will be the underlying population model in several subsequent sections.

Example 1.7. U.S. human population

In example 1.6 of the entire U.S. population from 1790 to 1950 (Braun 1983, pp. 32–34), a logistic model was determined, with the magnitude of r being 0.03134 and the value of K being 197 million. Starting with a population of 3.929 million in 1790, the predicted population size in 1950 is 149 million. The actual population in 1950 was 151 million, illustrating the good approximation of the logistic model to represent population growth. According to the model, the U.S. reached half its carrying capacity in 1913. ■

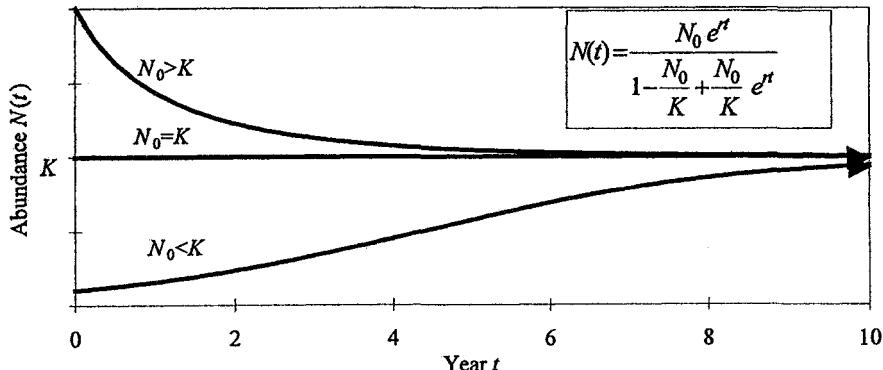


Figure 1.2. Time trajectories of the logistic growth law for population abundance when $N_0 < K$, $N_0 = K$, and $N_0 > K$.

Example 1.8. Solving for r and K

At times 10, 20, and 30, the sizes of a population that obeys the logistic law are 100, 150, and 175. In (1.9), the term t is replaced with $(t - 10)$ so that N_0 is the population size at time 10, which is 100. For the other two times, substitution of values into (1.9) yields

$$N(20) = 150 = \frac{100e^{r(20-10)}}{1 - 100/K + 100/Ke^{r(20-10)}}$$

$$\text{and } N(30) = 175 = \frac{100e^{r(30-10)}}{1 - 100/K + 100/Ke^{r(30-10)}},$$

which are two transcendental equations in two unknowns r and K . Either by trial-and-error or by solving these nonlinear equations with numerical methods, the solutions are $r = 0.125$ and $K = 188$. The extrapolated population size at time 0 from (1.9) and these parameter values is 46. ■

1.1.3. Time-Varying Parameters

Levins (1969) developed several extensions to the basic logistic model. Two important cases are when r is a function of time, say $r(t)$, and when K is a function of time, say $K(t)$. These cases provide additional biological realism for populations with seasonal variations or trends over time in conditions such as food supply or habitat. Levins derived the solutions for when only one of the parameters was time-varying. The general solution to the case when both r and K are functions of time can be derived (R.I. Fletcher, personal communication, 1990), as we now show. Let

$$r(t) = \text{intrinsic rate of increase as a function of time } t$$

$$s(t) = \int_0^t r(x) dx$$

$$K(t) = \text{carrying capacity as a function of time } t$$

$$g(t) = -r(t)/K(t)$$

$$y = 1/N$$

$$dN = -y^{-2} dy.$$

From (1.8) the differential equation with time-varying r and K is

$$\frac{dN}{dt} = r(t)N \left[1 - \frac{N}{K(t)} \right] = r(t)N + g(t)N^2. \quad (1.10)$$

If the change of variables from N to y is made, then (1.10) becomes

$$\begin{aligned} -y^{-2} \frac{dy}{dt} &= r(t)y^{-1} + g(t)y^{-2} \\ \text{or } \frac{dy}{dt} &= -r(t)y - g(t), \end{aligned} \quad (1.11)$$

which is the linear nonhomogeneous Bernoulli equation (Braun 1983). The general solution of (1.11) is

$$y = y_0 e^{-s(t)} - \left[e^{-s(t)} \int_0^t e^{s(x)} g(x) dx \right], \quad (1.12)$$

where y_0 is the initial condition at $t = 0$. Substituting in the original variables N and $K(t)$, (1.12) becomes

$$\begin{aligned} \frac{1}{N} &= \frac{1}{N_0} e^{-s(t)} + \left[e^{-s(t)} \int_0^t e^{s(x)} \frac{r(x)}{K(x)} dx \right] \\ \text{or } N &= \frac{N_0 e^{s(t)}}{1 + N_0 \int_0^t \frac{r(x) e^{s(x)}}{K(x)} dx}. \end{aligned} \quad (1.13)$$

If only r is a function of t (that is, K is constant), then the solution from (1.13) is

$$N(t) = \frac{N_0 e^{s(t)}}{1 - \frac{N_0}{K} + \frac{N_0}{K} e^{s(t)}}, \quad (1.14)$$

which is quite similar to the simple logistic solution (1.9).

If only K is a function of t (that is, r is constant), then the solution to this special case from (1.13) with $s(t) = rt$ is

$$N(t) = \frac{N_0 e^{rt}}{1 + r N_0 \int_0^t \frac{e^{rx}}{K(x)} dx}, \quad (1.15)$$

which corrects an error in (21) of Levins (1969). Inspection of (1.15) reveals that the effect of varying carrying capacity on abundance is as a weighted harmonic mean of previous carrying capacities $K(x)$, with the most recent carrying capacities having the greatest weights (e^{rx}).

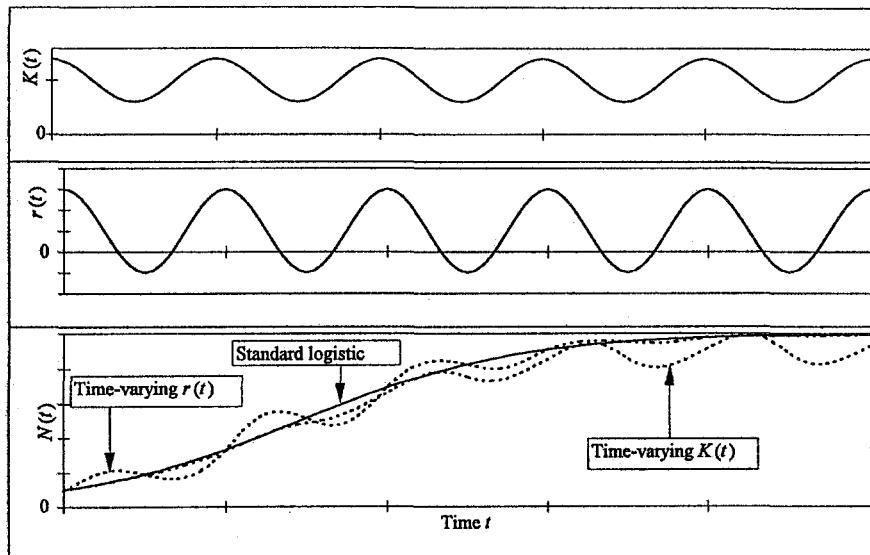


Figure 1.3. Time trajectories of the logistic growth laws for population abundance with time-varying intrinsic growth parameter $r(t)$ or carrying capacity $K(t)$. Each variation follows a sinusoidal function, as depicted in the upper panels. The standard logistic growth law with constant r and K is also shown for comparison.

Examples of varying either r or K in a sinusoidal manner are shown in figure 1.3, using (1.14) and (1.15). The integrals in (1.14) and (1.15) were evaluated numerically using Simpson's rule (Kennedy and Gentle 1980, pp. 87–88), although the constant K case can be resolved in closed form. Variations in r induce large effects on N when N is small. Variations in K induce large effects on N when N nears K .

Levins (1969) also considered the effect of stochastic variation on the exponential and logistic population models by adding a random error term to the respective differential equations and by letting r and K be random variables. For the exponential model, introduction of random error resulted in a left-skewed distribution of abundance and a higher expected population size. Random variation in r resulted in a lognormal distribution for abundance and a higher expected population size. For the logistic model, the introduction of random error resulted in a bimodal distribution, with values clustered near 0 and between $K/2$ and K . Variation in r resulted in either a bimodal or unimodal distribution, depending on the average value of r and the amount of random variation. Variation in K reduced the expected population size, which depended on the most recent values of K .

Rotenberg (1987) developed an extension of the logistic law with fluctuating carrying capacity that has a different intrinsic rate of increase when the population is above carrying capacity. Carrying capacity is modeled as a stochastic variable, such as uniform or normal, and the amount of time each carrying capacity is in effect is also stochastic, modeled as a Poisson variable. When such a population is harvested, population levels and harvest yields vary widely depending on the amount of fluctuation in carrying capacity, the time between environmental changes, and reproduction rates.

1.1.4. Multispecies Extensions

The ecological basis of the logistic model is that individuals of a species compete for limited resources, which results in increasing diminution of population growth rate with increasing population size. As summarized by Pianka (1974), the logistic law can be extended to incorporate a variety of similar ecological relationships between species. Competition between two species i and j is one such relationship, which can be symbolized as $(-, -)$, where species i has a negative effect on species j , and species j has a negative effect on species i . Some other ecological relationships and their symbols include predator-prey or parasite-host $(+, -)$, mutualism or protocooperation $(+, +)$, commensalism $(+, 0)$, and amensalism $(-, 0)$, where $+$ denotes a positive effect and 0 denotes no effect.

For a community of n species, let N_i be the abundance of species i ; r_i be the intrinsic rate of increase parameter for species i ; K_i be the carrying capacity parameter for species i ; and α_{ij} be the interaction parameter for the negative effect of species j on species i . The extension of the logistic for each species i from Pianka (1974) is then

$$\frac{dN_i}{dt} = r_i N_i \left(\frac{K_i - N_i - \sum_{j \neq i}^n \alpha_{ij} N_j}{K_i} \right). \quad (1.16)$$

This system of equations (1.16) is a special case of the more general quadratic form known as the Lotka-Volterra system, named after two scientists who independently developed these types of equations starting in the 1920s. As written, these equations pertain directly to the ecological notion of competition. Holding other species, j , constant and setting (1.16) to 0, equilibrium for species i is achieved at population level $N_i^* = K_i - \sum_{j \neq i}^n \alpha_{ij} N_j$, showing that the effect of competition is to lower equilibrium abundance below the carrying capacity of each species. Phase-plane analysis (see Pianka 1974) can be used to find joint equilibrium solutions and to determine direction of population change at different levels of each species.

This same system (1.16) can be used for predator-prey relationships, either by redefining α_{ij} to be positive for the predator population, i , or by replacing the negative sign in the equation with a positive sign. Frequently, the increase in a predator population is thought to be due exclusively to its predation of prey; hence the interaction term would be used in place of the intrinsic rate of increase term. Similar considerations apply to other ecological interactions. Further development and explanation of these models appears in the ecological literature; see Pianka (1974), May (1973), and Murray (1989).

Multispecies models are used further in later chapters, when needed to develop a particular model or to extend a particular method to a situation where species interactions are important. Generally, multispecies models have been used to explore interactions among species within an ecosystem and to tie together information from bioenergetics and food habits studies (e.g., Anderson and Ursin 1977, Laevastu and Larkins 1981). However, such models have generally had poor predictive capabilities and are rarely used for stock assessment and fisheries management. The reasons for this are complex, but perhaps the major difficulties are (1) the estimation of the interaction parameters, α_{ij} , due to high natural variability in the ecosystem, (2) several possible competing hypotheses to explain observations of population responses, and (3) uncertainty about the functional relationship between the various species.

1.2. THEORY OF MORTALITY

Most fish populations are composed of fish of different ages. A year-class, or cohort, of fish is defined as a group of fish that were spawned in the same year. Thus, the 1988 year-class is the group of fish at age 0 in 1988, age 1 in 1989, and so on. In this section, we treat age 0 as a reference age representing the first age at which the assumptions of the model are valid; the corresponding transformation to actual age should be implicitly understood.

An age-structured population model follows a year-class of fish through its life, rather than following a population over time as in section 1.1. Because time passes as year-classes age, there is a deliberate mixing of time and age in this section. In chapter 8, we derive the appropriate equations in terms of both time and age. Nevertheless, the following development also applies to a multiple age-structured population over a period of time when there is no recruitment of new fish and if parameters are constant for all individuals during the time period.

A guiding principle of year-class dynamics is that the abundance of a year-class decreases as it ages due to mortality. The following development of the mortality process is motivated from one in the classic handbook by Ricker (1975a). Let N_0 be the number of individuals in the year-class at age 0; $N(t)$ be the number of individuals in the year-class at age t ; Z be the instantaneous total mortality (units of t^{-1}); A be the annual death fraction; and S be the annual survival fraction. Initially it is assumed that instantaneous mortality Z is constant for all individuals and ages. Treating mortality as negative population growth, the differential equation for year-class size from (1.6) is then

$$\frac{dN}{dt} = -ZN, \quad (1.17)$$

where $N(0) = N_0$. The solution to (1.17) is

$$N(t) = N_0 e^{-Zt}, \quad (1.18)$$

showing that year-class abundance decreases exponentially over age under constant instantaneous mortality. After one year of life, year-class size is $N(1) = N_0 \exp(-Z)$. Hence the survival fraction over one year is the ratio of year-class abundances, or

$$S = \exp(-Z).$$

The annual death fraction, A , is the proportion of the starting population that dies, or

$$A = 1 - S = 1 - \exp(-Z).$$

For small Z , the approximation $A \approx Z$ is sometimes used. For example, if $Z = 0.10$, then $A = 0.095$. To convert from survival to instantaneous mortality,

$$Z = -\ln(1 - A) = -\ln(S).$$

This simple model is unrealistic for most fish populations across all ages because mortality changes as a function of age, being highest during the first year of life. To allow for differing mortalities as a function of age, let Z_x be the instantaneous mortality

at age x , starting at age 0. Each mortality, Z_x , is assumed constant for that age. The same equations presented above are used in this situation by subscripting the parameters Z , S , and A by x . Considering the start of each age in sequence, population sizes are

$$\begin{aligned} N_1 &= N_0 S_0 = N_0 \exp(-Z_0), \\ N_2 &= N_1 S_1 = N_0 S_0 S_1 = N_0 \exp[-(Z_0 + Z_1)], \\ N_t &= N_{t-1} S_{t-1} = N_0 \prod_{x=0}^{t-1} S_x = N_0 \exp \left[- \left(\sum_{x=0}^{t-1} Z_x \right) \right]. \end{aligned}$$

Cumulative survival up to the start of age t is $\prod_{x=0}^{t-1} S_x$, and cumulative instantaneous mortality is $\sum_{x=0}^{t-1} Z_x$. Note that annual rates of survival multiply to obtain cumulative survival, while instantaneous mortalities add to obtain cumulative instantaneous mortality. To find population size at some fraction of a year τ , (1.18) can be applied with N_0 redefined to be N_t ; hence

$$N(t + \tau) = N_t e^{-Z_t \tau}.$$

Example 1.9. Archetypal fish population

Consider a fish population with annual survivals $S_0 = 1 \times 10^{-6}$, $S_1 = 0.1$, $S_2 = 0.2$, $S_3 = 0.5$, and $S_4 = 0.9$. From the relationship $Z = -\ln(S)$, the corresponding instantaneous mortalities are $Z_0 = 13.82$, $Z_1 = 2.30$, $Z_2 = 1.61$, $Z_3 = 0.69$, and $Z_4 = 0.11$. Cumulative survival ($\prod S$), the product of the individual survivals, is 0.9×10^{-8} . Cumulative instantaneous mortality, the sum of the individual mortalities, is 18.53. Also note that $-\ln(\prod S) = 18.53$, showing that the relationship for individual survival and mortality also applies to cumulative survival and mortality. In order to have survivors, the number of eggs, N_0 , would have to be at least $1/(\prod S) = 1.1 \times 10^8$, >100 million eggs. This magnitude or greater is common for actual fish populations. For example, one large Pacific halibut can spawn >4 million eggs annually (Schmitt and Skud 1978), and its female population is on the order of millions. ■

1.2.1. Deterministic Theory of Fishing

For fish populations subjected to harvesting, total mortality is composed of mortality due to harvesting and mortality due to natural causes. Let F be the instantaneous fishing mortality; M be the instantaneous natural mortality; C be the catch (removals due to fishing); D be natural deaths (removals due to natural causes); and $T = C + D$ = total removals. Consider a year-class at that stage of life where instantaneous natural mortality M and instantaneous fishing mortality F are constant and assumed to operate concurrently and continuously, so that $Z = F + M$. Year-class size from (1.18) is then

$$N(t) = N_0 e^{-Zt} = N_0 e^{-(F+M)t}. \quad (1.19)$$

The corresponding differential equation,

$$\frac{dN}{dt} = -FN - MN, \quad (1.20)$$

is made up of the term FN to represent the rate of removals due to fishing and the term MN to represent the rate of removals due to natural causes. The catch rate is then

$$\frac{dC}{dt} = FN. \quad (1.21)$$

Similarly, the death rate due to natural causes is

$$\frac{dD}{dt} = MN.$$

Since $T = C + D$, the differential equation (1.20) can also be written

$$\frac{dN}{dt} = -\frac{dT}{dt} = -\left(\frac{dC}{dt} + \frac{dD}{dt}\right).$$

Integrating (1.21) over ages 0 to τ yields

$$\int_0^C dC = \int_0^\tau FN_0 e^{-Zt} dt$$

$$\text{or } C = \frac{F}{Z} N_0 \left(1 - e^{-Z\tau}\right). \quad (1.22)$$

Equation (1.22) is known as the Baranov catch equation, after the Russian scientist who derived it in the 1910s (Ricker 1975a).

For one year of aging,

$$C = \frac{F}{Z} N_0 \left(1 - e^{-Z}\right)$$

$$= \frac{F}{Z} N_0 A, \quad (1.23)$$

showing that the proportion of total deaths ($T = N_0 A$) due to fishing is F/Z . Similarly, the proportion of total deaths, T , due to natural causes is M/Z , and the number of deaths, D , due to natural causes is

$$D = \frac{M}{Z} N_0 A. \quad (1.24)$$

Further simplification of (1.22) occurs by considering average year-class size over a period of time. Define the integral average of a function $X(t)$ over the ages t_1 to t_2 as

$$\bar{X} = \int_{t_1}^{t_2} X(t) dt / (t_2 - t_1),$$

which is equivalent to the area under the curve, $X(t)$, divided by its length. For $X(t) = N(t)$, the integral average over ages 0 to τ is

$$\bar{N} = N_0 \left(1 - e^{-Z\tau}\right) / (Z\tau). \quad (1.25)$$

Comparing (1.22) and (1.25),

$$\frac{C}{\tau} = F\bar{N}, \quad (1.26)$$

showing that the catch over time period τ is proportional to instantaneous fishing mortality and average abundance during the interval of fishing. The term τ is necessary to reconcile the dimension of numbers per time in the equation. Using the usual time period of one year, (1.26) becomes

$$C = F\bar{N}. \quad (1.27)$$

This fundamental relationship will reappear frequently in later sections. These equations can be easily generalized for varying mortality among ages by considering time periods of one year and subscripting F and M by age (see chapter 8).

Example 1.10. Hypothetical fish population

Suppose that a population of 1000 individuals is subject to fishing mortality $F = 0.4$ and natural mortality $M = 0.2$ for a period of two years. Annual survival is $S = 0.549$, and the annual death fraction is $A = 0.451$. The proportion of deaths due to fishing is $\frac{F}{Z} = \frac{2}{3}$. Hence, the first year's catch is $C = 1000 \times 0.451 \times \frac{2}{3} = 301$, and the deaths due to natural causes is $D = 150$, resulting in total deaths $T = 451$ and a resulting population of 549. Average population abundance, \bar{N} , in the first year from (1.25) is $451/0.6 = 752$. From (1.27), a calculated catch of $0.4 \times 752 = 301$ agrees with the above. For the second year, the above calculations can be repeated with a starting population of 549, resulting in a catch of 165 and 83 natural deaths, for a total of 248 deaths and a resulting population of 301. The total catch over the two-year period summed from above is 466, which can also be obtained from (1.22) or (1.26) with $\tau = 2$. ■

Alternative formulations of competing sources of mortality can also be constructed. If instantaneous fishing or natural mortality occurs during only part of the year, piece-meal integration of the corresponding differential equations can be performed. For example, if fishing only occurs during the last half of a year, then the year-class size for a starting number N_0 and any time up to the middle of the year is $N_0 \exp(-Mt)$. In the last half of the year, it is $N_0 \exp(-\frac{1}{2}M) \exp[-Z(t - \frac{1}{2})]$.

In some cases, fishing occurs over such a short interval that it can be considered a pulse of removals. In this case, a differential equation is inappropriate. Suppose that all fishing occurs at the exact middle of the year. Then the year-class size is $N_0 \exp(-Mt)$ up to the middle of the year, $N_0 \exp(-\frac{1}{2}M) - C$ at the middle of the year, and $[N_0 \exp(-\frac{1}{2}M) - C] \exp[-M(t - \frac{1}{2})]$ for the last half of the year.

1.2.2. Stochastic Theory of Fishing

The deterministic theory of fishing presumes that there is no variability in catch for given levels of instantaneous fishing mortality, natural mortality, and initial population size. In reality, catches vary considerably due to the complex interactions that occur in the catching process and the underlying dynamics of a given population. A more realistic model would therefore incorporate variability into the mortality process.

The theory of stochastic processes (e.g., Parzen 1962, Chiang 1968), which incorporates such variability, has been used by Dupont (1983) and Sampson (1988a) to incorporate variability into the catch process and to provide alternative methods of

estimating abundance. The following derivation is based upon their approaches. As in the deterministic model, a single year-class is followed throughout its life, and time and age are used interchangeably.

Assumptions for a simple death process with fishing and natural death as the two sources of mortality are:

1. The probability of a fish being caught in the time interval $[t, t + \Delta t]$ is $\lambda(t)\Delta t + o(\Delta t)$, where $o(\Delta t)$ is a small deviation, such that $o(\Delta t)/\Delta t \rightarrow 0$ as $\Delta t \rightarrow 0$.
2. The probability of a fish dying from natural causes in the time interval $[t, t + \Delta t]$ is $\mu(t)\Delta t + o(\Delta t)$.
3. The probability of more than one fish dying in the time interval $[t, t + \Delta t]$ is $o(\Delta t)$.
4. There is no immigration, recruitment, or emigration from the population.

The terms $\lambda(t)$ and $\mu(t)$ correspond to F and M in the deterministic model but are allowed to be functions of time for greater generality. Let the initial year-class size at time 0 be N_0 and the year-class size at time t be $N(t)$. Consider the year-class over different periods of its life indexed by j , representing the interval $[t_j, t_{j+1}]$. From the above assumptions, the probability that an individual of the initial year-class is alive at time t is

$$r(t) = \exp \left[- \int_{t_0}^t (\lambda(x) + \mu(x)) dx \right],$$

and the probability that an individual is caught in the j th interval is

$$p_j = \int_{t_j}^{t_{j+1}} \lambda(t)r(t)dt.$$

The overall probability of an individual being caught during its lifetime is $p = \sum p_j$, and the probability of not being caught is $q = 1 - p$. From Dupont (1983), the probability of obtaining the catch distribution $\{C_j\}$ follows the multinomial distribution

$$P(\{C_j\}) = \binom{N_0}{C_1 C_2 \dots} \prod p_j^{C_j} q^{N_0 - \sum C_j}. \quad (1.28)$$

The expected value of catch in the j th interval is

$$E(C_j) = N_0 p_j \quad (1.29)$$

with variance

$$V(C_j) = N_0 p_j (1 - p_j) \quad (1.30)$$

and covariance

$$\text{cov}(C_j, C_k) = -N_0 p_j p_k. \quad (1.31)$$

Similarly, the number of individuals, $N(t)$, at time t follows a binomial distribution

$$P[N(t)] = \binom{N_0}{N(t)} r(t)^{N(t)} [1 - r(t)]^{N_0 - N(t)}. \quad (1.32)$$

The expected value of $N(t)$ is

$$E[N(t)] = N_0 r(t) \quad (1.33)$$

with variance

$$V[N(t)] = N_0 r(t)[1 - r(t)]. \quad (1.34)$$

Substituting $\lambda(t) = F$ and $\mu(t) = M$ into these equations produces the analogous equations for expected values of catch and abundance as obtained for deterministic values of catch and abundance in section 1.2.1. Dupont (1983) generalized the above treatment to include multiple year-classes and derived maximum likelihood estimators for abundance and mortality parameters. He also considered more complicated, realistic functions for $\lambda(t)$ and $\mu(t)$. Sampson (1988a) developed more complicated, realistic stochastic models which include migration, groups of animals, handling times, and multiple fishing operations. Further consideration of stochastic models of the fishing process is given in section 1.3.7.

Example 1.11. Hypothetical fish population

Consider the population from example 1.10 of 1000 individuals subject to fishing mortality $F = 0.4$ and natural mortality of $M = 0.2$. With mortality as a stochastic process, the expected values of catch and abundance after the first year from (1.29) and (1.33) are 301 and 549, respectively, which are the same as the deterministic values. Square roots of the variances from (1.30) and (1.34) are 15 and 16; 95% of the catches and abundances obtained from replications of this stochastic model should occur within 1.96 times these values. For catch, this interval is (271, 331); for abundance, this interval is (517, 581). Similar results can be obtained for other times. The key point is that catch and abundance are both considered to be realizations of random processes. ■

1.3. CATCH-PER-UNIT-EFFORT AND THE FISHING PROCESS

Because catch is the product of fishing mortality and abundance in (1.27), trends in catch over time may reflect changes in fishing mortality, changes in abundance, or both. Further information from a fishery is required to separate these confounded effects. Let

E = fishing effort over a time period τ

$U = \frac{C}{E}$ = the catch-per-unit-effort

q = catchability coefficient

a = amount of area fished by the gear

A = amount of area occupied by the population

$D = \frac{N}{A}$ = the population density (number per unit area).

Suppose that the fishing effort, E , from a fishery is known. Fishing effort may be measured by the number of vessels, number of fishers, amount of time, number of hooks, or other measurable variables. Considerable energy has been applied by fisheries researchers to develop reliable measures of fishing effort; consult Gulland (1983), Skud and Hamley (1978), and Ricker (1975a) for examples.

16 QUANTITATIVE FISH DYNAMICS

Assume that each unit of fishing effort operates independently and additively. The instantaneous change in catch would then be proportional to fishing effort per unit time and abundance, or

$$\frac{dC}{dt} = q \frac{dE}{dt} N, \quad (1.35)$$

where the catchability coefficient, q , has units of (effort units) $^{-1}$. Seber (1982) gave an alternative stochastic model with a parameter similar to q representing the probability of catching a fish with one unit of effort. Comparing (1.35) with (1.21), it follows that

$$F dt = q dE.$$

Assuming from time 0 to time τ that effort goes from 0 to E , we can then integrate to obtain

$$F\tau = q E, \quad (1.36)$$

which shows that each unit of fishing effort has a direct incremental effect on fishing mortality. From (1.27) and (1.36),

$$\begin{aligned} C &= F\tau \bar{N} = q E \bar{N} \\ \text{or } U &\equiv \frac{C}{E} = q \bar{N}. \end{aligned} \quad (1.37)$$

Thus, catch-per-unit-effort (CPUE), U , is proportional to average abundance. Even if q is not known, CPUE can still be used as an index of abundance over time, in the sense that proportional changes in CPUE are equal to proportional changes in abundance. If q is known, then average abundance can be estimated by U/q .

If the amount of effective fishing area of a particular gear type can be determined, then abundance can be estimated by projecting the catch in the sample area, a , to the total area, A , occupied by the population, or

$$\bar{N} = \frac{A}{a} C \quad (1.38)$$

(Paloheimo and Dickie 1964, Gulland 1983). The density (or concentration), D , of fish in an area is the number of fish per unit area, or

$$D = \bar{N}/A. \quad (1.39)$$

If it is assumed that fishing area is proportional to fishing effort, or $a = q'E$, then (1.38) becomes

$$U = q'D, \quad (1.40)$$

showing that CPUE is proportional to population density. For trawl data, the effective area is length of tow times the width of the trawl opening (with some corrections). This “area-swept” approach is frequently used in surveys to determine population abundance. For longline data, information on hook spacing has been incorporated into a model to estimate effective width based on a uniform circle of attraction about a hook (Eggers et al. 1982). More realistic models and additional experimental data are needed for the shape and strength of the attraction area.

1.3.1. Regional Considerations

Comparison of CPUE among regions requires consideration of the amount of fishing area covered by the fishing effort (Quinn et al. 1982). Let the subscript r denote region. If a small fishing area had the same CPUE as a large fishing area, the concentration of fish in both areas would be the same, but their abundances would differ greatly. Thus, CPUE in a region r is proportional to population density, or

$$U_r = q' \frac{\bar{N}_r}{A_r} = q' D_r, \quad (1.41)$$

which follows directly from (1.40) and (1.39).

Density for the entire population is the combination of regional densities weighted by habitat area, since

$$\begin{aligned} \bar{N} &= \sum_r \bar{N}_r = \sum_r A_r D_r \\ \text{and } D &= \frac{\bar{N}}{A} = \frac{\sum_r \bar{N}_r}{\sum_r A_r} = \sum_r \frac{A_r}{A} D_r. \end{aligned}$$

Hence, using (1.41), CPUE for the population should also be weighted by habitat area, or

$$U_A = \sum_r \frac{A_r}{A} U_r. \quad (1.42)$$

In practice, CPUE may indicate a higher density than actually occurs in the entire population area, if fishing takes place only on fishing grounds with the highest densities. Nevertheless, comparisons are still valid if there is consistency in fishing grounds selected over time and region. Another important consideration is that population area may change over time (Kearney 1991), whether due to environmental change or over-fishing. For example, if CPUE increases by a factor of 1.5 from one year to the next but population area is halved, then population abundance decreases to 0.75 of that in the first year. If the population contraction is unobserved, then the qualitative inference of increasing abundance from CPUE is completely wrong.

Example 1.12. Pacific halibut CPUE

Pacific halibut effort is measured in skates (1800 feet of groundline with 100 equally-spaced hooks attached) and catch is measured in pounds (Quinn et al. 1982). In 1980, CPUE in southeastern Alaska was 82.0 pounds per skate and CPUE in British Columbia was 68.4 pounds per skate. Bottom area inhabited by halibut for southeastern Alaska is 45,000 km² and 59,000 km² for British Columbia. Calculating $(A_r/A)U_r$ results in the values 35.3 and 39.0, showing that relative abundances in the two areas in 1980 were 48% and 52%, respectively. The overall measure of CPUE across both areas in 1980 from (1.42) was 74.3 pounds per skate. This is closer to British Columbia's CPUE because of its larger bottom area. ■

Overall CPUE could also be calculated as

$$U_E = \frac{\sum_r C_r}{\sum_r E_r} = \frac{C}{E} = \sum_r \left(\frac{E_r}{E} \right) U_r, \quad (1.43)$$

which shows that pooling catch and effort to obtain CPUE leads to effort-weighting of individual CPUEs. This method is inaccurate, except when certain conditions of similarity derived by Quinn et al. (1982) are satisfied. One of the obvious conditions is for relative fishing effort to be equal to relative bottom area, which could occur if harvesters distribute themselves uniformly in relation to fish habitat.

1.3.2. Standardization and Gear Selectivity

The assumption of constant catchability has been well studied in fisheries (Gulland 1983). For each fishery, component groups have been compared in an effort to standardize for fishing differences. In longline fisheries, Olsen and Laevastu (1983) describe 32 factors affecting longline CPUE and build a model incorporating such factors. Nevertheless, studies of soak time, hook-spacing, hook size, line depth, bait, and other gear differences predominate for fixed gear types such as longlines, handlines, and crab pots (Murphy 1960, Maéda 1967, Skud and Hamley 1978, Ralston 1982, Myhre and Quinn 1984, Somerton and Merritt 1986, Hinton 1996). In trawl fisheries, tonnage of vessel, mesh size, and modern electronics are major factors (Gulland 1983, Hilborn and Walters 1992). In recreational fisheries, the presence of a guide may have a major effect, and the skill level of individual fishers can vary widely. In purse seine fisheries, vessel speed and size, presence of helicopters, communication groups, and radar are important (Allen and Punsley 1984). In all commercial fisheries, the expertise of a vessel's skipper can have a pronounced effect on fishing success. In any fishery, technological advances or learning can result in an increase in catchability over time. If not corrected for, then an increase in CPUE over time may be mistakenly interpreted as an increase in abundance.

Standardization

Two different approaches are possible. The first is direct experimentation. The experimental design varies depending on the purpose of the study, but essentially, all gear types of interest are fished in the same area and CPUEs from all gear types are compared to a standard gear type. This results in the calculation of fishing power coefficients, P_i , for gear type i , or $P_i = U_i/U_s$, where U_s is CPUE from the standard gear type. Effective effort for each gear type is then $\tilde{E}_i = P_i E_i$, and total effective effort is $\tilde{E} = \sum \tilde{E}_i$. The quantity \tilde{E} is then used in place of E in further analysis. Not only are comparisons possible within a major gear type; it is possible to fish widely different gear types such as trawl and setline (Hoag et al. 1984). Comparative experiments can also be used to estimate selectivity of gear as a function of age or length, as discussed later in this section.

A second approach involves the comparison of CPUE data over a number of years (Gavaris 1980). A general linear model can be used to separate effects from many factors. Let U_R be the reference CPUE at one level of each of the factors. Subscript i refers to the factors, and subscript j refers to the levels within each factor. Define P_{ij} as the relative fishing power for the j th level of the i th factor. For the reference level of each factor, P_{ij} is set to 1. Let X_{ij} be equal to 1 when a datum refers to the j th level of the i th factor and 0 otherwise. The general model of CPUE for one combination of levels of the factors based on the lognormal distribution is then

$$U = U_r \prod_i \prod_j P_{ij}^{X_{ij}} e^\epsilon, \quad (1.44)$$

where ϵ is a normal random variable with mean 0 and constant variance σ^2 . A logarithmic transformation of (1.44) results in a linear regression model of the form

$$\begin{aligned} \ln U &= \ln U_r + \sum_i \sum_j X_{ij} \ln P_{ij} + \epsilon \\ \text{or } Y &= \beta_0 + \sum_k \beta_k X_k + \epsilon, \end{aligned} \quad (1.45)$$

where the subscript k subsumes i and j , the y -intercept β_0 is the reference log CPUE, and the parameters $\{\beta_k\}$ are logarithms of the power coefficients. In application, Gavaris (1980) considered the following factors: country, gear type, tonnage class, month, area fished, and year. He also determined a bias correction factor to obtain an unbiased estimate of mean CPUE. Such a correction is not needed if interest is in median-unbiased estimators. This statistical model can also be used for the direct experimentation approach described above, omitting factors such as year that are not applicable.

Trivial generalizations of (1.45) are possible with modern statistical software that permit one to replace the linear right-hand side of (1.45) with smooth functions of the independent variables and/or to replace the normal error assumption with a Poisson-like or other statistical distribution [see, for example, the generalized additive models in Hastie and Tibshirani (1990) and alternative statistical distributions in National Research Council (1994)].

For other similar approaches, consult Gulland (1983), Beverton and Holt (1957), Kimura (1981, 1988), and Hilborn and Walters (1992). Murphy and Elliott (1954), Pella and Psaropoulos (1975), Allen and Punsley (1984), Punsley and Deriso (1991), and Punsley and Nakano (1992) developed general linear models for yellowfin tuna catches (one of the largest databases of this kind in the world), including further consideration of weighting observations, spatial and temporal relationships, and expansions to actual abundance. Baelde (1991) applied basic standardization techniques and the general linear model to a prawn fishery to be able to use CPUE as a measure of relative abundance. Quinn (1987) considered standardization for short-term changes in catchability. Hilborn and Ledbetter (1985) and Hilborn (1985) used general linear models to consider individual vessel performance and its effect on catch rates. Tsou and Yeh (1991) applied a method of Honma (1974) to standardize CPUE, which involves several assumptions of constant parameters among months, areas, and years.

Example 1.13. Shrimp in the Gulf of Mexico

A subset of catch and CPUE data from interviews in the Gulf of Mexico shrimp trawl fishery in the month of October is shown in table 1.1 (J.M. Nance, SE Fisheries Center, Galveston, TX, personal communication, 1992). Data have been obtained monthly since 1981 for seven areas (subarea groups 1–3, 4–9, 10–12, 13–14, 15–17, 18–19, and 20–21) and two depth zones (≤ 15 , > 15 fathoms). Different vessels concentrate in shallow versus deep waters, and an important question is whether standardization is needed. The general linear model provides an answer by considering consistency in trends over various combinations of factors. Another use of the general linear model

Table 1.1. Gulf of Mexico shrimp trawl data, setup for general linear model, and predicted values.

y	a	d	C	U	ln(U)	X dummy variables												$\ln(\hat{U})$	\hat{U}
						82	83	84	85	86	87	88	89	90	91	7	2		
1981	6	1	2256174	824	6.71	0	0	0	0	0	0	0	0	0	0	0	0	6.77	869
1982	6	1	1882430	540	6.29	1	0	0	0	0	0	0	0	0	0	0	0	6.29	539
1983	6	1	1197020	594	6.39	0	1	0	0	0	0	0	0	0	0	0	0	6.22	501
1984	6	1	1942472	644	6.47	0	0	1	0	0	0	0	0	0	0	0	0	6.31	552
1985	6	1	1090424	639	6.46	0	0	0	1	0	0	0	0	0	0	0	0	6.57	712
1986	6	1	1568922	637	6.46	0	0	0	0	1	0	0	0	0	0	0	0	6.45	633
1987	6	1	886527	547	6.30	0	0	0	0	0	1	0	0	0	0	0	0	6.15	467
1988	6	1	1016833	411	6.02	0	0	0	0	0	0	1	0	0	0	0	0	6.18	485
1989	6	1	552482	435	6.08	0	0	0	0	0	0	0	1	0	0	0	0	6.17	479
1990	6	1	1208500	559	6.33	0	0	0	0	0	0	0	0	1	0	0	0	6.22	505
1991	6	1	784267	456	6.12	0	0	0	0	0	0	0	0	0	1	0	0	6.24	515
1981	7	1	482618	660	6.49	0	0	0	0	0	0	0	0	0	0	1	0	6.55	698
1982	7	1	295983	451	6.11	1	0	0	0	0	0	0	0	0	0	1	0	6.07	432
1983	7	1	181244	357	5.88	0	1	0	0	0	0	0	0	0	0	1	0	6.00	402
1984	7	1	117113	346	5.85	0	0	1	0	0	0	0	0	0	0	1	0	6.09	443
1985	7	1	386042	582	6.37	0	0	0	1	0	0	0	0	0	0	1	0	6.35	571
1986	7	1	146769	531	6.27	0	0	0	0	1	0	0	0	0	0	1	0	6.23	508
1987	7	1	195104	400	5.99	0	0	0	0	0	1	0	0	0	0	1	0	5.93	374
1988	7	1	244780	406	6.01	0	0	0	0	0	0	1	0	0	0	1	0	5.96	390
1989	7	1	143183	382	5.94	0	0	0	0	0	0	0	1	0	0	1	0	5.95	384
1990	7	1	113565	434	6.07	0	0	0	0	0	0	0	0	1	0	1	0	6.01	405
1991	7	1	235076	459	6.13	0	0	0	0	0	0	0	0	0	1	1	0	6.02	414

1981	6	2	1306583	934	6.84	0	0	0	0	0	0	0	0	0	0	0	1	6.74	849	
1982	6	2	745286	601	6.40	1	0	0	0	0	0	0	0	0	0	0	0	1	6.27	526
1983	6	2	1254905	543	6.30	0	1	0	0	0	0	0	0	0	0	0	0	1	6.19	489
1984	6	2	1017088	556	6.32	0	0	1	0	0	0	0	0	0	0	0	0	1	6.29	539
1985	6	2	918823	784	6.66	0	0	0	1	0	0	0	0	0	0	0	0	1	6.54	695
1986	6	2	941452	623	6.43	0	0	0	0	1	0	0	0	0	0	0	0	1	6.43	618
1987	6	2	960756	362	5.89	0	0	0	0	0	1	0	0	0	0	0	0	1	6.12	455
1988	6	2	930981	459	6.13	0	0	0	0	0	0	1	0	0	0	0	0	1	6.16	474
1989	6	2	906506	433	6.07	0	0	0	0	0	0	0	1	0	0	0	0	1	6.15	467
1990	6	2	734020	429	6.06	0	0	0	0	0	0	0	0	0	1	0	0	1	6.20	493
1991	6	2	1573642	472	6.16	0	0	0	0	0	0	0	0	0	0	1	0	1	6.22	503
1981	7	2	1451699	690	6.54	0	0	0	0	0	0	0	0	0	0	1	1	6.52	681	
1982	7	2	652734	354	5.87	1	0	0	0	0	0	0	0	0	0	0	1	1	6.05	422
1983	7	2	472851	335	5.81	0	1	0	0	0	0	0	0	0	0	0	1	1	5.97	392
1984	7	2	617821	460	6.13	0	0	1	0	0	0	0	0	0	0	0	1	1	6.07	432
1985	7	2	1074922	540	6.29	0	0	0	1	0	0	0	0	0	0	0	1	1	6.32	558
1986	7	2	937706	469	6.15	0	0	0	0	1	0	0	0	0	0	0	1	1	6.21	496
1987	7	2	743222	368	5.91	0	0	0	0	0	1	0	0	0	0	0	1	1	5.90	365
1988	7	2	1314478	445	6.10	0	0	0	0	0	0	0	1	0	0	0	1	1	5.94	380
1989	7	2	1129580	448	6.11	0	0	0	0	0	0	0	0	1	0	0	1	1	5.93	375
1990	7	2	1486298	384	5.95	0	0	0	0	0	0	0	0	0	1	0	1	1	5.98	396
1991	7	2	840176	438	6.08	0	0	0	0	0	0	0	0	0	0	1	1	1	6.00	404

Data are for the month of October. Factors include year (y), area (a), and depth (d). Total Catch C is in pounds and CPUE (U) is in pounds per day.

Table 1.2. Estimates of regression coefficients, related statistics, and transformations to power coefficients P_{ij} in the general linear model for Gulf of Mexico shrimp trawl data.

Factor level	Coef.	Est.	SE	P-value	LCI	UCI	P_{ij}	LCI	UCI
In U_r	β_0	6.768	0.071	.000	6.624	6.912	869	753	1004
Year 82	β_1	-0.478	0.092	.000	-0.666	-0.291	0.620	0.514	0.747
Year 83	β_2	-0.552	0.092	.000	-0.739	-0.364	0.576	0.478	0.695
Year 84	β_3	-0.454	0.092	.000	-0.642	-0.267	0.635	0.526	0.766
Year 85	β_4	-0.200	0.092	.035	-0.387	-0.013	0.819	0.679	0.987
Year 86	β_5	-0.317	0.092	.001	-0.504	-0.129	0.728	0.604	0.879
Year 87	β_6	-0.622	0.092	.000	-0.810	-0.435	0.537	0.445	0.647
Year 88	β_7	-0.583	0.092	.000	-0.770	-0.396	0.558	0.463	0.673
Year 89	β_8	-0.597	0.092	.000	-0.784	-0.410	0.550	0.456	0.664
Year 90	β_9	-0.543	0.092	.000	-0.730	-0.356	0.581	0.482	0.701
Year 91	β_{10}	-0.523	0.092	.000	-0.710	-0.336	0.593	0.491	0.715
Area 7	β_{11}	-0.220	0.039	.000	-0.300	-0.140	0.803	0.741	0.869
Depth 2	β_{12}	-0.024	0.039	.540	-0.104	0.056	0.976	0.901	1.057

Factors considered are year (1981–1991), area (6,7), and depth (1,2) for the month of October.

LCI and UCI denote lower and upper 95% confidence limits, respectively.

is that if CPUE is missing for some combination of factors (and, indeed, it is for some other factor combinations than those used here), then it can be estimated from the predictive equation.

This analysis is undertaken only with respect to three factors (year, area, and depth) with 11 levels of the year factor (1981–1991), two levels of the area factor (6 and 7), and two levels of the depth zone factor (1 and 2). The reference CPUE is selected as year 1981, area 6, and depth zone 1 for convenience. The X variables needed to perform the general linear model analysis are shown in table 1.1, along with the logarithm of CPUE as the dependent variable. Note that no X variables are included for factor levels corresponding to the reference CPUE because these levels are obtained by setting the other variables to zero.

The general linear model fits the data well, with an R^2 of 80% and an F -statistic of 10.1 with 12 and 31 degrees of freedom ($p < .001$). Estimates of regression coefficients and summary statistics are shown in table 1.2; all are highly significant except for depth zone. Exponentiating these estimates yields estimates of “power” coefficients and 95% confidence intervals. The reference CPUE obtained from the intercept is 869. From the year coefficients, CPUE in all other years is significantly different from the reference year 1981; the power coefficients for years show the relative trend in CPUE relative to that year. In this case, no real trend is indicated and values range from 54 to 82% of CPUE in 1981. CPUE for area 7 averages 80% of area 6, which is a significant difference. This difference could be due to either catchability or average shrimp density differences. The power coefficient of 98% for depth zone is not significantly different from 1, as seen from the confidence interval. Hence, there is no need to standardize for depth zone, and a more parsimonious model could be fit without this factor. For illustrative purposes, we will proceed with the model including depth zone.

Predicted $\ln(\text{CPUE})$ and CPUE obtained from the linear regression model are shown in table 1.1 and plotted in figure 1.4. The plot shows the good fit of the model to the data, the overall difference between the two areas, and the overall lack of difference

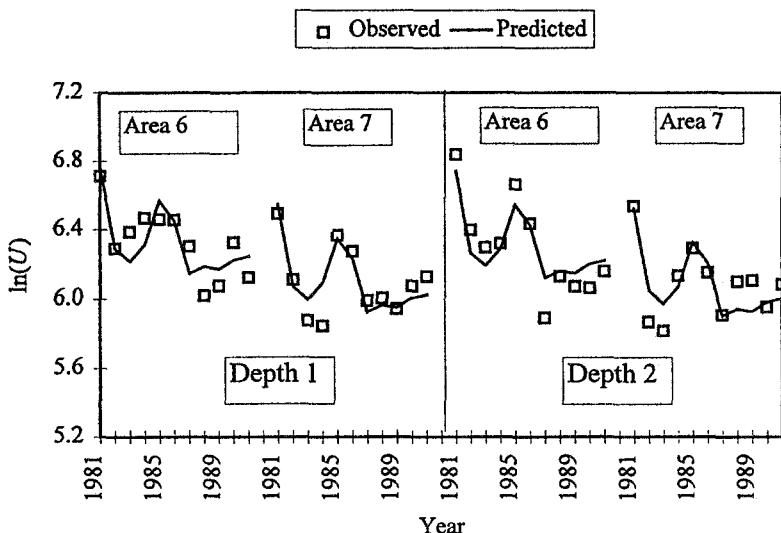


Figure 1.4. Observed and predicted $\ln(\text{CPUE})$ of Gulf of Mexico shrimp trawl data from the month of October as a function of year, area, and depth zone.

between the two depth zones. A consequence of the general linear model is that the same trend over time is imposed on each combination of other factors.

Suppose that it is desired to estimate total effort by standardizing data from depth zone 2 to those of depth zone 1. The process would first estimate effort from depth zone 1 by dividing catch by CPUE, as shown in table 1.3. For depth zone 2, effort would be estimated in the same way but modified to be effective effort by multiplying by the power coefficient of 0.97611 (table 1.3). Then the estimates would be summed over depth zone. Note that this process is equivalent to dividing total catch by CPUE of the first (reference) depth zone as shown in table 1.3, because standardization essentially converts effort from different groups into equivalent effective units.

The preceding calculations were all done with predicted CPUE from the general linear model. The same calculations could also be done with observed CPUE, although the analysis would still need to be done to obtain parameter estimates. The advantage of using predicted CPUE is that a smoothed series of estimates with the same trend across factors is used. The disadvantage is that each year produces a new addition of data for the general linear model. Rerunning the model will produce different estimates of predicted CPUE and estimated effort, which then has repercussions for all subsequent analyses. ■

Gear selectivity

Any fishing operation is more likely to catch fish of a particular range of sizes or ages than other ranges, a phenomenon known as gear selectivity. Consequentially, fishing mortality and catchability are functions of gear selectivity. Let x be the label for categories of interest, say size or age; F be the fishing mortality applied to fully selected categories; s_x be the gear selectivity for category x ; and q_x be the catchability for category x . Fishing mortality for category x is then

Table 1.3. Standardization of shrimp trawl data for two depth zones in Area 6 for the month of October, 1981–1991. (Catch in pounds, effort in days)

P _{d2} : 0.97611								
Depth 1				Depth 2				Effective Effort
Year	Catch	CPUE	Effort	Catch	CPUE	Effort		
1981	2256174	869	2595	1306583	849	1540	1503	
1982	1882430	539	3494	745286	526	1417	1383	
1983	1197020	501	2390	1254905	489	2567	2506	
1984	1942472	552	3520	1017088	539	1888	1843	
1985	1090424	712	1532	918823	695	1323	1291	
1986	1568922	633	2477	941452	618	1523	1486	
1987	886527	467	1900	960756	455	2110	2059	
1988	1016833	485	2095	930981	474	1965	1918	
1989	552482	479	1154	906506	467	1940	1894	
1990	1208500	505	2392	734020	493	1489	1453	
1991	784267	515	1522	1573642	503	3129	3054	

Depths 1 and 2				Sum of Eff. Effort
Year	Catch	CPUE	Effort	
1981	3562757	869	4098	4098
1982	2627716	539	4877	4877
1983	2451925	501	4897	4897
1984	2959560	552	5363	5363
1985	2009247	712	2823	2823
1986	2510374	633	3964	3964
1987	1847283	467	3960	3960
1988	1947814	485	4013	4013
1989	1458988	479	3048	3048
1990	1942520	505	3845	3845
1991	2357909	515	4576	4576

$$F_x = s_x F,$$

where $s_x = 1$ for fully selected categories. From the relationship $F = qE$, it follows that catchability for a category is

$$q_x = qs_x,$$

where q is catchability for fully selected categories. The relationship between CPUE and abundance from (1.37) is then

$$U_x = qs_x \bar{N}_x = q_x \bar{N}_x.$$

If two gear types 1 and 2 are fished simultaneously in the same area and if fishing mortality is small enough not to affect average abundance (as in an experiment or survey), then

$$U_{x1}/U_{x2} = q_{x1}/q_{x2} = q_1 s_{x1}/q_2 s_{x2},$$

showing that the ratio of CPUEs can be used to measure relative catchability, the ratio of catchability between two gear types. The right-hand side of the equation shows the

confounding of selectivity and full-selection catchability, so that selectivity of a gear type is determinable only in a relative sense. Even if one gear type is fully selective ($s_x = 1$) over a range of categories, the ratio of full-recruitment catchabilities, q_1/q_2 , remains in the equation, preventing absolute determination of selectivity. Rewriting this equation in terms of a reference gear type r in place of gear type 2 and category x ,

$$U_{x1} = U_r P_{x1},$$

where $P_{x1} = q_{x1}/q_r$. Thus, analysis of gear selectivity is simply a special case of the general linear model for standardization of CPUE presented earlier, where relative catchability here is equivalent to relative fishing power earlier.

Both standardization and analysis of gear selectivity could be undertaken jointly in a number of ways. First, standardization could be done for each category separately, which would provide category-specific estimates of fishing power. Second, a joint linear model with category-specific data could be done by adding category to the list of factors considered in the standardization model.

Third, models are frequently used for gear selectivity as a function of age or size. The typical functional form for monotonic selectivity curves (those that rise to an asymptotic value of 1 at older ages or larger sizes) is the logistic curve. This and other potential forms are described in chapter 4 in the context of growth and fecundity models. An estimation approach for experimental situations called SELECT (Share Each Length's Catch Total) uses the logistic and generalized logistic curves and allows for different fishing and sampling intensities and for more than two experimental gear types (Millar 1992, Xu and Millar 1993). It is assumed that one gear type is a control with full selectivity for all ages or sizes. For nonmonotonic selectivity curves, a variety of curves such as the normal, lognormal, and gamma have been used (see Millar 1995), as well as others described in chapters 8 and 9. It is not possible to deduce the selectivity curve when there is no nonselective control gear (Millar 1995), which is a consequence of the relative nature of CPUE ratios shown above. Nevertheless, it is possible to eliminate some functional forms when comparing catches from different gear types using statistical methods described in Millar (1995).

The experimental investigation of the selective properties of fishing gear is useful but not mandatory. In chapters 8 and 9, catch-age and catch-length methods estimate gear selectivity directly, obviating the need to perform selectivity experiments. Those methods determine absolute estimates of abundance, which allow absolute estimates of selectivity to be determined. Here, only relative estimates of abundance (CPUEs) are used, so that only relative estimates of gear selectivity are obtained. Some alternate treatments of selectivity and some examples of corrections for selectivity are given by Hamley (1975), Doubleday et al. (1984), Huson et al. (1984), Rudstam et al. (1984), and Willis et al. (1985). Skalski and Perez-Comas (1993) developed a nonparametric method for estimating gear selectivity.

1.3.3. Sampling for Catch and Effort

Sampling considerations are important in resolving CPUE relationships both for fishery catches and for surveys. The collection of papers in the volume edited by Doubleday and Rivard (1981) provides understanding of several factors for bottom trawl surveys. Smith (1980) considered different sampling estimators, depending on how the variance

of catch relates to catch itself. Our approach follows basic sampling methodology laid out in Quinn et al. (1982).

Catch is made up of what is landed and what is discarded. Sampling for landing information is usually straightforward for commercial fisheries because fish tickets are usually available. Accurate discard information usually requires some type of observer program. Discards should be explicitly considered in stock assessment, but often discard mortality is not considered due to lack of information. Effort information from commercial fisheries is usually obtained from a logbook program. The logbooks need to contain information on fishing effort and all other factors of importance in standardization. In sport fisheries, catch and effort information is often collected in a creel survey or a mail survey.

In the following development, let

r = region

f = a set of auxiliary factors such as season, country, and gear-type

x = the sampling unit such as vessel-day, vessel-trip, or fishing party

X = total number of sampling units

X' = number of sampling units in the sample

C'_{xrf} = logbook catch for sampling unit x

E'_{xrf} = logbook standardized effort for sampling unit x .

It is assumed that total catch, C_{rf} , is known. The goal is to estimate catch-per-unit-effort, U , and total effort, E , for each combination of r and f , for each region, r , by combining over f , and for all areas by combining over r . It is presumed that fishing effort has already been standardized by the methods in section 1.3.2.

The first task is to obtain CPUE and an estimate of its variance for each region and set of auxiliary factors. Assuming within each region that the sampling is done according to simple random sampling (with or without replacement) and that the variance of each catch sampled is proportional to fishing effort, Quinn et al. (1982) showed that the appropriate estimator is the ratio estimator

$$\widehat{U}_{rf} = \frac{\sum_{x=1}^{X'} C'_{xrf}}{\sum_{x=1}^{X'} E'_{xrf}} \quad (1.46)$$

with variance estimator

$$\widehat{V}(\widehat{U}_{rf}) = \frac{X'}{X' - 1} \frac{\sum_x (C'_{xrf} - \widehat{U}_{rf} E'_{xrf})^2}{\left(\sum_x E'_{xrf} \right)^2}. \quad (1.47)$$

The total effort fished can be extrapolated from the sample as

$$\widehat{E}_{rf} = \frac{C_{rf}}{\widehat{U}_{rf}}. \quad (1.48)$$

Its estimated variance can be obtained from the knowledge that the coefficients of variation (CV) of \widehat{E} and \widehat{U} are approximately the same; hence

$$\widehat{V}(\widehat{E}_{rf}) \approx \widehat{E}_{rf}^2 \text{ CV}^2(\widehat{U}_{rf}).$$

The next task is to combine across auxiliary factors, f , to obtain regional estimates of CPUE, or

$$\widehat{U}_r = \frac{\sum_f C_{rf}}{\sum_f \widehat{E}_{rf}} = \frac{C_r}{\widehat{E}_r}. \quad (1.49)$$

Its variance estimate from Quinn et al. (1982) is

$$\widehat{V}(\widehat{U}_r) = \widehat{U}_r^2 \sum_f \left(\frac{\widehat{E}_{rf}}{\widehat{E}_r} \right)^2 \frac{\widehat{V}(\widehat{U}_{rf})}{\widehat{U}_{rf}^2}. \quad (1.50)$$

The final task is to combine across regions, which was presented in section 1.3.1. The estimator of CPUE using the method of area-weighting from (1.42) is

$$\widehat{U}_A = \sum_r \frac{A_r}{A} \widehat{U}_r \quad (1.51)$$

with variance estimate

$$\widehat{V}(\widehat{U}_A) = \sum_r \left(\frac{A_r}{A} \right)^2 \widehat{V}(\widehat{U}_r). \quad (1.52)$$

The associated estimator of effort is $\widehat{E}_A = C/\widehat{U}_A$ with estimated variance $\widehat{V}(\widehat{E}_A) \approx \widehat{E}_A^2 \widehat{V}(\widehat{U}_A)$.

The estimator of CPUE using the method of effort-weighting from (1.43) is

$$\widehat{U}_E = \frac{C}{\widehat{E}} = \frac{\sum C_r}{\sum \widehat{E}_r} = \sum_r \frac{\widehat{E}_r}{\widehat{E}} \widehat{U}_r. \quad (1.53)$$

Its variance estimate in analogy to (1.50) is

$$\widehat{V}(\widehat{U}_E) = \widehat{U}_E^2 \sum_r \left(\frac{\widehat{E}_r}{\widehat{E}} \right)^2 \frac{\widehat{V}(\widehat{U}_r)}{\widehat{U}_r^2}. \quad (1.54)$$

The associated estimator of effort is $\widehat{E} = \sum \widehat{E}_r$ with estimated variance $\widehat{V}(\widehat{E}) = \sum \widehat{V}(\widehat{E}_r)$.

Example 1.14. Trout creel survey

A small lake is stocked with rainbow trout. In a creel survey, residents and visitors were interviewed. Three resident anglers reported catches of 0, 1, and 2 trout for 8, 3, and 1 hours of effort, respectively. CPUE \widehat{U}_{11} is 0.25, with variance 0.0742, standard error 0.27, and coefficient of variation 1.08. The survey determined that the catch from all resident anglers was 30, resulting in an estimated total effort of $30/0.25 = 120$ hours. Similarly, visitors obtained a CPUE \widehat{U}_{12} of 0.15, with variance 0.0025, standard

error 0.05, and coefficient of variation 0.33. Visitor catch was 75, resulting in estimated visitor fishing effort of 500 hours. Overall, total catch was $30 + 75 = 105$, and total effort was $120 + 500 = 620$, resulting in CPUE \widehat{U}_1 of $105/620 = 0.17$. This is closer to visitor CPUE because of higher visitor effort. Estimated variance was 0.0034, standard error 0.058, and coefficient of variation 0.34. These data could then be combined with other lakes, using the lake areas or lake efforts for weighting. ■

1.3.4. More Complex Models

Nonlinear models

In practice, catchability may not be constant due to such factors as random variation, gear competition or cooperation, and spatial and temporal effects (Rothschild 1977). A more general framework for the relationship between catch, effort, and abundance postulates that catch is related nonlinearly to effort and abundance as

$$C = q E^{\alpha+1} N^{\beta+1} \quad (1.55)$$

$$\text{or } U = (q E^\alpha N^\beta) N, \quad (1.56)$$

where α and β are model parameters (Bannerot and Austin 1983). The term $q E^\alpha N^\beta$ in parentheses in (1.56) matches the catchability coefficient in (1.37), showing that this model assumes that catchability is proportional to power functions of effort and abundance. Tsoa et al. (1985) provided an estimation procedure using this relationship based on a surplus production equation described in section 2.2.7. Quinn and Collie (1990) used regression techniques with CPUE and biomass estimates of walleye pollock to find a square root relationship between CPUE and abundance ($\beta = -0.5$).

This model allows concave upward, linear, and concave downward relationships between CPUE and abundance depending on β , as shown in figure 1.5. Hilborn and Walters (1992) termed the situation where $-1 < \beta < 0$ as “hyperstability” because CPUE does not change as much as abundance at high levels of abundance. In theory, a virgin population would be at a high level of abundance and fished down to lower levels. Under hyperstability, the population would be fished down more rapidly than would be indicated by following trends in CPUE. Conversely, they termed the situation where $\beta > 0$ as “hyperdepletion” because CPUE changes more rapidly than abundance at higher levels of abundance. Under hyperdepletion, the trend in CPUE would overstate the declining trend in the population.

If parameter $\alpha \neq 0$, then a nonlinear relationship exists between fishing mortality and fishing effort. In this case, catch per power function of effort $U^* = C/E^{\alpha+1}$ would provide a proportional measure of $N^{\beta+1}$. The situation where $-1 < \alpha < 0$ represents gear saturation, where each unit of new gear added to the fishery results in less net incremental catch. The opposite situation, where $\alpha > 0$, represents gear synergy, where each unit of new gear results in greater net incremental catch. Angelsen and Olsen (1987) provided an approach for estimating α and β using fishery data with independent estimates of fish availability. Shardlow et al. (1985) discussed the possibility of spurious nonlinear catchability effects due to measurement error in abundance.

An alternative nonlinear model given by Richards and Schnute (1986) provides a general model of the form

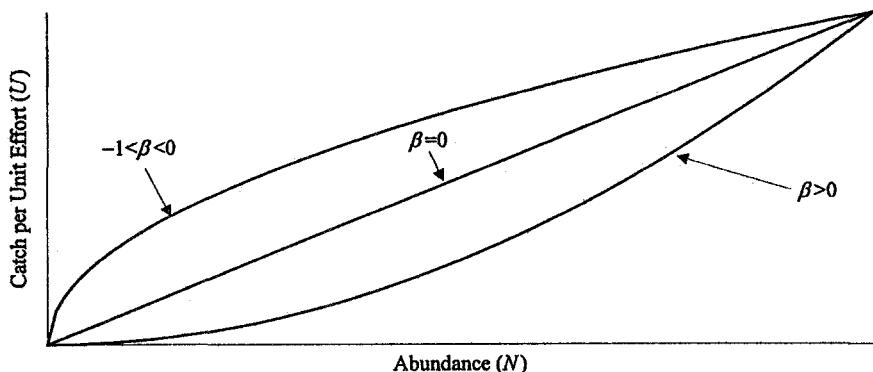


Figure 1.5. Relationship between CPUE and abundance in the Bannerot-Austin model for three ranges of β values.

$$U = \begin{cases} \frac{p + qN}{1 + rN}, & \text{for } N > -\frac{p}{q} \\ 0, & \text{for } N \leq -\frac{p}{q}, \end{cases} \quad (1.57)$$

where p , q , and r are parameters, and N is population abundance or density. This model represents five different cases of possible relationships between CPUE and abundance, depending on the values of the parameters. Richards (1987) further allowed measures of abundance and CPUE to be subject to measurement error. Some examples from this model are shown in figure 1.6. The model is more general than (1.56) in that it does not go through the origin when $p \neq 0$. Thus, a positive x -intercept or a positive y -intercept may occur depending on the parameter values. When $r = 0$, then a linear relationship between CPUE and abundance occurs. Both concave upward and downward curves occur, but the flexibility is limited to some extent by the lack of a power relationship.

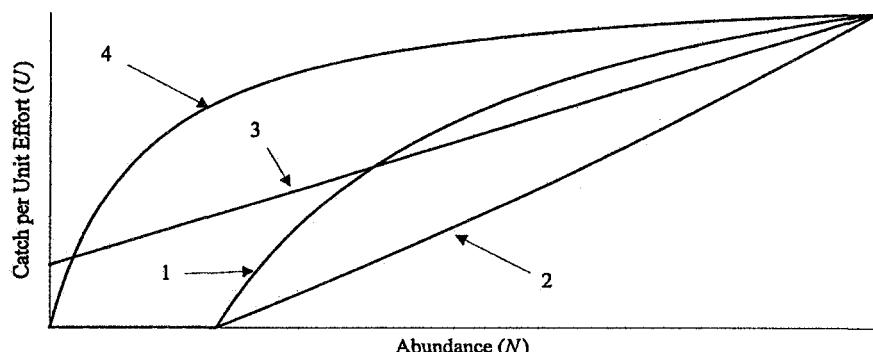


Figure 1.6. Relationship between CPUE and abundance in the Richards-Schnute model for four situations: 1, $p < 0, q, r > 0$; 2, $p, r < 0, q > 0$; 3, $p, q > 0, r = 0, q > 0$; 4, $p = 0$.

Statistical models

Regardless of the relationship between CPUE and abundance, it is important to understand the underlying statistical distribution of CPUE data. Among the useful statistical models for analyzing CPUE data, Gavaris (1980) (see section 1.3.2) and many others postulated a lognormal distribution for CPUE. Reed (1986) developed a stochastic model for catch as a function of effort based on the Poisson distribution and approximates it by the root-normal distribution. Bannerot and Austin (1983) determined experimentally that a measure of CPUE related to the proportion of zero catches had the best correlation with independent estimates of abundance obtained through sampling. Pennington (1983) modeled CPUE as a mixture of a discrete probability for observations of zero catch and a statistical distribution for nonzero observations (the delta distribution). Lo et al. (1992) developed indices of abundance using the delta distribution combined with lognormal linear models.

A general methodological approach follows Quinn (1985a) and Richards and Schnute (1992). Quinn (1985) used transformations to uncover a root normal distribution for Pacific halibut CPUE data. Richards and Schnute (1992) generalized Quinn's approach to consider general transformations in a likelihood setting and to consider the bivariate distribution between catch and effort in developing a statistical approach. Only the univariate situation will be given here.

Suppose that a set of CPUE data $\{U_i = C_i/E_i, i = 1, \dots, n\}$ is collected, where the data are assumed to be independently and identically distributed. Specifically, it is assumed that some transformation of the data results in an underlying normal distribution. Two possible candidates are the Box-Cox transformation

$$T(U) = \begin{cases} \frac{U^\alpha - 1}{\alpha}, & \text{for } \alpha \neq 0 \\ \ln U, & \text{for } \alpha = 0, \end{cases} \quad (1.58)$$

and the Schnute-McKinnell transformation

$$T(U) = \begin{cases} \frac{U^\alpha - u_1^\alpha}{u_2^\alpha - u_1^\alpha}, & \text{for } \alpha \neq 0 \\ \frac{\ln(U) - \ln(u_1)}{\ln(u_2) - \ln(u_1)}, & \text{for } \alpha = 0. \end{cases} \quad (1.59)$$

Parameter α is the transformation parameter, and u_1 and u_2 are user-specified constants, such as the lowest and highest observed CPUE values (Richards and Schnute 1992). Let the back-transformation from T to U be denoted S , where

$$S(T) = T^{-1}(T(U)) = U. \quad (1.60)$$

For example, the Box-Cox back-transformation from (1.58) is

$$U = S(T) = \begin{cases} (\alpha T + 1)^{1/\alpha} & \text{for } \alpha \neq 0 \\ \exp(T) & \text{for } \alpha = 0. \end{cases} \quad (1.61)$$

From the normality assumption, the probability density function for T is

$$f(T) = (2\pi\sigma^2)^{-1/2} \exp\left[-\frac{1}{2\sigma^2}(T - \mu)^2\right], \quad (1.62)$$

where μ and σ^2 are the mean and the variance of the distribution. Importantly, the median and mode are the same as the mean. The probability density function for U , obtained by transformation of the density function for T , from Richards and Schnute (1992) is

$$g(U) = f(T(U)) \frac{\partial T}{\partial U}, \quad (1.63)$$

which for the Box-Cox transformation is

$$g(U) = (2\pi\sigma^2)^{-1/2} U^{\alpha-1} \exp\left[-\frac{1}{2\sigma^2}(T(U) - \mu)^2\right]. \quad (1.64)$$

The density function (1.63) is not that for the normal distribution because of the partial derivative, showing that the distribution of a nonlinear function of a normally distributed variable is not normal.

The mean and other moments of U do not appear to have closed-form solutions for arbitrary α , although they can be derived for some special cases. For the case where $\alpha = 1/n$ with n an integer, let $x = \alpha T + 1$. The distribution of x is then normal with mean $\alpha\mu + 1$ and variance $\alpha^2\sigma^2$. The mean (expected value) of U is then

$$\begin{aligned} E(U) &= E(\alpha T + 1)^{1/\alpha} \\ &= E(x^n) \quad \text{the non-central } n\text{th moment} \\ &= m^{(n)}(t) \Big|_{t=0}, \end{aligned} \quad (1.65)$$

where the last term is the n th derivative of the moment-generating function of a normal distribution evaluated at 0.

The median of U is simply the back-transformation (1.60) of the median (and the mean) of T because the transformations (1.58) and (1.59) are monotone functions of U . Hence, the median can be written $m = S(\mu)$ using (1.60). For the Box-Cox transformation using the back-transformations (1.61), the median is

$$m = \begin{cases} (\alpha\mu + 1)^{1/\alpha}, & \text{for } \alpha \neq 0 \\ \exp(\mu), & \text{for } \alpha = 0. \end{cases} \quad (1.66)$$

The easiest way to find the mode is to numerically find the largest value of $g(U)$ for several values of U . Quinn (1985) and Richards and Schnute (1992) argued that the median, m , may be the best measure of central tendency in contrast to the mean and the mode, with one-half of the distribution always found on either side of it.

Estimation of the three parameters α , μ , and σ^2 , which characterize the distribution of U , can be undertaken using maximum likelihood methods. The log-likelihood of the data from (1.62) and (1.63) is

$$\begin{aligned} \ln \mathcal{L} &= \ln \left[\prod_i^n g(U_i) \right] = -\frac{n}{2} \ln(2\pi\sigma^2) - \frac{1}{2\sigma^2} \sum_i^n (T_i - \mu)^2 \\ &\quad + \sum_i^n \ln \left(\frac{\partial T}{\partial U} \Big|_{U=U_i} \right), \end{aligned} \quad (1.67)$$

where $T_i = T(U_i)$, which is the transformation of U_i . For the Box-Cox transformation, the third term in (1.67) is $(\alpha - 1) \sum \ln(U_i)$ (including $\alpha = 0$). Maximum likelihood estimates (MLEs) follow by taking the derivative of (1.67) with respect to each parameter, setting the result equal to 0, and solving. As the third term in (1.67) is only a function of α , the maximum likelihood estimates of μ and σ^2 follow from the theory of normal distributions, which are

$$\hat{\mu} = \frac{1}{n} \sum_i^n T_i \quad (1.68)$$

$$\hat{\sigma}^2 = \frac{1}{n} \sum_i^n (T_i - \hat{\mu})^2, \quad (1.69)$$

where T_i is evaluated at the maximum likelihood estimate $\hat{\alpha}$. The transcendental equation which results for α is not particularly useful; it is simpler to obtain $\hat{\alpha}$ by maximizing the likelihood (1.67) directly using numerical methods, after substituting (1.68) and (1.69) into (1.67). Note that the maximum log likelihood as a function of α simplifies to

$$\max [\ln \mathcal{L}(\alpha)] = -\frac{n}{2} \left[\ln(2\pi\hat{\sigma}^2 + 1) \right] + \sum_i^n \ln \left(\frac{\partial T}{\partial U} \Big|_{U=U_i} \right). \quad (1.70)$$

The estimate of the median is then

$$\hat{m} = S(\hat{\mu}) \quad (1.71)$$

using (1.60). A numerical estimate of the mean can be made using

$$\hat{U} = \int_0^\infty U \hat{g}(U) dU, \quad (1.72)$$

where $\hat{g}(U)$ is the probability density function (1.63) evaluated at the maximum likelihood estimates. Alternatively, the mean can be estimated by using (1.65) with the MLEs when appropriate. The mode can be found as the maximum value of $\hat{g}(U)$ with respect to U . In most cases, it is easiest to determine the mean and mode numerically rather than formulaically. One method of estimating the variance of an estimate of central tendency, say the estimated median \hat{m} , is to use the delta method (Seber 1982, pp. 7–9), which results in

$$\hat{V}(\hat{m}) \approx \left(\frac{\partial S}{\partial T} \Big|_{T=\hat{\mu}} \right)^2 \hat{V}(\hat{\mu}), \quad (1.73)$$

where $\hat{V}(\hat{\mu}) = \hat{\sigma}^2/n$, and n is sample size.

Given the likelihood function and the maximum likelihood estimates, several different analyses can be undertaken, as shown by Richards and Schnute (1992). First, univariate and multivariate confidence intervals for the parameters can be constructed. Second, hypothesis tests can be performed; it is frequently of interest to test whether the data follow a log-normal ($\alpha = 0$), root-normal ($\alpha = \frac{1}{2}$), or normal ($\alpha = 1$) distribution. This is usually done using large-sample theory that minus twice the log

likelihood is distributed as a chi-square distribution. A straightforward approach is to construct a confidence interval for α as follows. The conditional log likelihood (1.70) is maximized as a function of α . A critical value, X , is calculated from the maximum likelihood estimates as

$$X = \ln \mathcal{L}(\hat{\alpha}) - \frac{1}{2} \chi_p^2(1), \quad (1.74)$$

where the latter term is the χ^2 critical value at level p with 1 degree of freedom. The lower and upper confidence limits for α correspond to the two places where the log likelihood is equal to X , which is illustrated graphically in the example below. Confidence intervals for μ and σ^2 , if desired, follow from the standard theory of normal distributions, which for μ is simply $\hat{\mu} \pm 1.96 \hat{\sigma}_{\mu}$. Joint confidence intervals for parameters can be obtained by applying a modification of (1.74), where the degrees of freedom equal the number of fixed parameters, as shown by Richards and Schnute (1992).

There are at least three direct ways to obtain confidence intervals for the median. One way is to reparameterize the model in terms of m in place of μ and then to maximize the likelihood with respect to α and σ^2 as a function of m . The confidence limits are the two values of m where the conditional maximum likelihood equals the critical value X in (1.74) (Richards and Schnute 1992). An approximate method is to use $\hat{m} \pm 1.96 \hat{\sigma}_m$ from (1.73). The third way is to back-transform the confidence interval for μ using (1.61) with $\hat{\alpha}$, which is also an approximate method because the statistical properties of $\hat{\alpha}$ are ignored. Alternatively, variance and interval estimation for any measure of central tendency can be obtained by application of the jackknife, the parametric bootstrap, or the nonparametric bootstrap (Efron 1982, Efron and Tibshirani 1993).

Comparison of estimates for different data sets reveals whether the distributions of CPUE data are consistent. Comparisons between years are suggestive of changes in stock abundance, if there is a monotonic relationship between CPUE and abundance.

Further modifications to this general model can be undertaken. See Richards and Schnute (1992) for the appropriate formulae and rationale for the Schnute-McKinnell transformation, a slightly different parameterization of the univariate case, the comprehensive treatment of the bivariate case, and an example showing the greater information contained in bivariate data. See Quinn et al. (1985) for treatment of CPUE data when variance of CPUE depends on the amount of effort and formulae for the root normal distribution, and for an example showing application of those formulae.

Example 1.15. Tiger prawns in Torres Strait, Australia

In February–March, 1986, a research trawl survey for tiger prawns sampled 28 stations (Blyth et al. 1990). Each “shot” was 60 minutes long, covering an effective area of 2.24 ha, except for station 14 which was 65 minutes long. The distribution of CPUE (numbers per ha) across stations is heavily right-skewed (table 1.4, figure 1.7), suggesting that transformation parameter α is much less than 1. The sample variance (391) is much greater than the mean (22), the observed median (18) is less than the mean, and the observed mode falls in the interval (15, 20).

Maximum likelihood estimates are found using numerical techniques to maximize (1.67) or (1.70); calculations of transformation T_i from (1.58), and individual log likelihood $\ln g(U_i)$ using (1.64) for each station i , and its sum [$\ln \mathcal{L}$ in (1.70)] are

Table 1.4. Tiger prawn CPUE U_i (numbers per ha) at 28 stations in Torres Strait, Australia from a research survey in February/March, 1986, along with transformations T_i and likelihood calculations $\ln g(U_i)$ using the MLEs. Also shown are the observed mean, sample variance, and median of the $\{U_i\}$ and $\{T_i\}$, and the maximum log likelihood value $\max(\ln \mathcal{L})$.

Station	CPUE U_i	T_i	$\ln g(U_i)$
1	6.25	2.15	-3.28
2	11.17	2.99	-3.37
3	17.87	3.73	-3.69
4	16.08	3.56	-3.59
5	11.62	3.05	-3.38
6	9.38	2.73	-3.31
7	9.83	2.80	-3.32
8	32.17	4.75	-4.50
9	19.66	3.89	-3.79
10	69.25	6.23	-6.50
11	19.66	3.89	-3.79
12	16.53	3.60	-3.62
13	17.87	3.73	-3.69
14	17.32	3.68	-3.66
15	16.53	3.60	-3.62
16	42.44	5.26	-4.45
18	35.29	4.92	-4.68
19	4.02	1.57	-3.38
20	18.32	3.77	-3.71
21	42.89	5.28	-5.11
22	88.46	6.75	-7.42
25	22.78	4.14	-3.96
26	1.79	0.61	-3.83
27	5.36	1.95	-3.30
28	2.68	1.07	-3.57
29	3.13	1.26	-3.49
30	20.10	3.93	-3.81
Observed Mean	21.78	3.56	
Sample Variance	391	2.19	
Observed Median	17.60	3.71	
$\max(\ln \mathcal{L})$	-112.88		
n	28		

shown in table 1.4 using the MLEs. The observed mean of the transformed CPUEs $\{T_i\}$ (3.56) is less than the observed median (3.71), and the sample variance (2.19) is less than the mean. The MLE $\hat{\alpha}$ is about 0.17 (table 1.5), close to the value for a log-normal distribution. The corresponding calculations of MLEs $\hat{\mu}$ from (1.68) and $\hat{\sigma}^2$ from (1.69) are shown in table 1.5. The curve corresponding to $\hat{g}(U)$ is superimposed on the observed histogram in figure 1.7, showing a good fit to the data.

The estimate of the median from (1.71) and its standard error from (1.73), and the estimates of the mean from (1.72) and the mode [the maximum value of $\hat{g}(U)$] using numerical methods are shown in table 1.5. These likelihood estimates of central tendency are not the same as the observed measures. The mode, in particular, differs markedly from its observed counterpart (as can be seen in figure 1.7), which suggests

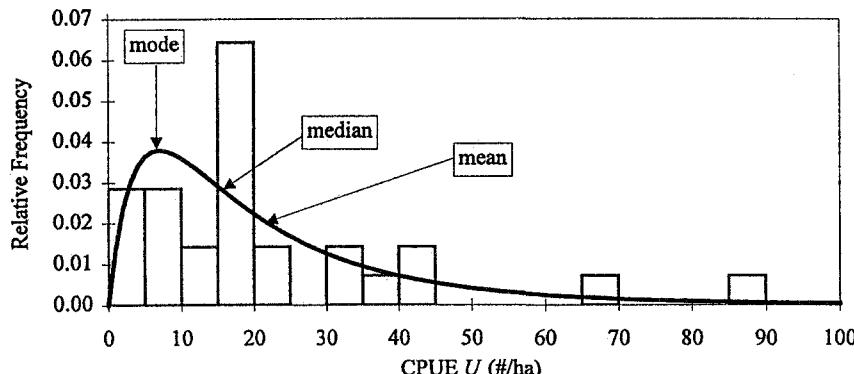


Figure 1.7. Tiger prawn CPUE histogram and fitted probability density function $\hat{g}(U)$ using the maximum likelihood estimates. Relative frequency for the histogram is determined as the proportion of observations divided by the interval width (5).

the mode is not a stable measure of central tendency. The mean lies far from the center of the distribution due to the heavy tail of the CPUE distribution, suggesting that the median is the best measure of central tendency in this case.

The 95% confidence interval for α is found by first maximizing the conditional likelihood $\ln \mathcal{L}(\alpha)$ in (1.70) as a function of α ; the corresponding likelihood profile is shown in figure 1.8. The critical value X from (1.74) is plotted as a straight line in figure 1.8; the intersections with the likelihood profile yield the lower and upper confidence limits for α of $(-0.18, 0.52)$. Hence, neither the log-normal ($\alpha = 0$) nor the root-normal ($\alpha = \frac{1}{2}$) can be rejected as the underlying distribution of prawn CPUE, although the log-normal is more likely. The normal distribution can be handily rejected. The 95% confidence intervals for μ and m in table 1.5 follow the methods described above. The three ways of doing it for m are fairly similar; the likelihood approach should be the most accurate although the most time-consuming. ■

Table 1.5. Maximum likelihood estimates of α , μ , and σ^2 for tiger prawn CPUE; corresponding estimates of measures of central tendency (mean, median, and mode); and 95% confidence intervals for selected parameters.

Parameter	Estimate	95% C.I.	
		Lower	Upper
α	0.17	-0.18	0.52
μ	3.56	3.02	4.09
σ^2	2.11		
median m	16.1		
using MLE approach		11.0	22.8
using $\hat{\sigma}_m = 2.7$		10.7	21.4
using back-transformation		11.4	22.2
mean \hat{U}	20.9		
mode	7.0		

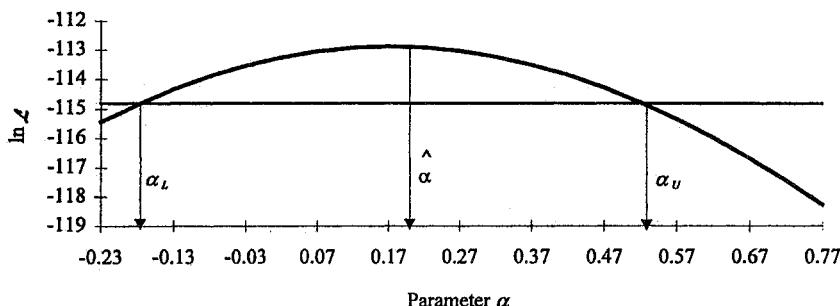


Figure 1.8. The likelihood profile as a function of α , and the critical value X plotted as a straight line. The maximum likelihood occurs at the top of the likelihood profile, and the two intersections denote the confidence limits.

Other considerations

Other factors may also be important in understanding CPUE. Rudstam et al. (1984) modeled gillnet catches as a function of the probability of encountering the net and the probability of retention after encounter. Sampson (1991) constructed an economic model relating CPUE to technical parameters of fishing vessels as well as biomass. Hilborn and Walters (1992) described several technical factors which could affect CPUE.

It is often necessary to forecast CPUE in the near future for management purposes. Models in later chapters use underlying processes in the population to do so, but sometimes simpler methods will suffice (Stocker and Hilborn 1981, Roff 1983, Schnute 1985). For example, a linear regression of $CPUE_t$ versus $CPUE_{t-1}$ for recent data could be used to establish a short-term trend for a population and then used to forecast $CPUE_{t+1}$. If the fishing effort E_{t+1} is prescribed or forecasted, then catch is forecasted as the product $\widehat{CPUE}_{t+1} E_{t+1}$. Along these lines, time-series methods are designed for forecasting and have been applied to many fisheries data sets (e.g., Quinn and Marshall 1989).

1.3.5. Schooling and Search

Many fish populations are found in schools, a fact which heretofore we have not considered in the fishing process. For passive fishing gear, where fish make a direct response to the gear (e.g., biting a hook, entering a trap), the effect of schooling would be to increase the variance in CPUE due to aggregation in the population. No bias would be expected to occur, unless competition for bait is severe or the fishery operates selectively in areas of high abundance (Murphy and Elliott 1954, Maéda 1967, Skud and Hamley 1978).

For active fishing gear, where vessels first search for schools of fish and then encircle or trawl through the schools (e.g., purse seining, trawling), the effect of schooling on CPUE may be dramatic. For example, if a random search process is used for schools and a small fraction of a school is caught, then the total number of schools remains constant, while the actual population goes down. The encounter rate of schools would then be a valid index of the number of schools, but not of the total population. If the amount of fish in a school caught per encounter is constant, then catch per set or trawl,

a common CPUE statistic, remains constant, despite a decline in the actual population. Several mathematical models for schooling populations have been constructed that show the lack of a relationship between CPUE and abundance for schooling populations (Paloheimo and Dickie 1964, W. Clark 1975, C. Clark and Mangel 1979, Quinn 1980). In the ecological literature, several studies on predator-prey relationships have revealed complicated effects on prey encounter and consumption rates due to the effects of schooling, aggregation, interference, multiple predators, and patchy environments (Brock and Riffenburgh 1960, further references in Quinn 1980). The theory of search (Saila and Flowers 1967, Paloheimo 1971, Koopman 1980, Mangel and Clark 1983, Mangel 1985; see also section 1.3.7) also has revealed complexities in the encounter process, which suggests that traditional techniques for the relationship between CPUE and abundance may not be appropriate. Mangel and Beder (1985) develop a general theory for estimating stock size for schooling populations from search data, including depletion.

A simple model from the ecological literature, called the Holling disk or Michaelis-Menton equation (Holling 1966), relates prey encounter rate to prey density and predator search and handling time. Let

$$\begin{aligned} n &= \text{number of encounters with prey by a predator} \\ D &= \text{density of prey (numbers per area)} \\ \tau_s &= \text{time spent searching by a predator} \\ \tau_h &= \text{time spent handling and consuming one prey} \\ \tau_t &= \tau_s + n\tau_h = \text{total time available} \\ a &= \text{search rate (area searched per unit of time).} \end{aligned}$$

The number of encounters, n , is then

$$\begin{aligned} n &= a\tau_s D = a(\tau_t - n\tau_h)D \\ \text{so that } n &= a\tau_tD / (1 + a\tau_h D). \end{aligned} \tag{1.75}$$

In (1.75), the number of encounters increases as prey density increases and eventually levels off due to partitioning of total time available into search and handling time. Modifications of (1.75) exist for multiple predators, interference between predators, aggregation of predators into areas of high prey densities, and stochasticity in the encounter process. (See references in Quinn 1980; see section 1.3.7 for more details.)

The Holling disk equation (1.75) is applicable to schooling populations where the prey item is the school. The implication is that search time is an important component of the fishing process and should be measured. The density of schools in the population is directly related to the number of schools encountered divided by the search time; hence a measure of density of schools is $\text{CPUE} = n/\tau_s$. The Holling disk equation appears in many models for the fishing process (e.g., Paloheimo and Dickie 1964, Eggers 1976, Mangel 1982, 1985). Another implication of this model is that independent information on the spatial distribution of fish and fishing effort and on the parameters of schooling is necessary to determine the relationship between abundance and CPUE in a schooling population.

A different approach to modeling the search process for schooling populations from Quinn (1980) involves the theory of line transects (Seber 1982, Buckland et al.

1993). The first part of the fishing process is conceptualized as a search for schools along a transect line. At each time, t , a search along a transect line is made and some proportion of each school encountered is harvested. Let

- A = area occupied by the population
- N_t = number of schools in the population at time t
- n_t = number of schools encountered at time t
- L_t = length of the search along the transect
- \bar{S}_t = average school size at time t
- $c(\bar{S}_t)$ = effective width of search along the transect
- C_t = total catch of individuals at time t .

According to line transect theory, the expected number of schools encountered is

$$E(n_t) = \frac{2L_t c(\bar{S}_t)}{A} N_t, \quad (1.76)$$

which implies that the ratio of expected encounters to abundance is equal to the ratio of the effective area covered to population area. The effective width, c , is modeled as a function of school size in (1.76) because larger schools should be encountered more often. The actual mathematical relationship used depends on the encounter mechanism and species. For species that are sighted, such as whales and porpoises, a linear relationship of logarithmic school size

$$c(\bar{S}_t) = a + b \ln(\bar{S}_t) \quad (1.77)$$

is often used (Quinn 1985b, Buckland et al. 1993). In a three-dimensional setting, a function of the cube root of school size has been used (Brock and Riffenburgh 1960). If the radius of a school is important in the encounter process, then effective width is proportional to \bar{S}_t .

The mortality process can be modeled in different ways. First, it could be assumed that a fixed number of fish per school, \bar{C} , are killed, resulting in a total catch of

$$C_t = \bar{C} n_t. \quad (1.78)$$

Second, it could be assumed that a fixed proportion of a school, p_C , is killed, resulting in a total catch of

$$C_t = p_C \bar{S}_t n_t. \quad (1.79)$$

In this case the average number of fish killed per school is $\bar{C} = p_C \bar{S}_t$. In either case, the number of individuals at time $t + 1$ is

$$T_{t+1} = T_t - C_t. \quad (1.80)$$

One additional process that might be incorporated is the effect of the fishing process on the school structure. If fragmentation of a school occurs due to the fishing operation,

let x be the number of pieces that the school breaks into. Then the number of schools at time $t + 1$ is

$$N_{t+1} = N_t + (x - 1)n_t. \quad (1.81)$$

Similarly, attraction of schools might be incorporated into the dynamics of schools based on empirical or theoretical principles.

If the only data collected during the fishing process are the number of schools encountered, the length of search, and the catch of fish from each encounter, then only three CPUE measures are available: schools per length searched, $U_{t1} = n_t/L_t$, kill per length searched, $U_{t2} = C_t/L_t$, and kill per set, $U_{t3} = C_t/n_t$. The expected value of the first CPUE measure from (1.76) and (1.77) is

$$E(U_{t1}) = 2[a + b \ln(\bar{S}_t)]N_t/A, \quad (1.82)$$

when effective width is a linear function of $\ln(\bar{S}_t)$. The expected value (1.82) is not proportional to the abundance of schools, the abundance of individuals, nor to the average school size in general. If effective width is constant as a function of school size ($b = 0$), then the expected value is proportional to abundance of schools N_t .

The expected value of the second CPUE measure from (1.78) and (1.82) is

$$E(U_{t2}) = 2[a + b \ln(\bar{S}_t)]N_t\bar{C}/A, \quad (1.83)$$

which is also not proportional to any population parameter of interest in general. If effective width is constant as a function of school size, and average catch per school is proportional to average school size \bar{S}_t as in (1.79), then the expected value (1.83) is proportional to abundance of individuals because $N_t\bar{S}_t = T_t$. Similarly, if average catch per school is constant, then the expected value is proportional to abundance of schools.

The expected value of the third CPUE measure from (1.78) is

$$E(U_{t3}) = \bar{C}. \quad (1.84)$$

If average catch per school is proportional to average school size, \bar{S}_t , then the expected value is proportional to average school size. Similarly, if average catch per school is constant, then the expected value is constant, regardless of the actual school dynamics.

Example 1.16. Hypothetical schooling population

To further illustrate the vagaries of school dynamics on measures of CPUE, a hypothetical example is constructed using the school dynamics described above. A population of $N_1 = 100$ schools has an average school size of 10 individuals at time 1, resulting in a total population T_1 of 1000 individuals. The population area, A , is 100 and the length searched, L_t , is 10. After each school is encountered, the number of individuals killed, \bar{C} , is 3 and the school fragments into 2 pieces. The encounter parameters a and b are both 0.5. Table 1.6 shows the calculation of the number of animals encountered using (1.79) and (1.80) and CPUE statistics using (1.82–1.84) for two subsequent time periods. The abundance of individuals, T , decreases from 1000 to 778, the number of schools, N , increases markedly from 100 to 174, and the average school size, \bar{S} , decreases markedly from 10 to 4.5. The first CPUE measure increases modestly from

Table 1.6. Population changes from exploitation and CPUE estimates for a hypothetical population. Parameters: $A = 100$, $L = 10$, $a = b = 0.50$.

t	N_t	\bar{S}_t	T_t	n_t	C_t	U_{t1}	U_{t2}	U_{t3}
1	100	10.0	1000	35	105	3.5	10.5	3
2	135	6.6	895	39	117	3.9	11.7	3
3	174	4.5	778	43	129	4.3	12.9	3

3.5 to 4.3, the second CPUE measure increases modestly from 10.5 to 12.9, and the third CPUE measure remains constant at 3. Thus, none of the available CPUE measures accurately reflects changes in the population parameters of interest. ■

This model shows the complications of schooling in interpreting CPUE as a measure of abundance for a schooling population. A different model with schooling dynamics produces the same conclusions (Clark and Mangel 1979). Without information about the dynamics of schooling populations (encounter parameters, fragmentation and attraction rates, and school size), the ability to understand changes in a schooling population is limited. Further consideration of search and schooling is given in section 1.3.7.

1.3.6. Effects of Catchability Differing Between Individuals

Catchability can differ between individuals for several reasons, including their propensity to take baited hooks, their habitat preference, and their avoidance capabilities. As a consequence, the average catchability of a year-class can change over time. Those individuals with high catchability are more likely to be caught, and so they tend to dominate the catch in the initial time periods. Following the removal of the more catchable individuals, fish with lower q coefficients remain. This systematic shift in average q of fish in the catch can occur without any direct interference competition between individuals for the fishing gear, in contrast to what occurs in the stochastic angling models considered in section 1.3.7.

A model for the catchability process can be derived by partitioning the time interval into T time periods. During any given time period, assume that the risk of capture for an individual depends on that individual's catchability coefficient, q . Specifically assume that the probability of capture, $u(t, q)$, for an individual of catchability q in time period, t , is given by

$$u(t, q) = 1 - e^{-q E_t}, \quad (1.85)$$

where E_t is the amount of fishing effort expended in time period t . Natural mortality is assumed to occur after all fishing occurs in each time period. Equation (1.85) implies that the probability an individual of catchability q avoids capture in time period t can be written as

$$P(\text{survive fishing}|q) = e^{-q E_t}.$$

The probability density function (PDF) for q as a function of time period can be derived. Let $f_t(q|\text{prior fishing})$ denote the PDF of q at the beginning of time period t prior to fishing in that period. The PDF of q after fishing can be written with Bayes theorem as a recursive equation, following Deriso and Parma [1987, equation (6)] by analogy. The PDF after fishing is the posterior density function given by

$$f_t(q|\text{fish survives}) = \frac{e^{-qE_t} f_t(q|\text{prior fishing})}{\int_{-\infty}^{\infty} e^{-xE_t} f_t(x|\text{prior fishing}) dx}. \quad (1.86)$$

The meaning of (1.86) is that the probability density of any specific catchability, q , for those individuals that avoided capture in the t th time period is the same as the probability of survival for an individual with that given catchability, q , times the probability density of that catchability coefficient prior to fishing in that time period, all normalized so that the integral across q sums to 1.

Equation (1.86) does not account for the finite nature of the population under study because actual catch data are not used for the posterior update. Perhaps a better model of the change in q would account for specific removals of fish, but such a model is not considered here. On the other hand, (1.86) does show the shift in probability density that occurs when catchability is variable. Discrete probability density functions are modeled with (1.86) by replacing the integral in that formula with a summation, but again this will not cause the posterior density to be conditional on actual catch removals.

Next we consider two different kinds of prior density functions for catchability; namely, the normal and the gamma probability density functions. Both of them admit analytical solutions.

Normal density function

Here we assume that at the beginning of the depletion experiment, the PDF of q is normal with mean Q_1 and variance σ^2 ; that is,

$$f_1(q|\text{prior fishing}) \sim N(Q_1, \sigma^2).$$

By assuming that the initial PDF of q is normal, we get the well-known result that the posterior density function in (1.86) is also normal. By induction, it follows that the posterior density function is a normal density for all time periods of the experiment. The mean of q at the beginning of the t th time period is derived similar to the ones given in Deriso and Parma (1987, appendix I). Here mean catchability is given by

$$Q_t = Q_1 - \sigma^2 E_{t-1}^*, \quad (1.87)$$

where cumulative effort is defined as

$$E_{t-1}^* = \sum_{j=1}^{t-1} E_j.$$

As a consequence of (1.87), the decrease in mean catchability after each time period is proportional to fishing effort expended in that time period; the proportionality constant is σ^2 , the variance of the distribution for catchability. The variance of q in the model is not affected by the fishing process; it equals σ^2 at any time t .

One possible objection to the normal PDF used in the above example is that animals do not have a negative catchability, and thus, at best, q has a truncated, normal-type density. This biological limitation motivates one to consider an alternative model.

Gamma density function

Here one assumes that the initial PDF of q is gamma with mean r/λ_1 and variance r/λ_1^2 . The right-hand side of equation (1.86) is easily solved in this case (A. Parma, personal communication, 1987). The posterior density of q is also a gamma PDF, but the lambda parameter is shifted to $\lambda_2 = \lambda_1 + E_1$. By induction, it follows that the posterior density function is a gamma density for all time periods of the experiment. The gamma PDF at the t th time period is characterized by its mean and variance, given as follows:

$$Q_t = r/\lambda_t \quad (1.88)$$

$$V_t(q) = r/\lambda_t^2, \quad (1.89)$$

where λ_t is given recursively by

$$\lambda_t = \lambda_{t-1} + E_{t-1}. \quad (1.90)$$

From (1.88) and (1.89) combined with (1.90), mean catchability and variance in q decrease each time interval inversely proportional to cumulative fishing effort.

Both of the above functions illustrate the main qualitative feature of a decline in average catchability with age of a year-class. Conversely, vulnerability to fishing gear often increases with age in the younger age classes as individuals recruit to fishing grounds and become large enough to be captured. By combining these two trends in catchability, a dome-shaped relationship between catchability and age of the fish can occur.

1.3.7. Stochastic Fishing Models

Anyone who has ever tried to catch a fish knows that the fishing process is stochastic in nature. Even for larger fishing operations, such as those involving a commercial fishing vessel, the catch rate obtained in the course of a single trip is often quite variable. On the other hand, for fisheries where a large number of boats are involved, then the sample average catch rate for the aggregate fleet would be expected to be close to the true mean catch rate. Exceptions to the large-sample rule include those situations where the fleet does not operate as a large number of statistically independent sampling units or where the fleet does not randomly sample the entire fish habitat. Three types of stochastic models are described below: a purse seine fishery model, an angling gear model, and a longline model.

Purse seine model

A purse seine fishing model was first derived by Neyman (1949) and then generalized by Pella (1969). The fishing process is treated as a Markov process, as shown below, which involves transitions to alternative states of searching or setting on a school. Pella divided the process into five states to accommodate two species of tunas and whether or not a purse seine set results in catch, which results in a semi-Markov process. Time spent in a state is considered a random variable with distribution dependent on the state occupied.

Assume that K schools of fish are distributed randomly within an area of size A . If a vessel can search through an area of size a per unit of time, then the probability that

k schools are discovered is given by the binomial density function and approximated as a Poisson process where

$$p_t(k) = \frac{(\lambda t)^k}{k!} e^{-\lambda t},$$

and $\lambda = (a/A)K$. The mean and variance of a Poisson process are $E(k) = \lambda t$ and $V(k) = \lambda t$, respectively. The waiting time between discoveries, say u , is a random variable with the negative exponential distribution for a Poisson process. It follows that $E(u) = 1/\lambda$ and $V(u) = 1/\lambda^2$ are the mean and variance of the waiting time.

By application of renewal theory, Pella (1969) showed that the expected number of entries, $n_t(i)$, into any state, i , of the system is given approximately by

$$E[n_t(i)] \approx \frac{t}{\tau_{ii}} + \frac{\tau_{ii}^{(2)}}{2\tau_{ii}^2} - \frac{\tau_{oi}}{\tau_{ii}}, \quad (1.91)$$

where τ_{ii} is the mean recurrence time to state i ; τ_{oi} is the mean first passage time from state o to state i ; and $\tau_{ii}^{(2)}$ is the second moment about the origin of the length of time between entries into state i .

It was also assumed in the above derivation that the process began in a search state. A method for approximating the general solution is given in Pella's paper.

Example 1.17. Purse seine model with two states

The simple two-state model of Neyman (1949) can be solved for expected catch. Assume that the process is made of two states—searching for fish and catching fish (all sets are assumed successful)—and that time spent in the catching state is a fixed constant h . Equation (1.91) can be applied to this problem, as shown in Pella's paper. Expected catch (number of purse seine sets) over a time interval of length t is given by

$$E(C_t) \approx \frac{t}{1/\lambda + h} + \frac{h^2}{2(1/\lambda + h)^2}.$$

The first term on the right-hand side is the simple approximation one would expect: total time divided by expected search plus set time for each set. The second term is insignificant for practical values of λ and h . ■

Several extensions of the purse seine model and, more generally, the application of search theory to fisheries models have been considered in several papers by Mangel and co-workers (e.g., Mangel 1982, 1985; Mangel and Clark 1983; Mangel and Beder 1985).

Angling gear model

The angling gear model of Deriso and Parma (1987) is similar to Neyman's (1949) purse seine model. The angling process of “fish–handle gear–fish” can be thought of as a renewal process. Let $E[r(t)]$ be the expected value of $r(t)$, the number of gear retrievals during time interval $[0, t]$, then apply the definition of a renewal equation in stochastic processes to get

$$E[r(t)] = \int_0^t E[r(t-y)]dF(y) + F(t),$$

where $F(y)$ is the probability distribution function of time y elapsed before the first gear retrieval occurs; time elapsed includes handling time. Asymptotic formulae for renewal processes (Karlin and Taylor 1975) show, as $t \rightarrow \infty$, that $r(t)$ is distributed as a normal random variable:

$$r(t) \sim N(t/\mu, \sigma^2/\mu^3), \quad (1.92)$$

when time, y , elapsed between any two successive gear retrievals is a random variable with distribution $F(y)$, and mean μ and variance σ^2 .

Example 1.18. A fishing line with a single hook and bait

Following Deriso and Parma (1987), assume that the gear is retrieved after each attack by fish, either to be rebaited or have the bait checked. The random encounter assumption implies

$$P(\text{gear is attacked during a small time } \Delta t) = \lambda(\Delta t) + o(\Delta t),$$

where λ is the attack rate by all species, and $o(\Delta t)$ denotes terms of smaller order than Δt . Notice that attack rate, λ , is also assumed to be a constant in our model. For a single species, assume $\lambda = aX$, where X is species density and a is per capita attack rate. The above is just a typical structure of a Poisson process, and thus, $F(y)$ is a truncated exponential distribution. To see this result, note that

$$P(\text{no attacks up to time } y - h) = e^{-\lambda(y-h)}$$

for $y > h$. Therefore, the mean and variance of the exponential distribution, truncated of account for handling time h , can be written, respectively,

$$\begin{aligned} \mu &= \frac{1 + \lambda h}{\lambda}, \\ \sigma^2 &= \frac{1}{\lambda^2}. \end{aligned}$$

By substitution into (1.92) one obtains that $r(t)$ is normally distributed with mean and variance given by

$$\begin{aligned} E[r(t)] &= \frac{\lambda t}{1 + \lambda h}, \\ V[r(t)] &= \frac{\lambda t}{[1 + \lambda h]^3}. \end{aligned} \quad (1.93)$$

By rearranging (1.93), the relationship between attack rate and expected number of retrievals is

$$\lambda = \frac{E[r(t)]}{t - hE[r(t)]}. \quad (1.94)$$

By further assuming that catch on a given attack occurs with a constant probability, one concludes that expected catch is proportional to the expected number of gear retrievals, or $E[c(t)] \propto E[r(t)]$. Because attack rate λ is itself proportional to fish density, then an index of fish density from (1.94) is proportional to catch per unit soak time because

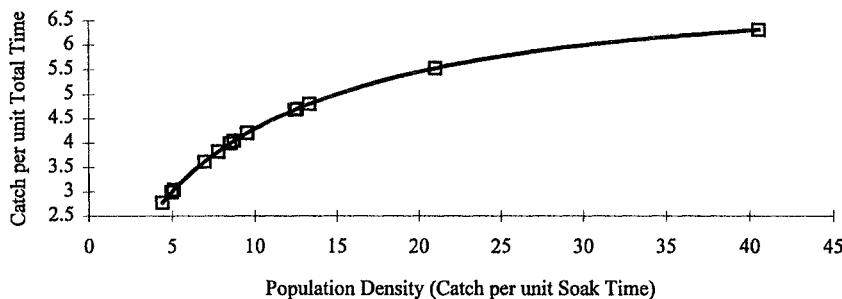


Figure 1.9. Relationship between expected CPUE (catch divided by total fishing time) and population density for Pacific Ocean snappers. Open squares represent CPUE data from Polovina (1986) for three combined groundfish species, paired to corresponding X-axis moment estimators (catch divided by soak time) for total species density. Time is measured in hours and h is fixed at 8 minutes. (Adapted from Deriso and Parma 1987.)

$$\lambda \propto \frac{E[c(t)]}{t - h E[r(t)]}. \quad (1.95)$$

This index is related to a moment estimator for λ ; the maximum likelihood estimator is derived by Deriso and Parma (1987). The relationship between catch per unit soak time given by (1.95) is nonlinearly related to catch per unit of total fishing time [that is, where the denominator in (1.95) is given simply by t], as illustrated in figure 1.9.

■

Multiple species generalization

The angling model of Deriso and Parma (1987) was extended in their paper to multi-species fishing. With only competition for the gear considered, the Poisson parameter, λ , is a linear function of abundances of all species, *viz.*,

$$\lambda = a_1 X_1 + a_2 X_2 + \cdots + a_n X_n,$$

where each species' density, X_i , is multiplied by the species-specific attack rate, a_i , and then summed over all species. If there is interference competition between two species so that one inhibits access to the gear of the other, then the equation for λ needs to be modified. Deriso and Parma considered such a case for three species where species 1 inhibits species 2; a_{12} denotes the inhibition factor. By assuming the interference is based on random encounters,

$$\lambda = a_1 X_1 + (a_2 - a_{12} X_1) X_2 + a_3 X_3$$

is an appropriate model when the act of inhibition by species 1 does not (significantly) affect its own attack rate.

Expected catch of the i th species is the product of a multinomial probability of catching the i th species out of all possible n species that could be present on a given hook and expected aggregate catch. Deriso and Parma showed this results in an expected catch of the i th species of

$$E[c_i(t)] = \frac{a'_i X_i t}{1 + \lambda' h} \quad (1.96)$$

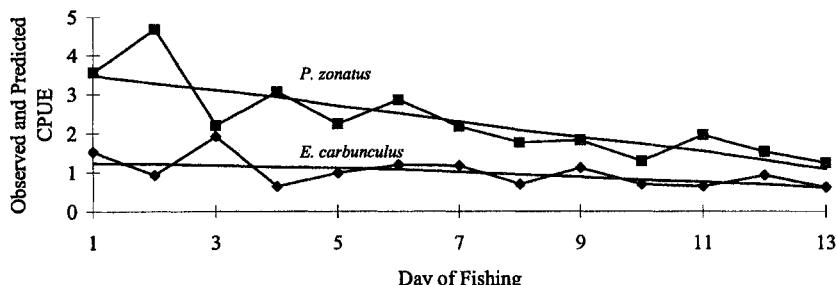


Figure 1.10. Observed CPUE (catch per hours fishing) for each day of fishing for two species of snappers, *Pristipomoides zonatus* (squares) and *Etelis carbunculus* (diamonds), from Polovina (1986). The smooth curve running through the middle of observed data is the trajectory for predicted CPUE (the expected value). (Adapted from Deriso and Parma 1987.)

where the prime symbol denotes that the a_i coefficients are replaced by a product of species-specific hooking success and attack rate.

Note that (1.96) is similar to (1.93), but that now handling time is taken for gear retrievals of all species. Expected catch per unit of time fishing is proportional to species abundance when $h = 0$ (no handling time). With handling time, however, the denominator in (1.96) is a function of abundance for the total species complex; here, catch for any given species depends nonlinearly on abundance of other species, and the catch can increase or decrease solely as a result of changes in abundance of other fishes. Therefore, an increase over time in CPUE of one species does not imply that this species is being directly affected by the behavior of another species, but rather it can be due, in a sense, to competition for limited handling time.

The effect that the abundance of one species can have on catches of another species is illustrated in the application of the above angling model to three species of snappers caught during a depletion experiment in the Mariana Island region. The fishing area was thought to contain a closed population for the duration of the experiment (Polovina 1986), and thus abundance of each species should have declined with fishing removals. Figures 1.10 and 1.11 show CPUE (catch per hours fishing, including handling time) for the three species along with expected catch (1.96) under the assumption of no direct interference competition. The increase in observed CPUE for *Pristipomoides auricilla* is accounted for simply by competition with the two species depicted in figure 1.10 for the limited amount of handling time available on the deep-sea handline fishing gear used in the experiment. The figures illustrate the importance of measuring soak time in the experiment; catch per unit soak time is a better measure of fish density.

Longline model

Multispecies competition for gear affects the interpretation of data collected in the course of longline fishing. Both deterministic models (Murphy 1960) and stochastic models (Rothschild 1967) show that abundance of a given target species is nonlinearly related to CPUE (target species catch per number of hooks of long-line fishing gear). The nonlinearity is caused by both interspecific and intraspecific competition for available baits. A similar nonlinearity occurs with angling gear, as seen above.

The longline model developed below is based on the simplifying assumption that

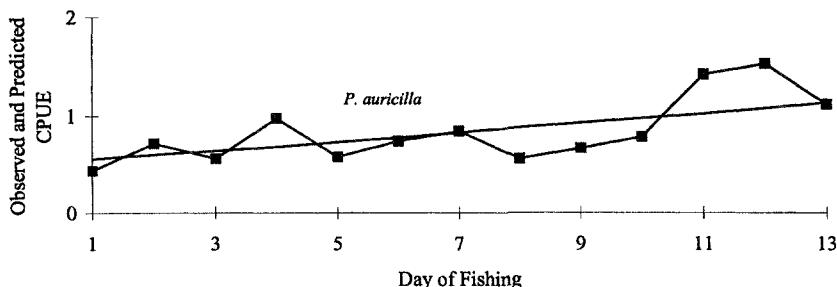


Figure 1.11. Observed CPUE (catch per hours fishing) for each day of fishing for the snaper, *Pristipomoides auricilla*, from Polovina (1986). The smooth curve running through the middle of observed data is the trajectory for predicted CPUE (the expected value). (Adapted from Deriso and Parma 1987.)

attacks on each baited hook occur randomly and that the bait is removed during the attack, irrespective of whether a fish is caught. In addition, the assumption is made that bait either deteriorates or is removed by uncatchable species (such as starfish) during a short time period, Δt , with probability $d\Delta t$. Specifically, the model is based on the assumption that

$$P(\text{hook is emptied during a small time } \Delta t) = (\lambda + d)\Delta t + o(\Delta t),$$

where λ is the aggregate attack rate of all catchable species and $o(\Delta t)$ denotes terms of smaller order than Δt . By following a limiting process, similar to that given in Rothschild (1967, p. 104), as $\Delta t \rightarrow 0$, we see that

$$P(\text{hook is not emptied during a fishing period}) = e^{-(\lambda+d)T}, \quad (1.97)$$

where T is the amount of time in a fishing period. Equation (1.97) is essentially a survival probability for baits, similar in its derivation to conventional competing risk models of survival (Chiang 1968). In the model, λ is treated as a constant during any given fishing period with no adjustment made for changes in species abundance.

With only competition for a given hook considered, the attack rate λ for multiple species fishing is a linear function of all species abundances,

$$\lambda = a_1 X_1 + a_2 X_2 + \cdots + a_n X_n,$$

where each species density X_i is multiplied by the species-specific attack rate, a_i , and then the products are summed over all n species being considered. This competition equation is identical to the one given earlier for angling gear.

Fish may attack a baited hook, remove the bait, but not get hooked in the process. Let θ_i be the probability that an individual of species i is hooked when it attacks a baited hook. The probability, p_i , that an individual of species i will be on a given hook when the gear is hauled can be written as a product of three probabilities:

$$p_i = \theta_i \frac{a_i X_i}{\lambda + d} [1 - e^{-(\lambda+d)T}].$$

Starting from right to left, these probabilities are the probability that the bait is taken in a fishing period of duration T times the probability that species i attacked the hook, given that the bait was taken, times the probability that the attack results in a catch.

Following Rothschild (1967), assume that species-specific catch on a unit of long-line gear is distributed multinomially. In essence, this means that all H hooks on the gear are treated as statistically independent. Independence is probably a reasonable assumption for solitary predators, like Pacific halibut, but less likely for schooling fishes because neighboring hooks are more likely to return with catch of the same schooling species than would be expected based on the species population density. The probability of obtaining a given set of species-specific catches is given by a multinomial distribution:

$$P(C_1, \dots, C_n) = \frac{H!}{(H - \Sigma C_i)! (\prod C_i!)} (1 - \sum p_i)^{(H - \Sigma C_i)} \prod_{i=1}^n p_i^{C_i},$$

where C_i is the number of individuals of species i caught on a unit of gear, and H is the total number of hooks on a unit of gear. The summation symbol indicates summation across all n species unless subscripts indicate otherwise.

As the competition model now stands, there are too many fundamental parameters ($\{a_i, \theta_i, X_i\}$, d) to see clearly some basic properties of the resultant estimators of fish density. In an application to a depletion experiment on Pacific halibut (R. B. Deriso, unpublished manuscript), the following simplifications were made. The first simplifying assumption is that $\theta = 1$. Second, virtually no bait is left intact after a typical several-hour gear-soak time. Therefore, the probability in (1.97) of bait remaining on a hook is nearly zero; this can be due to a high d value for losses due to deterioration and other causes. Finally, reparameterize the model, let $\tilde{a}_i = a_i/d$, then, together with the above simplifications, get the following approximation to p_i :

$$p_i \approx \frac{\tilde{a}_i X_i}{\sum \tilde{a}_i X_i + 1}. \quad (1.98)$$

Maximum likelihood estimates (MLEs) of species density can now be found. MLEs of the p_i are solved in the usual manner to get $\hat{p}_i = C_i/H$. By the invariance principle of MLEs, the MLE of species density is solved by substituting \hat{p}_i into (1.98) to get

$$\widehat{\tilde{a}_i X_i} = \frac{C_i}{H - \Sigma C_i}, \quad (1.99)$$

because

$$\tilde{a}_i X_i = p_i / (1 - \sum p_i).$$

The MLE of a given species population density above can be written in words as

$$\text{Population density} \propto \frac{\text{Catch}}{\text{Total number of hooks} - \text{Catch}},$$

which shows, by analogy to the angling model, that the denominator takes into account the adjustment of nominal effort by subtracting hooks removed from fishing by the catch.

Variance of the MLE for \hat{p}_i is given by $V(\hat{p}_i) = p_i(1 - p_i)/H$, the variance of $(1 - \Sigma \hat{p}_i)$ is given by $V(1 - \Sigma \hat{p}_i) = \Sigma p_i(1 - \Sigma p_i)/H$, and the covariance between those terms is $\text{cov}[\hat{p}_i, (1 - \Sigma \hat{p}_i)] = -p_i(1 - \Sigma p_i)/H$ (Mardia et al. 1979). Species density in (1.99) is a ratio of the p_i parameters, and its variance can be approximated with the delta method (Seber 1982):

$$V(\widehat{\tilde{a}_i X_i}) \approx \frac{\tilde{a}_i X_i}{H - E(\Sigma C_i)} (1 + \tilde{a}_i X_i),$$

where $E(\Sigma C_i)$ is expected value of the aggregate catch of all species.

Stock Productivity and Surplus Production

2.1. THEORY OF STOCK PRODUCTIVITY

Much of fish population dynamics focuses on harvesting. Given the latent productivity of a population (defined formally below), it is of interest to determine what surplus is available for harvesting, after replenishment of the population through recruitment and fish growth and diminishment of the population through natural mortality. In dealing with dynamics under harvesting, we use one concept of a stock being the aggregate of a population that can be managed as a discrete unit. In commercial fisheries, stock size and amount of harvest are often given in units of weight. Thus, our development refers to stock biomass as the weight of all fish in the stock and yield as the weight of fish harvested in aggregate. As we introduce more complex features into population models, we will return to the term “population.”

In this section, mathematical models of stock productivity are developed, and the amount of surplus production available for harvest is determined. The relationships of yield to biomass, fishing mortality and fishing effort are derived, and time-dependent behavior is described. Methods for estimating surplus production are presented in section 2.2. The relationship between surplus production and recruitment, growth, and natural mortality is described in section 2.3.

The stock is modeled simplistically; no direct account is made of recruitment, fish growth, natural mortality, age structure, or interactions with other species. Let $B = B(t)$, the stock biomass at time t , and $Y = Y(t)$, the cumulative yield from harvesting up to time t . These quantities are analogous to abundance, N , and catch, C , used in previous sections through the transformation of average fish weight, \bar{W} , which is represented by

$$B = N\bar{W} \text{ and } Y = C\bar{W}.$$

Frequently, we use “dot notation” for instantaneous rates; for a variable X ,

$$\dot{X} \equiv \frac{dX}{dt}.$$

Latent productivity, \dot{P} , is defined as the instantaneous rate of biomass production in the absence of fishing ($\dot{Y} = 0$). We consider models of latent productivity which are a

function of stock biomass alone, or $\dot{P} \equiv \dot{P}(B)$. Specific models for latent productivity, $\dot{P}(B)$, are given in subsequent sections.

From the definition of biomass, $B = N\bar{W}$, latent productivity can be expanded as

$$\dot{P} = \dot{B} = N\dot{\bar{W}} + \dot{N}\bar{W}.$$

Thus, latent productivity has two components: the first component represents changes due to growth of individuals, and the second component represents abundance changes such as death or recruitment. Allen (1971) examined the weight change component, $\dot{P}_1 = N\dot{\bar{W}}$, for a single cohort and for multiple cohorts by using different models for weight and abundance. He defined production as the “total amount of tissue elaborated in the population,” represented by $\int \dot{P}_1 dt$. The ratio of production to integrated biomass (or, equivalently, productivity component, \dot{P}_1 , to mean biomass) is often used as a comparative tool among cohorts, species, and communities. In our treatment, we use both components of productivity and define production, P , as $\int \dot{P} dt$.

In the presence of fishing, the instantaneous rate of change in biomass, also called “net productivity,” is equal to latent productivity decremented by the accrual rate of yield, or

$$\dot{B} = \dot{P} - \dot{Y}. \quad (2.1)$$

This fundamental relationship, derived by Fletcher (1978a), shows that biomass increases when latent productivity exceeds yield rate ($\dot{P} > \dot{Y} \Rightarrow \dot{B} > 0$), and vice versa. In the absence of fishing, the instantaneous change in biomass from (2.1) is equal to latent productivity ($\dot{B} = \dot{P}$ when $\dot{Y} = 0$).

When biomass does not change ($\dot{B} = 0$), the stock is said to be at equilibrium; equilibrium quantities are denoted with an asterisk. A general relationship between yield and biomass at equilibrium follows by setting $\dot{B} = 0$ in (2.1); thus $\dot{Y} = \dot{P}$, and with initial condition $Y(0) = 0$,

$$\begin{aligned} \int_0^{Y_*} dY &= \int_0^{\tau} \dot{P}(B_*) dt \\ \Rightarrow Y_*/\tau &= \dot{P}(B_*), \end{aligned} \quad (2.2)$$

because equilibrium latent productivity, $\dot{P}(B_*)$, is constant as a function of time, t . If time is measured in annual units, then for a one-year period ($\tau = 1$), the important concept emerges that annual surplus production (the integral of productivity) can be taken as equilibrium yield through harvesting.

In the presence of fishing, a general relationship between yield rate, \dot{Y} , fishing mortality, $F(t)$, and biomass, $B(t)$, analogous to that for catch rate in (1.21), is

$$\dot{Y} = F(t) B(t). \quad (2.3a)$$

To obtain equilibrium solutions, fishing mortality is assumed constant [$F(t) = F_*$], so that

$$\dot{Y} = F_* B(t). \quad (2.3b)$$

This linear relationship between yield rate and biomass is shown in figure 2.1. If the population is at equilibrium [$B(t) = B_*$], integration of (2.3b) with initial condition $Y(0) = 0$ results in

$$Y_*/\tau = F_* B_*. \quad (2.4a)$$

Thus, equilibrium fishing mortality can be found from the equation

$$F_* = (Y_*/\tau)/B_* = \dot{P}(B_*)/B_* \quad (2.4b)$$

with the use of (2.2). Conversely, (2.4b) can be solved for B_* as a function of F_* . If fishing mortality is proportional to fishing effort, as in (1.36), equilibrium fishing effort from (2.4b) is then

$$E_* = F_* \tau / q = Y_*/(q B_*). \quad (2.4c)$$

A typical latent productivity relationship, $\dot{P}(B)$, starts at 0 at $B = 0$, increases to maximum productivity, m , at stock biomass B_m , and decreases to 0 at stock biomass B_∞ . The special case of a parabolic relationship is shown in figure 2.1 and is fully described in the section 2.1.1. Parameter B_∞ is called the asymptotic (or “pristine,” “virgin,” “unfished”) stock biomass, analogous to the logistic K (see section 1.1.2). When the stock is not fished, the stock will tend toward B_∞ . When the stock is fished, the stock will tend toward a new equilibrium, B_* , and equilibrium yield (per unit time), fishing mortality, and fishing effort are determined from (2.4a,b,c). Maximum equilibrium yield, commonly known as “maximum sustainable yield” (MSY), is equal to maximum productivity, m , by examination of (2.2), where a unit time period ($\tau = 1$) is implicit. Thus, the stock biomass that produces MSY is B_m , and fishing mortality, F_m , and fishing effort, E_m , follow from (2.4b) and (2.4c) by replacing $*$ with m .

2.1.1. Graham-Schaefer Model

The first example of latent productivity, the Graham-Schaefer system, stems from the classic logistic law, discussed in section 1.1.2. As a fisheries model, this system has been explored by Graham (1935), Schaefer (1954, 1957), Ricker (1975a), Fletcher (1978a), and Gulland (1983). Latent productivity is modeled variously as

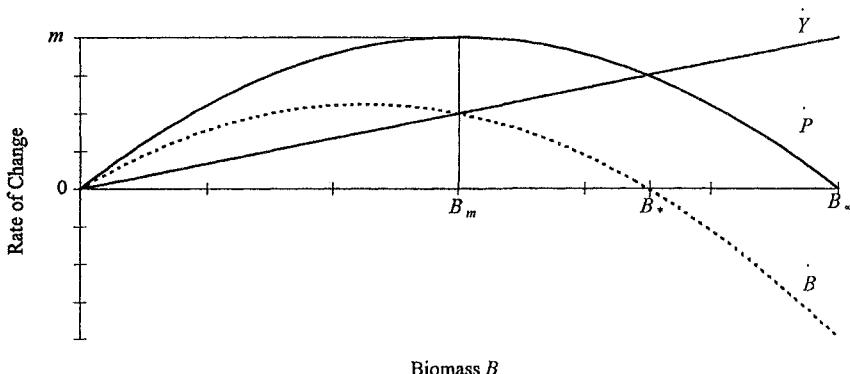


Figure 2.1. Latent productivity, \dot{P} ; yield rate, $\dot{Y} = F_* B$, and rate of change of biomass, $\dot{B} = \dot{P} - \dot{Y}$ as a function of biomass, B , for the Graham-Schaefer surplus production model. Reference points include pristine biomass, B_∞ ; maximum productivity, m ; biomass, B_m , at which maximum productivity occurs; and equilibrium biomass, B_* , for fishing mortality, F_* .

$$\dot{P}(B) = \begin{cases} k \left(1 - \frac{B}{B_\infty}\right) B & (\text{Graham, Schaefer, Ricker}) \\ r' (B_\infty - B) B & (\text{Gulland}) \\ \frac{4m}{B_\infty} \left(1 - \frac{B}{B_\infty}\right) B & (\text{Fletcher}), \end{cases} \quad (2.5)$$

where k is an intrinsic growth parameter analogous to the logistic r , and $r' = k/B_\infty$. Fletcher's formulation is used in subsequent development because of the inherent utility of its parameters.

First, an equilibrium analysis is made to determine when the stock is stable. In the absence of fishing, equilibrium occurs when $\dot{P} = 0$, or from (2.5), when

$$\frac{4m}{B_\infty} \left(1 - \frac{B}{B_\infty}\right) B = 0.$$

This equation has two solutions, $B = 0$ and $B = B_\infty$. The biomass, B_m , at which maximum productivity, m , occurs is obtained from

$$\begin{aligned} \frac{d\dot{P}}{dB} &= \frac{4m}{B_\infty} - \frac{8mB}{B_\infty^2} = 0 \\ \Rightarrow B_m &= \frac{B_\infty}{2}. \end{aligned}$$

Substituting B_m into (2.5) yields maximum productivity, m :

$$\begin{aligned} \dot{P}(B_m) &= \frac{4m}{B_\infty} \left(1 - \frac{B_m}{B_\infty}\right) B_m \\ &= m. \end{aligned}$$

Figure 2.1 shows the parabolic curve for latent productivity (2.5) as a function of biomass between 0 and B_∞ with a maximum at m . The parameters m and B_∞ define a family of latent productivity curves, as shown by Fletcher (1978a).

In the presence of fishing, the resultant differential equation from (2.1), (2.3a), and (2.5) is

$$\begin{aligned} \dot{B} &= \frac{4m}{B_\infty} \left(1 - \frac{B}{B_\infty}\right) B - F(t) B \\ &= \left[\frac{4m}{B_\infty} - F(t) \right] B - \frac{4m}{B_\infty^2} B^2. \end{aligned} \quad (2.6)$$

When fishing occurs at level F_* as in (2.3b), \dot{B} is a parabolic function of B , as shown in figure 2.1.

At equilibrium [$\dot{B} = 0$ and $F = F_*$ in (2.6)], there are two solutions: $B = 0$ and

$$B_* = B_\infty - \frac{B_\infty^2}{4m} F_*, \quad (2.7)$$

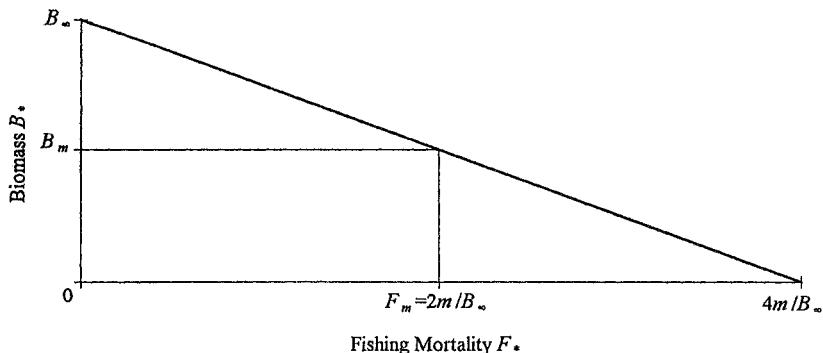


Figure 2.2. The linear relationship between equilibrium biomass and fishing mortality for the Graham-Schaefer surplus production model. When fishing mortality is greater than or equal to $4m/B_\infty$, equilibrium biomass is 0. Fishing mortality, F_m , which produces maximum sustainable yield is $2m/B_\infty$; the corresponding biomass, B_m , occurs at $B_\infty/2$.

showing that the relationship between equilibrium biomass and fishing mortality is linear (figure 2.2). For a positive equilibrium biomass to occur, fishing mortality must be less than $4m/B_\infty$; otherwise the stock crashes.

For clarity, further equilibrium relationships are given only for a unit time period ($\tau = 1$). Equilibrium yield is a parabolic function of equilibrium biomass from (2.2) and (2.5), or

$$Y_* = \frac{4m}{B_\infty} \left(1 - \frac{B_*}{B_\infty} \right) B_*. \quad (2.8a)$$

By substituting (2.7) into (2.4a) [or into (2.8a)], equilibrium yield is also a parabolic function of fishing mortality, or

$$Y_* = F_* B_* = B_\infty F_* - \frac{B_\infty^2}{4m} F_*^2, \quad (2.8b)$$

a consequence of the negative linear relationship (2.7). The relationship between equilibrium yield and fishing effort, E_* , from (2.4c) and (2.8b) is also parabolic, or

$$Y_* = q E_* B_* = q B_\infty E_* - \frac{q^2 B_\infty^2}{4m} E_*^2, \quad (2.8c)$$

because $F_* = q E_*$. These three relationships (2.8a, b, c) are illustrated in figure 2.3.

Maximum sustainable yield (Y_m) is equivalent to maximum productivity, $P(B_m) = m$, as a consequence of (2.2) and occurs at $B_m = B_\infty/2$. From (2.4b), fishing mortality that produces MSY is

$$F_m = Y_m/B_m = m/B_m = 2m/B_\infty.$$

Fishing effort that produces MSY from (2.4c) is

$$E_m = F_m/q = 2m/(q B_\infty).$$

These values are indicated in figures 2.1–2.3.

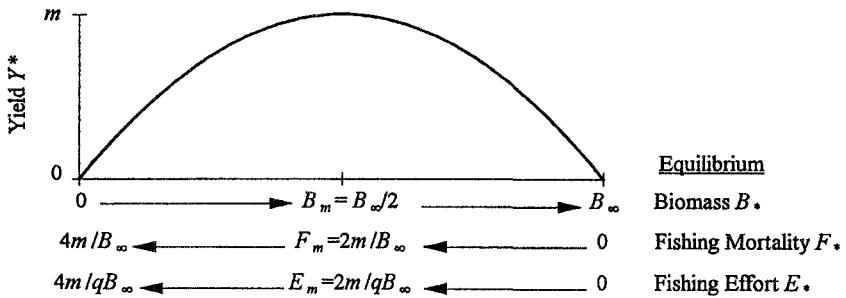


Figure 2.3. Parabolic relationships between equilibrium yield and equilibrium biomass, fishing mortality, and fishing effort for the Graham-Schaefer surplus production model. The maximum sustainable yield (MSY) is m ; corresponding values for B_m , F_m , and E_m are shown.

The time-dependent behavior for biomass in the Graham-Schaefer system is obtained by integrating (2.6) over a time period where $F = F_*$ is constant. The steps in the solution are the same as those for the logistic law in section 1.1.2. Given the initial condition B_0 at $t = 0$, the solution is

$$B(t) = \frac{B_*}{1 + \frac{B_* - B_0}{B_0} e^{-(4m/B_\infty - F_*)t}}, \quad (2.9)$$

where B_* is given in (2.7). When stock biomass $B(t)$ is below equilibrium biomass, B_* , it increases toward B_* in a sigmoidal manner. If $B(t)$ is above B_* , it decreases exponentially toward B_* . If F_* changes, then a new equilibrium biomass is defined, and the stock will move toward that new level.

When $F = 4m/B_\infty$, the first term on the right-hand side of (2.6) drops out, and the solution to the differential equation is then

$$B(t) = \left(\frac{1}{B_0} + \frac{4m}{B_\infty^2} t \right)^{-1},$$

which goes to 0 as $t \rightarrow \infty$. As $4m/B_\infty$ is equal to the intrinsic growth parameter k in (2.5), fishing at rates $F \geq k$ sends the stock to extinction.

The time-dependent behavior for yield is obtained by integrating (2.3b) with (2.9) for $B(t)$. Given the initial condition $Y_0 = 0$ at $t = 0$, Fletcher (1978a) showed that the solution for cumulative yield, $Y_C(t)$, from time 0 up to time t is

$$Y_C(t) = \begin{cases} (B_\infty - B_*) \ln \left[1 + \frac{B_0}{B_*} \left\{ e^{(4m/B_\infty - F_*)t} - 1 \right\} \right], & F \neq 4m/B_\infty \\ B_\infty \ln \left(1 + \frac{4m B_0}{B_\infty^2} t \right), & F = 4m/B_\infty \end{cases}, \quad (2.10)$$

where B_* is given in (2.7). For a time unit of one year, annual yield, Y_t , from t to $t + 1$ is calculated as

$$Y_t = Y_C(t + 1) - Y_C(t),$$

or directly from (2.10) with $t = 1$ and $B_0 = B(t)$. Annual yield approaches equilibrium yield, Y_* , in a manner similar to how biomass approaches equilibrium biomass. When F changes, a new equilibrium yield is defined, and annual yield moves toward the new equilibrium.

Example 2.1. Hypothetical stock

Suppose that a stock follows a Graham-Schaefer system, for which production parameter, m (MSY), is 1000 units and pristine biomass, B_∞ , is 10,000 units. Therefore B_m is 5000 units and F_m is 0.2. The catchability parameter, q , is 0.01, and starting biomass, B_0 , is 10,000 units. The stock is harvested for 30 years under three fishing mortality regimes: $F = 0.45$ for the first 10 years, $F = 0.05$ for the second 10 years, and $F = 0.2$ for the last 10 years. Calculations of B_* and B_t are given in table 2.1, with the time-dependent behavior illustrated in figure 2.4. Biomass levels after each change in F are calculated by redefining B_0 to be the biomass at the time when F changes. Equilibrium and annual yields are also calculated in table 2.1 and shown in figure 2.4. In the final period when $F = F_m$, the yield approaches $m = \text{MSY}$. ■

2.1.2. Pella-Tomlinson Model

The Graham-Schaefer model has been criticized for its lack of flexibility, in that MSY must occur at 50% of pristine biomass, B_∞ . Pella and Tomlinson (1969) provided a more general model with an additional parameter to allow the biomass level, B_m , at MSY to be shifted to the left or right. Its most common representation for latent productivity is

$$\dot{P}(B) = \pm aB^n \mp bB, \quad a, b > 0, \quad (2.11)$$

where the positive case is used when $0 < n < 1$ and the negative case is used when $n > 1$. When $n \rightarrow 1$, the special limiting case is called the Gompertz-Fox model, discussed in section 2.1.3.

Fletcher (1978b), by a convenient reparameterization, was able to recast the two equations (2.11) into a single equation, with parameters m and B_∞ identical to those for the Graham-Schaefer model. This three-parameter model for latent productivity is

$$\dot{P} = \gamma m \left(\frac{B}{B_\infty} \right) - \gamma m \left(\frac{B}{B_\infty} \right)^n, \quad (2.12)$$

where

$$\gamma = \frac{n^{n/(n-1)}}{n-1}.$$

The parameter γ is positive when $n > 1$ and negative when $0 < n < 1$. The relationship between latent productivity and biomass is shown in figure 2.5 for four values of n , showing that n controls the shape of the relationship, whereas m controls the extremum along the \dot{P} -axis and B_∞ controls the root along the B -axis. Equations for converting between (2.11) and (2.12) are

$$B_\infty = \left(\frac{a}{b} \right)^{1/(1-n)} \quad \text{and} \quad m = \pm \frac{b(1-n)}{n} \left(\frac{an}{b} \right)^{1/(1-n)}.$$

The biomass, B_m , at which maximum productivity, m , occurs [ρ in Fletcher (1978b)] is found by setting the derivative of (2.12) with respect to B to 0, or

Table 2.1. Equilibrium biomass, B_* , biomass, B_t , at the start of each year t , equilibrium annual yield, Y_* , and annual yield, Y_t , for a Graham-Schaefer population with initial biomass, B_0 , of 10,000 units, pristine biomass, B_∞ , of 10,000 units, maximum productivity, m , of 1,000 units, and fishing mortality, F_t , of 0.45 for the first 10 years, 0.05 for the second 10 years, and 0.2 ($= F_m$) for the last 10 years.

t	F_t	B_*	B_t	Y_*	Y_t
0	0.45	-1250	10000	0	3706
1	0.45	-1250	6843	0	2662
2	0.45	-1250	5137	0	2055
3	0.45	-1250	4071	0	1658
4	0.45	-1250	3342	0	1379
5	0.45	-1250	2812	0	1171
6	0.45	-1250	2410	0	1011
7	0.45	-1250	2096	0	884
8	0.45	-1250	1843	0	781
9	0.45	-1250	1635	0	696
10	0.05	8750	1462	438	85
11	0.05	8750	1939	438	111
12	0.05	8750	2518	438	142
13	0.05	8750	3189	438	178
14	0.05	8750	3926	438	215
15	0.05	8750	4689	438	253
16	0.05	8750	5434	438	289
17	0.05	8750	6119	438	321
18	0.05	8750	6715	438	349
19	0.05	8750	7210	438	371
20	0.20	5000	7605	1000	1451
21	0.20	5000	6949	1000	1341
22	0.20	5000	6490	1000	1263
23	0.20	5000	6158	1000	1206
24	0.20	5000	5910	1000	1162
25	0.20	5000	5721	1000	1129
26	0.20	5000	5575	1000	1103
27	0.20	5000	5461	1000	1083
28	0.20	5000	5372	1000	1067
29	0.20	5000	5300	1000	1054
30			5243		

$$0 = \frac{\gamma m}{B_\infty} - \frac{\gamma mn}{B_\infty} \left(\frac{B_m}{B_\infty} \right)^{n-1}$$

$$\Rightarrow B_m = n^{1/(1-n)} B_\infty, \quad (2.13)$$

which shows that the positioning of B_m in relation to pristine biomass is solely a function of n . Figure 2.5 shows the shifting of B_m as a function of exponent n for given B_∞ and m . Substituting (2.13) for B in (2.12) shows that maximum productivity is indeed m .

In the presence of fishing, the Pella-Tomlinson system from (2.1), (2.3a), and (2.12) becomes

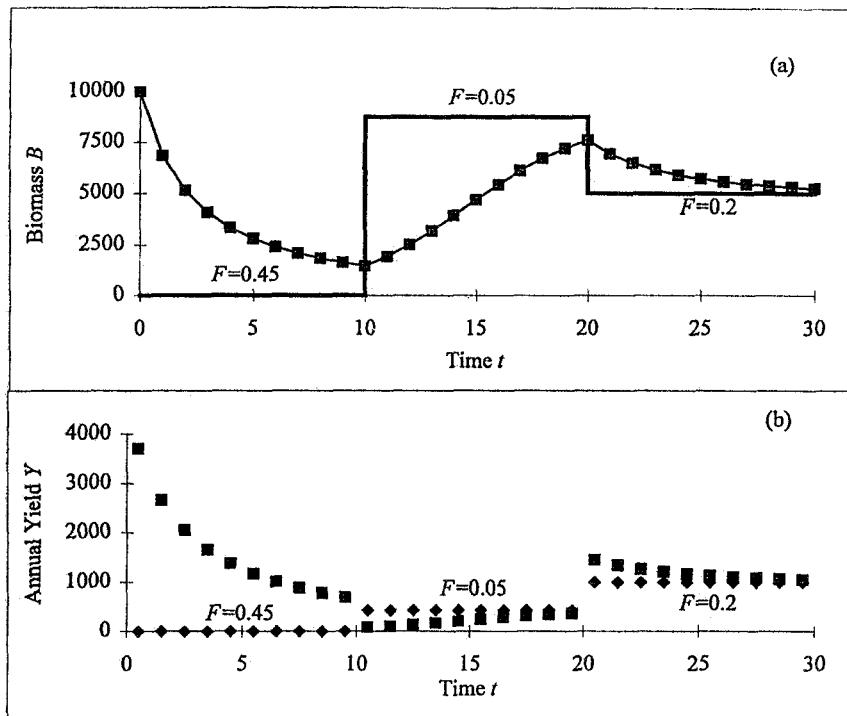


Figure 2.4. Time trajectories of (a) biomass and (b) annual yield (squares) for a stock following the Graham-Schaefer surplus production model with $m = 1000$ and $B_\infty = 10,000$. The stock starts at B_∞ and is fished for three 10-year fishing periods with the shown values of fishing mortality; the last corresponds to the rate producing MSY. Equilibrium biomass (solid line) and yield (diamonds) corresponding to the fishing mortalities are also depicted.

$$\dot{B} = \left[\frac{\gamma m}{B_\infty} - F(t) \right] B - \frac{\gamma m}{B_\infty^n} B^n. \quad (2.14)$$

At equilibrium ($\dot{B} = 0$ and $F = F_*$), there are two solutions: $B = 0$ and

$$B_* = B_\infty \left(1 - \frac{B_\infty}{\gamma m} F_* \right)^{1/(n-1)}. \quad (2.15)$$

This nonlinear relationship between equilibrium biomass and fishing mortality varies dramatically as a function of n (figure 2.6). This equation has the interesting property that $B_* > 0$ no matter what the value of F_* when $0 < n < 1$. When $n > 1$, note that for a positive equilibrium biomass to occur, fishing mortality should be less than $\gamma m / B_\infty$.

The relationships between yield, biomass, and fishing mortality at equilibrium are obtained analogously to the Graham-Schaefer system. For a unit time period, equilibrium yield is

$$Y_* = \dot{P}(B_*) = \frac{\gamma m}{B_\infty} B_* - \frac{\gamma m}{B_\infty^n} B_*^n. \quad (2.16)$$

This relationship is akin to the latent productivity relationship (2.12) shown in figure 2.5. By substituting (2.15) into (2.4a) [or into (2.16)],

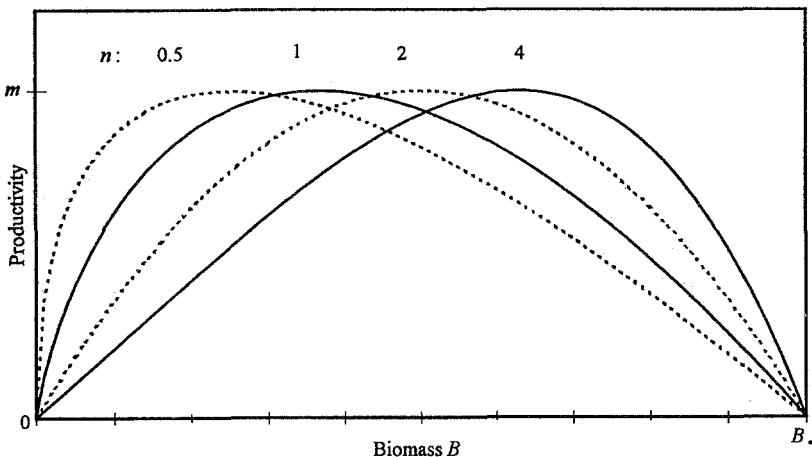


Figure 2.5. The relationship between latent productivity, \dot{P} , and biomass, B , for four cases of the Pella-Tomlinson surplus production model: $n = 0.5$, $n = 1$ (Gompertz-Fox), $n = 2$ (Graham-Schaefer), and $n = 4$. Maximum productivity, m , and equilibrium unfished biomass, B_∞ , are kept constant among the cases to show only the effect of varying n . Values of B_m for these four cases are $\frac{1}{4}$, $\frac{1}{e}$, $\frac{1}{2}$, and $\sqrt[3]{\frac{1}{4}} \approx 0.63$ of B_∞ from (2.13).

$$Y_* = F_* B_\infty \left(1 - \frac{B_\infty}{\gamma m} F_* \right)^{1/(n-1)}. \quad (2.17)$$

The shape of this relationship is strongly influenced by n (figure 2.7). The relationship between equilibrium yield and fishing effort, E_* , is obtained by substituting $q E_*$ for F_* in (2.17).

Maximum sustainable yield is equal to m as before and occurs at B_m , given in (2.13). Hence, fishing mortality that produces MSY is

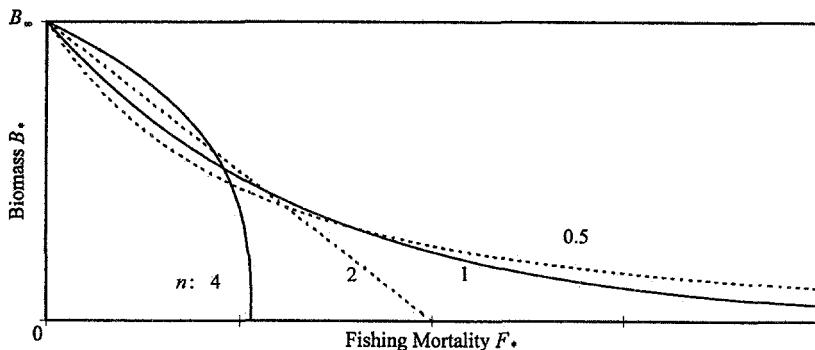


Figure 2.6. The relationship between equilibrium biomass and fishing mortality for four cases of the Pella-Tomlinson surplus production model. The parameter n controls the shape of the decline. When $n \leq 1$, there is no finite value of fishing mortality that gives a nonpositive equilibrium biomass.

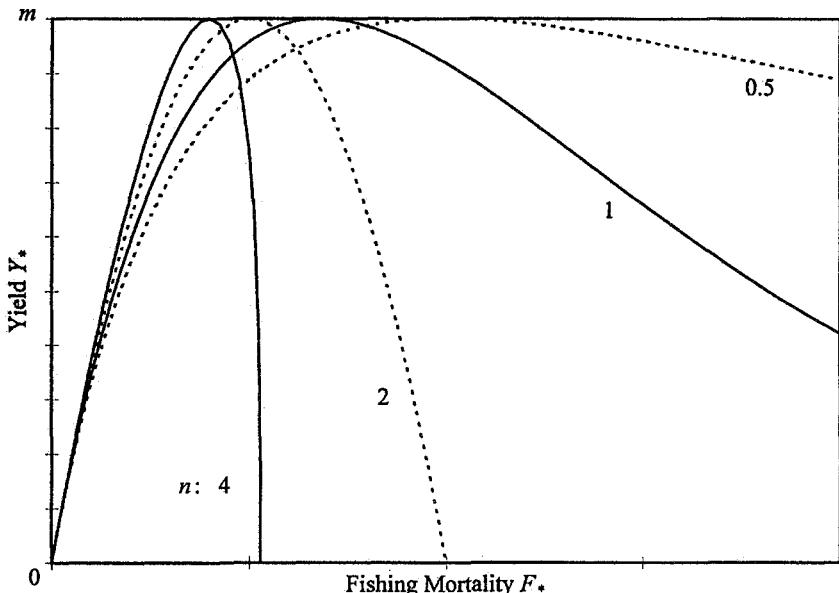


Figure 2.7. The relationship between equilibrium yield and fishing mortality for four cases of the Pella-Tomlinson surplus production model. The parameter n controls the shape and the extent of the relationship. When $n \leq 1$, there is no finite, positive value of fishing mortality that gives a nonpositive equilibrium yield.

$$F_m = \frac{m}{B_m} = \frac{n-1}{n} \left(\frac{\gamma m}{B_\infty} \right),$$

and fishing effort at MSY is

$$E_m = \frac{F_m}{q} = \frac{n-1}{n} \left(\frac{\gamma m}{q B_\infty} \right).$$

The time-dependent behavior for biomass in the Pella-Tomlinson system is obtained by integrating (2.14) with $F = F_*$ and initial condition B_0 at time 0, which produces

$$B(t) = \left[B_*^{1-n} + (B_0^{1-n} - B_*^{1-n}) e^{(\gamma m / B_\infty - F_*)(1-n)t} \right]^{1/(1-n)}, \quad (2.18)$$

where B_* is given in (2.15).

The time-dependent behavior for cumulative yield from (2.3b) and (2.18) for the initial condition $Y_0 = 0$ at $t = 0$ and $F = F_*$ is

$$Y_C(t) = F_* B_* \int_0^t \left\{ 1 - \left[1 - (B_0 / B_*)^{1-n} \right] e^{(\gamma m / B_\infty - F_*)(1-n)t} \right\}^{1/(1-n)} dt, \quad (2.19)$$

(Fletcher 1978b), where B_* is given in (2.15). Equation (2.19) can be integrated by using series expansions, or numerically if a numerical upper limit is of interest. The time-dependent behavior of the Pella-Tomlinson system is similar to the Graham-Schaefer system, except that the inflection point of the curves is now controlled by the parameter n . For a time unit of one year, annual yield, Y_t , is calculated as the difference, $Y_C(t+1) - Y_C(t)$, or directly from (2.19) with $t = 1$ and $B_0 = B(t)$.

2.1.3. Gompertz-Fox Model

The Gompertz-Fox model, a special case of the Pella-Tomlinson model with $n = 1$, is obtained as a limiting form of (2.12) as $n \rightarrow 1$ (Fox 1970, Fletcher 1978b). The “Gompertz” designation refers to a general growth model developed by Gompertz (see section 4.3.3). The resultant differential equation for latent productivity is

$$\dot{P} = -em \frac{B}{B_\infty} \ln \left(\frac{B}{B_\infty} \right). \quad (2.20)$$

Equation (2.20) is controlled by the same two parameters m and B_∞ of the Graham-Schaefer system, but its shape is quite different (case $n = 1$ in figure 2.5). The biomass, B_m , at which maximum productivity, m , occurs is found by setting the derivative of (2.20) with respect to B to 0; thus,

$$B_m = B_\infty/e \approx 0.368B_\infty. \quad (2.21)$$

Thus, the biomass B_m at which maximum productivity occurs is fixed at 36.8% of pristine biomass, which is less than the 50% of pristine biomass for the Graham-Schaefer system. So, the Gompertz-Fox model is as inflexible as the Graham-Schaefer model. Substituting B_m into (2.20) shows that maximum productivity is indeed m .

In the presence of fishing, the differential equation for biomass from (2.1), (2.3a), and (2.20) is

$$\dot{B} = -em \frac{B}{B_\infty} \ln \left(\frac{B}{B_\infty} \right) - F(t)B. \quad (2.22)$$

At equilibrium ($\dot{B} = 0, F = F_*$), there are two solutions: $B = 0$ and

$$B_* = B_\infty \exp \left(-\frac{B_\infty}{em} F_* \right) = B_\infty \exp \left(-\frac{B_m}{m} F_* \right). \quad (2.23)$$

Thus, the relationship between equilibrium biomass and fishing mortality is an exponentially decreasing function, controlled by the inverse of the ratio of maximum productivity, m , to the biomass at which it occurs, B_m . The relationship is shown in figure 2.6 for the case $n = 1$. In common with the cases $0 < n < 1$ in the Pella-Tomlinson model, this equation has the interesting property that $B_* > 0$ no matter what the value of F_* .

The relationships between yield, biomass, and fishing mortality at equilibrium for the Gompertz-Fox system are obtained analogously to the Pella-Tomlinson system. For a unit time period, equilibrium yield is

$$Y_* = \dot{P}(B_*) = -em \frac{B_*}{B_\infty} \ln \left(\frac{B_*}{B_\infty} \right), \quad (2.24)$$

which is akin to the productivity–biomass relationship (case $n = 1$ in figure 2.5). By substituting (2.23) into (2.4a) [or into (2.24)],

$$Y_* = F_* B_\infty \exp \left(-\frac{B_\infty}{em} F_* \right) \quad (2.25)$$

which is shown as case $n = 1$ in figure 2.7. The relationship between equilibrium yield and fishing effort, E_* , is obtained by substituting qE_* for F_* in (2.25). Corresponding parameters at the level producing MSY can be found from (2.4a,b,c) with the substitution of m for Y_* and B_m for B_* .

The time-dependent behavior for biomass in the Gompertz-Fox system over a time period when $F = F_*$ is obtained by integrating (2.22), or

$$B(t) = B_* \exp \left[\left(\frac{B_\infty}{em} F_* + \ln \frac{B_0}{B_\infty} \right) e^{-(em/B_\infty)t} \right], \quad (2.26)$$

where B_* is given in (2.23). The time-dependent behavior for cumulative yield by using (2.26) and the initial condition $Y_0 = 0$ at $t = 0$ is

$$Y_C(t) = F_* B_* \int_0^t \exp \left[\left(\frac{B_\infty}{em} F_* + \ln \frac{B_0}{B_\infty} \right) e^{-(em/B_\infty)t} \right] dt. \quad (2.27)$$

Annual yield, Y_t , is calculated in the same way as for previous models.

2.1.4. Fletcher Quadratic Model

An alternative means of providing greater complexity in production models was pioneered by Fletcher (1982). His original development was for growth models (Fletcher 1974), and the main derivation of the differential equation is found therein. He added rotation terms to the basic Graham-Schaefer model (2.5) to avoid the complications caused by the indeterminate exponent in the Pella-Tomlinson model (2.12). The general latent productivity equation is written in the quadratic form

$$\dot{P} + aB^2 - bB + g\dot{P}^2 + hB\dot{P} = 0, \quad a, b > 0, g \geq 0, h \text{ real}. \quad (2.28)$$

If $g = h = 0$, then (2.28) reduces to the Graham-Schaefer model. To obtain a parabola, the constraint $ag - h^2/4 = 0$ must be imposed, which results in three independent parameters $\{b, g, h\}$ plus an initial condition $B(0) = B_0$. The relationships between the four parameters in (2.28) and maximum productivity, m , the biomass, B_m , at which maximum productivity occurs, and pristine biomass, B_∞ are:

$$\begin{aligned} a &= \frac{4m}{B_\infty(4B_m - B_\infty)}, \\ b &= \frac{4m}{4B_m - B_\infty}, \\ g &= \frac{(B_\infty - 2B_m)^2}{mB_\infty(4B_m - B_\infty)}, \\ h &= \frac{4(B_\infty - 2B_m)}{B_\infty(4B_m - B_\infty)}. \end{aligned}$$

Differential equation (2.28) is quadratic in \dot{P} and hence can be written in the form $\tilde{a}\dot{P}^2 + \tilde{b}\dot{P} + \tilde{c} = 0$. Its two branches are then

$$\dot{P} = -\frac{1 + hB}{2g} \pm \frac{\sqrt{1 + (2h + 4bg)B}}{2g}. \quad (2.29)$$

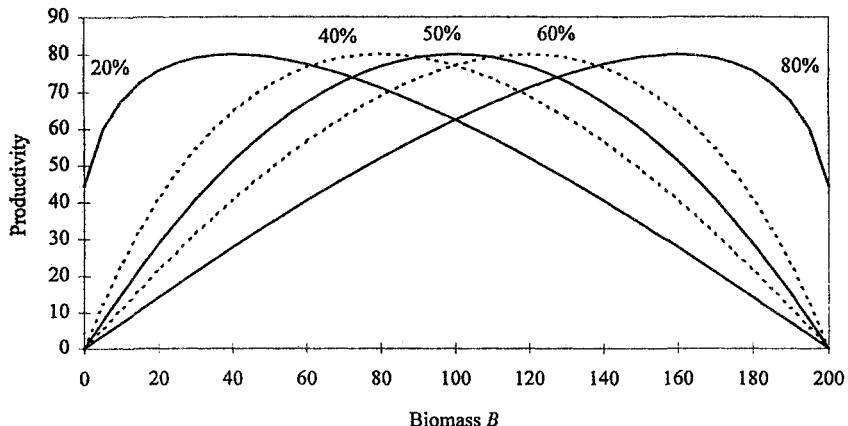


Figure 2.8. The relationship between latent productivity \dot{P} and biomass B for the Fletcher quadratic production model. Each curve shown is part of a parabola defined by equation (2.29). For each of the five cases shown, pristine biomass, B_∞ , is 200 units and maximum productivity, m , is 80 units. Five cases are shown where the biomass at maximum productivity, B_m , is 20, 40, 50 (the Graham-Schaefer model), 60, and 80% of pristine biomass. Note that the first and last cases do not have two crossings of the biomass axis, so are not valid production models.

Usually, the positive branch is used, as explained below. The effect of the added rotation terms in (2.28) is to rotate the traditional parabolic productivity curve to new axes, which allows it to resemble a skewed curve such as the Pella-Tomlinson (figure 2.8). When $B_\infty/4 < B_m < 3B_\infty/4$, the positive branch produces a productivity curve that rises from 0 at $B = 0$, rises to a maximum at $B = B_m$, and drops to 0 at $B = B_\infty$ (figure 2.8). When not in this range, the curve does not drop to 0 either at $B = 0$ or $B = B_\infty$ (figure 2.8); in most cases, a productivity curve would be considered valid only within the range $B_\infty/4 < B_m < 3B_\infty/4$.

When fishing occurs, the corresponding differential equation for biomass from (2.1), (2.3a), and (2.29) is

$$\dot{B} = -\frac{1 + (h + 2gF)B}{2g} + \frac{\sqrt{1 + (2h + 4bg)B}}{2g}. \quad (2.30)$$

With fishing mortality $F = F_*$, equilibrium biomass (when $\dot{B} = 0$) from (2.30) is

$$B_* = \frac{4g(b - F_*)}{(h + 2gF_*)^2}. \quad (2.31)$$

By equating equilibrium yield, Y_* , with latent productivity at B_* from (2.2) and (2.29), the relationship between equilibrium yield and biomass is

$$Y_* = -\frac{1 + hB_*}{2g} + \frac{\sqrt{1 + (2h + 4bg)B_*}}{2g}. \quad (2.32)$$

By equating Y_* with F_*B_* from (2.4a) and (2.31), the relationship between equilibrium yield and fishing mortality is

$$Y_* = \frac{4g(bF_* - F_*^2)}{(h + 2gF_*)^2}. \quad (2.33)$$

As in previous models, similar relationships with equilibrium effort can be defined by substituting qE_* for F_* . Also, fishing mortality that produces MSY can be found from $F_m = m/B_m$, and fishing effort at MSY can be found from $E_m = F_m/q$.

A closed form but implicit time-dependent solution of differential equation (2.30) exists. By letting

$$\begin{aligned} v &= h + 2gF, & u_1 &= 1/2g, \\ u_2 &= (h + 4bg - 2gF)/[2g(h + 2gF)], & u_3 &= 2h + 4bg, \\ u_4 &= u_2/u_1, & u_5 &= u_1v/2, \end{aligned}$$

equation (2.30) can be rewritten as

$$\dot{B} = u_1(-1 - vB + \sqrt{1 + u_3B}).$$

By the change of variables to $D = \sqrt{1 + u_3B}$, the solution to the resulting differential equation becomes tractable, resulting in the general solution to (2.30) of

$$\frac{\sqrt{1 + u_3B} - 1}{(\sqrt{1 + u_3B} - u_4)^{u_4}} = C_0 e^{(u_4 - 1)u_5 t}, \quad (2.34)$$

where initial condition $B(0) = B_0$ yields

$$C_0 = \frac{\sqrt{1 + u_3B_0} - 1}{(\sqrt{1 + u_3B_0} - u_4)^{u_4}}.$$

For comparison to Fletcher (1982), (2.34) may also be written

$$\frac{(Q(t) - u_2)^{u_2/u_1}}{Q(t) - u_1} = C'_0 e^{-(u_2/u_1 - 1)u_5 t}, \quad (2.35)$$

where $Q(t) = u_1\sqrt{1 + u_3B}$ and C'_0 is the integration constant. [Fletcher (1982) accidentally omitted the term $-u_5$.] As (2.34) can be written as a function of only u_2/u_1 , u_3 , u_5 , and C'_0 , it is a four-parameter solution, as is (2.34). As the solution is only implicit for $B(t)$, numerical integration of (2.30) may be desirable. A closed-form solution for yield $Y = \int FB(t)dt$ has not been found, but numerical methods can be used.

2.1.5. Threshold Models

For many fish stocks, productivity at low stock levels appears to be substantially reduced compared to MSY stock levels. When reduced to low levels, these stocks do not rebuild, even if fishing pressure is reduced. This failure to respond suggests that there may be a threshold level below which the capacity of the stock to rebuild is damaged. In chapter 3, this reduction is described as depensation, and the appropriate mathematical representation is given there. For production models, a threshold level is defined as a

biomass level below which latent productivity is zero or negative. Let T be the lower biomass level at which $\dot{P} = 0$; B_∞ be the upper biomass level at which $\dot{P} = 0$; and $m_0 = \dot{P}(0)$, the intercept on the \dot{P} -axis.

Any productivity function covered so far can be generalized to include a threshold by adding a constant term to the latent productivity equation (Fletcher 1982). Fletcher (1982) viewed the addition as an unwelcome refinement, because intolerable complications might arise in estimation procedures. Nevertheless, the additional parameter might be useful for certain stocks. For the Graham-Schaefer system (2.5), Quinn and Collie (1990) developed the corresponding threshold model, which is

$$\dot{P} = \frac{4m}{B_\infty - T}(B - T) - \frac{4m}{(B_\infty - T)^2}(B - T)^2, \quad (2.36)$$

which has $\dot{P} = 0$ at $B = T$ and $B = B_\infty$. The addition of parameter T essentially shifts the Graham-Schaefer parabola to the right, so that it goes through $(T, 0)$ rather than $(0, 0)$, as shown in figure 2.9. The value of parameter m_0 is

$$m_0 = -\frac{4mT}{B_\infty - T} \left(1 + \frac{4mT}{B_\infty - T} \right),$$

showing that $m_0 < 0$ for $T > 0$, which is shown in figure 2.9.

The most straightforward way to introduce fishing is to use (2.1) with (2.36) and

$$\dot{Y} = \begin{cases} F(B - T), & \text{for } B \geq T \\ 0, & \text{for } B < T \end{cases}.$$

The line for \dot{Y} for constant fishing mortality, $F = F_*$, and corresponding curve for \dot{B} are shown in figure 2.9. For a given fishing mortality, F_* , the equilibrium relationships are found analogously as in section 2.1.1. In particular, B_m is $(T + B_\infty)/2$, and fishing mortality at MSY is $F_m = m/(B_m - T)$. Quinn and Collie (1990) applied this approach to Bering Sea walleye pollock.

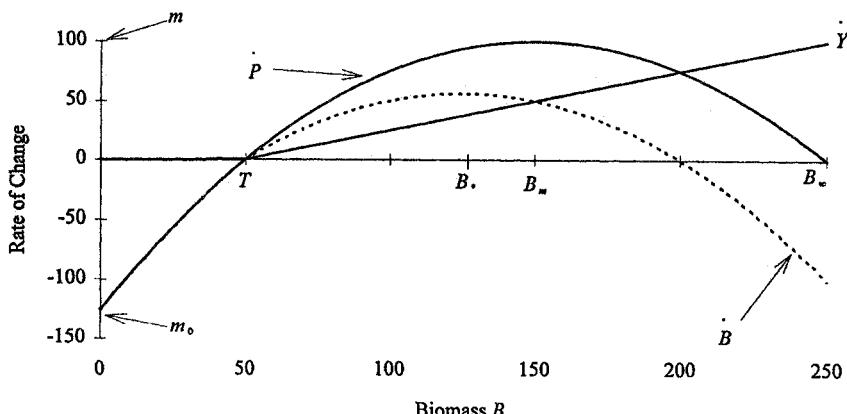


Figure 2.9. Latent productivity, \dot{P} , yield rate, $\dot{Y} = F_*(B - T)$, and rate of change of biomass $\dot{B} = \dot{P} - \dot{Y}$ as a function of biomass B for the Quinn-Collie surplus production model with threshold. Reference points include pristine biomass, B_∞ ; maximum productivity, m ; threshold, T ; biomass, B_m , at which maximum productivity occurs; latent productivity, m_0 , at zero biomass; and equilibrium biomass, B_* , for fishing mortality F_* .

Analogous threshold models can be developed for other production models by replacing B quantities with $B - T$ quantities. This procedure is equivalent to adding a constant to the latent productivity equation but makes it easier to obtain equilibrium relationships.

2.1.6. Models with Environmental Variables

One criticism of many population models, including surplus production models, is that their parameters are constant in time, whereas the environment in which the population is found is constantly changing. Thus, model parameters may in reality be a function of environmental variables. The ultimate question is, which parameters are affected by the environment and in what way?

Freon (1988) considered this question with respect to the Graham-Schaefer, Gompertz-Fox, and Pella-Tomlinson surplus production models. Environmental variation is allowed in B_∞ and q as functional forms of an environmental variable X , written $f_1(X)$ and $f_2(X)$, respectively. Freon wrote the Graham-Schaefer model (2.5) with fishing as

$$\dot{B} = r'[B_\infty - B]B - qEB = r'[f_1(X) - B]B - f_2(X)EB,$$

where $r' = 4m/B_\infty^2$ in our notation. Parameter r' is assumed constant, implying that the slope of the relative rate of change in biomass is constant and that the square root of maximum productivity is proportional to biomass. This assumption stems from conclusions in examining habitat considerations (see MacCall 1990); other assumptions can be made as well. Equilibrium relationships described in section 2.1.1 still apply but are now functions of the environmental variable. For example, (2.7) for equilibrium biomass becomes

$$B_*(X) = f_1(X) - f_2(X)E_*/r'.$$

Management quantities such as MSY, biomass, fishing mortality, and effort at MSY are also functions of the environment given by

$$\begin{aligned} Y_m(X) &= r' f_1^2(X)/4, \\ B_m(X) &= f_1(X)/2, \\ F_m(X) &= r' f_1(X)/2, \quad \text{and} \\ E_m(X) &= r' f_1(X)/[2f_2(X)]. \end{aligned}$$

Freon gives several graphical examples and shows how environmental variables can be used to explain actual fisheries time series better than models without environmental variables. A computer program is available for such analysis (Freon et al. 1990).

2.2. PARAMETER ESTIMATION

Given that few stocks are at equilibrium for even a short time, determining the parameters of the equilibrium stock-production relationships in section 2.1 is quite difficult. At a minimum, two such time periods when the stock was at equilibrium would be needed to isolate the parameters m and B_∞ of the Graham-Schaefer or Gompertz-Fox system, and three time periods would be needed for the parameters of the Pella-Tomlinson, Fletcher quadratic, or threshold system. Ricker (1975a) gives examples of such calculations.

It is assumed that the time unit is one year and that a time series of annual yield and fishing effort $\{Y_t, E_t\}$ is available for analysis; thus, a unit time period ($\tau = 1$) is used. In analogy to results in section 1.3, yield is assumed proportional to average biomass, or $Y = F\bar{B}$ [cf. (1.27)], and fishing mortality is assumed proportional to fishing effort, or $F = qE$ [cf. (1.36)]. Hence, catch-per-unit-effort (CPUE) is proportional to average biomass, or $U = q\bar{B}$ [cf. (1.37)]. Hence CPUE is a monitoring aid in determining the status of the stock as a proxy for biomass. For example, consider the Graham-Schaefer system and define $U_\infty = qB_\infty$ and $U_* = qB_*$. From the equilibrium yield–fishing effort relationship in (2.8c), the relationship between equilibrium CPUE and effort is then

$$U_* = \frac{Y_*}{E_*} = U_\infty - \frac{U_\infty^2}{4m} E_*. \quad (2.37)$$

This linear relationship could be used to determine the parameters U_∞ and m if two equilibrium points were known. If data are available from the onset of the fishery, CPUE from that period may be a reasonable approximation to U_∞ , requiring one other time period when the stock is thought to be at equilibrium to resolve the remaining parameter m .

It is not appropriate to apply the equilibrium relationships derived in section 2.1 for yield and biomass or for yield and fishing effort to annual fisheries data without additional methodology to account for nonequilibrium conditions. Various strategies have been proposed to handle nonequilibrium conditions, which are summarized in sections 2.2.1 to 2.2.8. In section 2.2.9, the Graham-Schaefer system is used to simulate a stock over 30 years with varying fishing mortality. The resulting information is used with each method to illustrate the aspects of parameter estimation and to determine whether any inherent bias is present.

2.2.1. Annual Surplus Production

The approach in this section is to obtain an annual estimate of surplus production, which is a function only of the data and is independent of any model. In this sense, the estimation of annual surplus production (ASP_t) is nonparametric. Annual yield is denoted Y_t . By recasting (2.1) in terms of \dot{Y} ,

$$\dot{Y} = \dot{P}(B) - \dot{B}.$$

This equation can be integrated from time t to time $t + 1$, assuming that biomass changes from B_t to B_{t+1} and yield changes from 0 to Y_t , which results in

$$\int_0^{Y_t} dY = \int_t^{t+1} \dot{P}[B(t)]dt - \int_{B_t}^{B_{t+1}} dB. \quad (2.38)$$

Note that B_t is the biomass at the start of time period t . Define $\Delta B_t = B_{t+1} - B_t$ to be the change in biomass in year t . Equation (2.38) becomes

$$\begin{aligned} Y_t &= \int_t^{t+1} \dot{P}dt - \Delta B_t \\ \Rightarrow ASP_t &\equiv Y_t + \Delta B_t = \int_t^{t+1} \dot{P}dt, \end{aligned} \quad (2.39)$$

where ASP_t is the annual surplus production in year t . Thus, annual surplus production is equivalent to the sum of yield and change in biomass. Consequently, annual surplus production is equivalent to the amount of yield that could have been taken in a given year that would have left the stock at equilibrium.

The integral of \dot{P} in (2.39) can be approximated by a rectangular area with a width of one and a length of $\dot{P}(B)$ evaluated at $B = \bar{B}_t$. Then, (2.39) becomes

$$\text{ASP}_t \equiv Y_t + \Delta B_t \approx \dot{P}(\bar{B}_t). \quad (2.40)$$

By comparing (2.40) with (2.2), surplus production parameters can be estimated by using annual surplus production, ASP_t , in place of equilibrium yield, Y_* , in any particular model and average biomass, \bar{B}_t , in place of equilibrium biomass, B_* .

Estimation of ASP in (2.40) requires information about yield and biomass each year. Yield is almost always available, but biomass is more problematic. Annual surveys that produce estimates of biomass could be used. Analysis of catch-age data produces age-structured estimates of abundance, $N_{a,t}$, at each age, a , and year, t (see chapter 8). These estimates are converted to stock biomass, $B_{a,t}$, by multiplying by age-specific average weight, $\bar{W}_{a,t}$, and stock biomass is the sum of age-specific biomass, or

$$B_t = \sum_a B_{a,t} = \sum_a N_{a,t} \bar{W}_{a,t}.$$

If CPUE data and an estimate of the catchability coefficient, q , are available, stock biomass can be estimated by an approach developed by Schaefer (1954, 1957). Average annual biomass is estimated by dividing CPUE by q , or

$$\bar{B}_t = U_t/q. \quad (2.41)$$

Biomass at the start of each time period can be approximated by linear interpolation as

$$B_t = (\bar{B}_{t-1} + \bar{B}_t)/2. \quad (2.42)$$

Annual change in biomass is estimated by

$$\Delta B_t = B_{t+1} - B_t = (\bar{B}_{t+1} - \bar{B}_{t-1})/2. \quad (2.43)$$

Finally, annual surplus production is estimated by

$$\text{ASP}_t = Y_t + \Delta B_t = Y_t + \left(\frac{Y_{t+1}}{q E_{t+1}} - \frac{Y_{t-1}}{q E_{t-1}} \right)/2. \quad (2.44)$$

Examples of calculation of ASP using CPUE are found in Schaefer (1954), Chapman et al. (1962), Ricker (1975a), and section 2.2.9. Examples of calculation of ASP using catch-age data are found in Deriso and Quinn (1983) and Quinn et al. (1984, 1985).

2.2.2. Surplus Production–Biomass Relationship

Estimation of surplus production parameters follows from the relationship of ASP and average biomass in (2.40) by using a particular surplus production model and specifying

the error structure. For the Graham-Schaefer system, by substituting ASP_t for Y_* and \bar{B}_t for B_* in (2.8a) and assuming an additive error structure, then

$$\text{ASP}_t = \frac{4m}{B_\infty} \bar{B}_t - \frac{4m}{B_\infty^2} \bar{B}_t^2 + \epsilon_t, \quad (2.45)$$

where ϵ_t is a random error with mean 0 and constant variance σ^2 . This equation has the form of a multiple linear regression through the origin

$$y = \alpha x_1 + \beta x_2 + \epsilon,$$

where the dependent variable is ASP_t and the two independent variables are \bar{B}_t and \bar{B}_t^2 . Parameter estimates a and b of α and β , respectively, are set equal to the respective coefficients in (2.45) to obtain estimates of m and B_∞ as

$$\hat{B}_\infty = -a/b \quad \text{and} \quad \hat{m} = -a^2/(4b).$$

Estimates of other surplus production parameters are

$$\hat{B}_m = \hat{B}_\infty/2, \quad \hat{F}_m = \hat{m}/\hat{B}_m, \quad \text{and} \quad \hat{E}_m = \hat{F}_m/q.$$

Measurement errors are likely to be present in the biomass estimates as well as in estimates of ASP. In practice, surplus production relationships are quite variable, which can result in poor or even nonsensical parameter estimates (e.g., negative estimates). Ricker (1975a) presents functional (GM) regression procedures that can alleviate some problems with measurement errors. Fuller (1987) gives a complete overview of measurement error models and methods of estimation (also see section 3.2.3).

Alternatively, if the variance of ASP_t is assumed equal to $\bar{B}_t^2 \sigma^2$, then the estimation equation is

$$\frac{\text{ASP}_t}{\bar{B}_t} = \frac{4m}{B_\infty} - \frac{4m}{B_\infty^2} \bar{B}_t + \epsilon_t, \quad (2.46)$$

where ϵ_t is again a random error with mean 0 and variance σ^2 . This equation has the form of a simple linear regression $y = \alpha + \beta x + \epsilon$, where the dependent variable is ASP_t/\bar{B}_t and the independent variable is \bar{B}_t . The formulae for the surplus production parameter estimates remain the same. In (2.46), average biomass appears on both sides of the equation, leading to an implicit negative correlation between the dependent and independent variables. This can produce the impression of a significant relationship between surplus production and biomass, even when no relationship is present. In practice, estimates are generally reasonable, but confidence in the results may be overstated.

For the Pella-Tomlinson model, by substituting ASP_t for Y_* and \bar{B}_t for B_* in (2.16) and assuming an additive error structure, then

$$\text{ASP}_t = \frac{\gamma m}{B_\infty} \bar{B}_t - \frac{\gamma m}{B_\infty^n} \bar{B}_t^n + \epsilon_t. \quad (2.47)$$

If n is fixed, then parameter estimates can be obtained from (2.47) by using linear regression techniques in a manner similar to the Graham-Schaefer model. If n is unknown, then (2.47) must be solved by nonlinear regression techniques (Draper and

Smith 1981, Bates and Watts 1988) for the parameters B_∞ , m , and n . With variance equal to $\bar{B}_t^2 \sigma^2$, the estimation equation is

$$\frac{\text{ASP}_t}{\bar{B}_t} = \frac{\gamma m}{B_\infty} - \frac{\gamma m}{B_\infty^n} \bar{B}_t^{n-1} + \epsilon_t, \quad (2.48)$$

which must also be solved by nonlinear regression techniques.

In practice, it is difficult with the Pella-Tomlinson model to obtain convergence of nonlinear regression techniques with surplus production information. The difficulty is with the parameter n , which can be traced to the flat behavior of the location of maximum biomass, B_m , in relation to B_∞ as a function of n (Fletcher 1978a).

For the Gompertz-Fox system, by substituting ASP_t for Y_* and \bar{B}_t for B_* in (2.24) and assuming an additive error structure, then

$$\text{ASP}_t = \frac{em \ln(B_\infty)}{B_\infty} \bar{B}_t - \frac{em}{B_\infty} \bar{B}_t \ln(\bar{B}_t) + \epsilon_t. \quad (2.49)$$

This equation has the form of a multiple linear regression through the origin $y = \alpha x_1 + \beta x_2 + \epsilon$, where the dependent variable is ASP_t and the two independent variables are \bar{B}_t and $\bar{B}_t \ln(\bar{B}_t)$. Parameter estimates a and b of α and β , respectively, are set equal to their respective coefficients in (2.49) to obtain estimates of m and B_∞ as

$$\hat{B}_\infty = \exp(-a/b) \quad \text{and} \quad \hat{m} = -b \hat{B}_\infty/e.$$

Estimates of other surplus production parameters are

$$\hat{B}_m = \hat{B}_\infty/e, \quad \hat{F}_m = \hat{m}/\hat{B}_m, \quad \text{and} \quad \hat{E}_m = \hat{F}_m/q.$$

With variance of ASP_t equal to $\bar{B}_t^2 \sigma^2$, then the estimation equation is

$$\frac{\text{ASP}_t}{\bar{B}_t} = \frac{em \ln(B_\infty)}{B_\infty} - \frac{em}{B_\infty} \ln(\bar{B}_t) + \epsilon_t. \quad (2.50)$$

This equation has the form of a simple linear regression $y = \alpha + \beta x + \epsilon$, where the dependent variable is ASP_t/\bar{B}_t and the independent variable is $\ln(\bar{B}_t)$. The formulae for the surplus production parameter estimates remain the same.

For the Fletcher quadratic model, the corresponding relationship between ASP_t and \bar{B}_t from (2.32) is

$$\text{ASP}_t = -\frac{1 + h \bar{B}_t}{2g} + \frac{\sqrt{1 + (2h + 4bg)\bar{B}_t}}{2g} + \epsilon_t, \quad (2.51a)$$

where b , g , and h are functions of the parameters m , B_∞ , and B_m (as given in section 2.1.4). If variance is assumed proportional to \bar{B}_t^2 , the estimation equation is

$$\frac{\text{ASP}_t}{\bar{B}_t} = -\frac{1 + h \bar{B}_t}{2g \bar{B}_t} + \frac{\sqrt{1 + (2h + 4bg)\bar{B}_t}}{2g \bar{B}_t} + \epsilon_t. \quad (2.51b)$$

In both cases [(2.51a) and (2.51b)], nonlinear least squares must be used. This model has better estimation properties than the Pella-Tomlinson because the power of the fitting is second degree, like the Graham-Schaefer model.

For the Quinn-Collie threshold model in section 2.1.5, ASP_t replaces \dot{P} , and \bar{B}_t replaces B in (2.36) in order to estimate parameters m , B_∞ , and T . Assuming an additive error structure, the resulting equation can be written

$$\text{ASP}_t = \alpha + \beta \bar{B}_t + \gamma \bar{B}_t^2 + \epsilon_t, \quad (2.52a)$$

which is in the form of a polynomial regression of order 2 (Quinn and Collie 1990). Hence the threshold model is fitted in the same way as the Graham-Schaefer model, except that the intercept is not set to 0. After obtaining corresponding parameter estimates a , b , and c , estimates of surplus production parameters from Quinn and Collie (1990) are

$$\begin{aligned}\hat{T} &= (-b + \sqrt{b^2 - 4ac})/(2c), \\ \hat{B}_\infty &= (-b - \sqrt{b^2 - 4ac})/(2c), \\ \hat{m} &= -(b^2 - 4ac)/(4c).\end{aligned}$$

Estimate c must be negative to obtain reasonable production parameter estimates. For an error structure with variance proportional to \bar{B}_t^2 , the estimation equation is

$$\text{ASP}_t/\bar{B}_t = \alpha(1/\bar{B}_t) + \beta + \gamma \bar{B}_t + \epsilon, \quad (2.52b)$$

which is in the form of a multiple linear regression. Noting that b is the y -intercept and a and c are the regression coefficients of the two independent variables, the same equations are again used to estimate production parameters.

2.2.3. Recruitment Adjustment

One would expect annual surplus production to be related to recruitment of fish into the stock (Ricker 1975a). In turn, anticipating the developments of chapter 3, recruitment should be related to the spawning stock in years past. One possible form for the relationship between recruitment, R , and spawning stock, S , is the Ricker equation

$$\begin{aligned}R &= S e^{\alpha - \beta S} \\ \Rightarrow \ln(R/S) &= \alpha - \beta S,\end{aligned}$$

where $\alpha > 0$ and $\beta > 0$. This equation produces a dome-shaped pattern of recruitment versus spawning stock (see section 3.1.2). Equating annual surplus production, ASP_t , with recruitment, R , and average biomass in past years thought to affect current recruitment, say \bar{B}_{past} , with spawning stock, S , the surplus production relationship adjusted for recruitment is

$$\ln(\text{ASP}_t/\bar{B}_{\text{past}}) = \alpha - \beta \bar{B}_{\text{past}} + \epsilon_t, \quad (2.53)$$

which is in the form of a linear regression. Given estimates a and b of α and β , respectively, estimates of production parameters from Ricker (1975a) are

$$\widehat{B}_m = 1/b, \quad \widehat{m} = e^a/(be), \quad \text{and} \quad \widehat{F}_m = m/B_m.$$

There is no parameter B_∞ for this model because $R \rightarrow 0$ only as $S \rightarrow \infty$.

This approach could also be used for any of the surplus production–biomass relationships in section 2.2.2 by replacing \overline{B} with $\overline{B}_{\text{past}}$. However, more appropriate methods for incorporating recruitment considerations into the dynamics of fish populations are given in later chapters (chapters 3, 5, 7, 8, 9). The choice of years to use in calculating $\overline{B}_{\text{past}}$ is arbitrary and depends on the life history of the species. In an application to Pacific halibut, Ricker used an average of 5–7 years prior to the current year based on halibut life history.

2.2.4. Surplus Production–Fishing Effort Relationship

Unlike the development of the surplus production–biomass relationship, there is no simple derivation of the relationship between surplus production and fishing effort. In analogy to section 2.2.2, parameter estimation could also be accomplished by substituting ASP_t for Y_* and E_t for E_* in the equilibrium yield–fishing effort relationship. However, this cannot be considered a formal approach but rather an ad hoc method. For comparison with later methods, parameters are formulated in CPUE units rather than biomass units. Thus, $U_\infty = q B_\infty$ and $U_m = q B_m$ will be used.

For the Graham-Schaefer system, the equilibrium–CPUE relationship is given in (2.37). By substituting ASP_t for Y_* and E_t for E_* in (2.8c) or (2.37) and assuming an additive error structure, then

$$\text{ASP}_t = U_\infty E_t - \frac{U_\infty^2}{4m} E_t^2 + \epsilon_t. \quad (2.54)$$

This equation has the form of a multiple linear regression through the origin, where the dependent variable is ASP_t , and the two independent variables are E_t and E_t^2 . Given parameter estimates a and b , estimates of m and U_∞ are

$$\widehat{U}_\infty = a \quad \text{and} \quad \widehat{m} = -a^2/(4b).$$

Direct estimates of other surplus production parameters are

$$\widehat{U}_m = \widehat{U}_\infty/2 \quad \text{and} \quad \widehat{E}_m = \widehat{m}/\widehat{U}_m.$$

If q is known, then

$$\widehat{F}_m = q \widehat{E}_m, \quad \widehat{B}_m = \widehat{U}_m/q, \quad \text{and} \quad \widehat{B}_\infty = \widehat{U}_\infty/q.$$

The alternative estimation equation for variance proportional to E_t^2 is

$$\frac{\text{ASP}_t}{E_t} = U_\infty - \frac{U_\infty^2}{4m} E_t + \epsilon_t, \quad (2.55)$$

which has the form of a simple linear regression with dependent variable $\text{ASP}_t/\overline{E}_t$ and independent variable E_t . The formulae for the surplus production parameter estimates remain the same. Equation (2.55) is similar to the equilibrium CPUE relationship (2.37).

For the Pella-Tomlinson system, the relationship between equilibrium CPUE and effort is

$$U_* = \frac{Y_*}{E_*} = U_\infty \left(1 - \frac{U_\infty}{\gamma m} E_*\right)^{1/(n-1)}, \quad (2.56)$$

obtained by substituting qE_* for F_* in (2.16) and then dividing by E_* . By assuming an additive error structure, the estimation equation for ASP_t is

$$\text{ASP}_t = E_t U_\infty \left(1 - \frac{U_\infty}{\gamma m} E_t\right)^{1/(n-1)} + \epsilon_t. \quad (2.57)$$

By assuming variance proportional to E_t^2 , the estimation equation is

$$\frac{\text{ASP}_t}{E_t} = U_\infty \left(1 - \frac{U_\infty}{\gamma m} E_t\right)^{1/(n-1)} + \epsilon_t. \quad (2.58)$$

In either case, the solution must be obtained by nonlinear regression.

For the Gompertz-Fox model, the relationship between equilibrium CPUE and effort from (2.24) is

$$U_* = \frac{Y_*}{E_*} = U_\infty \exp\left(-\frac{U_\infty}{em} E_*\right). \quad (2.59)$$

By assuming an additive error structure, the estimation equation is

$$\text{ASP}_t = E_t U_\infty \exp\left(-\frac{U_\infty}{em} E_t\right) + \epsilon_t. \quad (2.60)$$

By assuming variance proportional to E_t^2 , the estimation equation is

$$\frac{\text{ASP}_t}{E_t} = U_\infty \exp\left(-\frac{U_\infty}{em} E_t\right) + \epsilon_t. \quad (2.61)$$

These equations may be solved by nonlinear least squares. Alternatively, if a multiplicative error structure is assumed with variance proportional to E_t^2 , then the estimation equation becomes

$$\ln \frac{\text{ASP}_t}{E_t} = \ln U_\infty - \frac{U_\infty}{em} E_t + \epsilon_t, \quad (2.62)$$

which is in the form of a simple linear regression equation.

Similar approaches can be developed for the Fletcher quadratic and threshold models (see sections 2.1.4, 2.1.5).

2.2.5. Equilibrium Approximation

In the previous section, it was demonstrated that CPUE is a function of fishing effort at equilibrium. If not at equilibrium, CPUE is a function of recruitment and survival of a number of year-classes. Ignoring the recruitment effect, survival of a particular year-class is related to accumulated mortalities associated with fishing and natural causes (section 1.2). As fishing effort is directly related to fishing mortality (section 1.3), one would suppose that CPUE is related to average fishing effort over past years. In this

method of equilibrium approximation, equilibrium relationships between CPUE and effort are replaced with observed CPUE and average fishing effort in the past (Gulland 1983). As in section 2.2.4, there is no formal derivation of the relationship between CPUE and effort, so this must also be considered an ad hoc method.

Gulland (1961) originated this approach by using a simple average of fishing effort over T years, given by

$$\bar{E}_t = \sum_{i=0}^{T-1} E_{t-i} / T. \quad (2.63)$$

Gulland (1983) recommended that T be the average number of years that fish occur in the fishery, or approximately half the life span. Ricker (1975a) did not use effort in the current year in his application to Pacific halibut, but averaged effort from one to five years in the past. Fox (1975) argued that a weighted average of fishing effort is desirable because year-classes have had different lengths of time in the fishery at a particular time. If K is the number of years for which recruitment is thought to affect CPUE, then the weighted average is

$$\bar{E}_t = \sum_{i=0}^{K-1} (K-i) E_{t-i} / \sum_{i=0}^{K-1} (K-i). \quad (2.64)$$

The simplest course is to use the Graham-Schaefer system, in which the relationship between CPUE and effort is linear. Nevertheless, the approach of equilibrium approximation can be used with any of the models in section 2.2.4 by replacing the regressions of ASP_t/E_t versus E_t with regressions of observed CPUE U_t versus \bar{E}_t . For example, Yeh et al. (1991) used this method with the Pella-Tomlinson model. Estimates of production parameters are identical to those in section 2.2.4.

Although this method and the recruitment adjustment method of section 2.2.3 lack any rigorous development, the appreciation of lag effects on a population is worth noting. Rigorous models with time lags are considered in chapter 5. Also, the method of equilibrium approximation performed well in simulations of age-structured populations (Rivard 1987), but note its performance below (section 2.2.9).

2.2.6. Schnute's Nonequilibrium Method

By a novel treatment of the differential equation (2.6), Schnute (1977) derived a nonequilibrium method for the Graham-Schaefer system whereby production parameters m and B_∞ , and in addition, catchability, q , could be simultaneously estimated. Schnute used the continuous variable U to represent instantaneous CPUE over time, where $U = qB$. From (2.6), the equivalent differential equation for U is

$$\begin{aligned} \dot{U} &= q\dot{B} = \frac{4m}{B_\infty}U - \frac{4m}{qB_\infty^2}U^2 - qEU \\ \Rightarrow \frac{\dot{U}}{U} &= \frac{4m}{B_\infty} - \frac{4m}{qB_\infty^2}U - qE. \end{aligned} \quad (2.65)$$

By integrating (2.65) from time t to $t + 1$ and recalling the definition of an integral average in section 1.2.1, then

$$\begin{aligned} \int_{U_t}^{U_{t+1}} \frac{dU}{U} &= \frac{4m}{B_\infty} \int_t^{t+1} dt - \frac{4m}{q B_\infty^2} \int_t^{t+1} U dt - q \int_t^{t+1} E dt \\ \Rightarrow \ln \frac{U_{t+1}}{U_t} &= \frac{4m}{B_\infty} - \frac{4m}{q B_\infty^2} \bar{U}_t - q \bar{E}_t. \end{aligned} \quad (2.66)$$

By approximating \bar{U} and \bar{E} with averages at time t and $t + 1$, the final equation, after adding an error term, becomes

$$\begin{aligned} \ln \frac{U_{t+1}}{U_t} &= \frac{4m}{B_\infty} - \frac{4m}{q B_\infty^2} \frac{U_t + U_{t+1}}{2} - q \frac{E_t + E_{t+1}}{2} + \epsilon_{t+1} \\ \text{or } y &= \alpha + \beta x_1 + \gamma x_2 + \epsilon, \end{aligned} \quad (2.67)$$

which is in the form of a multiple linear regression with two independent variables. Given estimates a , b , and c of α , β , and γ , respectively, estimates of primary surplus production parameters are

$$\hat{q} = -c, \quad \hat{B}_\infty = a/(bc), \quad \text{and} \quad \hat{m} = a^2/(4bc).$$

The other parameter estimates are

$$\hat{B}_m = \hat{B}_\infty/2, \quad \hat{F}_m = \hat{m}/\hat{B}_m, \quad \hat{E}_m = \hat{F}_m/\hat{q}, \quad \text{and} \quad \hat{U}_m = \hat{m}/\hat{E}_m.$$

For the Schnute nonequilibrium method to produce reliable estimates, there must be good contrast in the data (Hilborn 1979). Potential correlation between the dependent variable and independent variables in (2.67) may result in poor estimates, as found in other surplus production models.

Rivard and Bledsoe (1978) also developed a nonequilibrium method, which uses numerical techniques to integrate the differential equations for productivity. Although their approach is fairly difficult to implement, it can be adapted to any production model.

2.2.7. Difference Equations for Surplus Production

The use of difference equations for production relationships was pioneered by Walters and Hilborn (1976) and Hilborn (1979) to produce simple recursive equations for estimating parameters and for projecting the stock into the future. In this approach, the differential equation is replaced with a difference equation in a manner similar to the simple exponential growth law in section 1.1. By using a time period of one year, the difference equation for the Graham-Schaefer system is

$$\frac{dB}{dt} \approx \Delta B_t = B_{t+1} - B_t = \frac{4m}{B_\infty} B_t - \frac{4m}{B_\infty^2} B_t^2 - Y_t. \quad (2.68)$$

Equation (2.68) can also be written as a projection equation for B_{t+1} as

$$B_{t+1} = \left(1 + \frac{4m}{B_\infty}\right) B_t - \frac{4m}{B_\infty^2} B_t^2 - Y_t. \quad (2.69)$$

In Hilborn's first model, the yield relationship is assumed to be

$$Y_t = q E_t B_t \quad \Rightarrow \quad U_t = q B_t.$$

Substitution of these two relationships into (2.68) and inclusion of an error term result in

$$\frac{U_{t+1}}{U_t} - 1 = \frac{4m}{B_\infty} - \frac{4m}{q B_\infty^2} U_t - q E_t + \epsilon_{t+1}, \quad (2.70)$$

which has the form of a multiple linear regression with two independent variables U_t and E_t . Equation (2.70) is quite similar to the Schnute nonequilibrium solution (2.67), and estimates of production parameters use the same formulae given in the preceding section. The major problem with this first formulation is that yield can exceed stock biomass given a high enough fishing effort, E_t .

In Hilborn's second model, the yield relationship is assumed to be asymptotic as fishing effort becomes large, or

$$Y_t = \mu_t B_t, \quad \mu_t = 1 - e^{-q'E_t}, \quad (2.71)$$

where μ_t is the annual exploitation fraction in year t . Thus, Y_t/μ_t , rather than CPUE, is the appropriate indicator of biomass in this model. Substitution of Y_t/μ_t for B_t in (2.69) and inclusion of an error term produce the estimation equation

$$Y_{t+1} = \mu_{t+1} \left[\left(1 + \frac{4m}{B_\infty} \right) \frac{Y_t}{\mu_t} - \frac{4m}{B_\infty^2} \left(\frac{Y_t}{\mu_t} \right)^2 - Y_t \right] + \epsilon_{t+1}. \quad (2.72)$$

Equation (2.72) is in the form of a nonlinear regression with three independent variables, E_{t+1} , Y_t , and E_t , and three parameters, q' , m , and B_∞ , because μ_t in (2.71) is a nonlinear function of q' and E_t . Other error assumptions could also be used.

Uhler (1980) indicated that the Schnute nonequilibrium model performs better than Hilborn's first model. By means of a simulation study, Hilborn (1979) compared the Schnute model and his first and second models under various management policies, such as constant effort, constant quota, and fixed escapement. He contrasted production parameter estimates with the situation where perfect information is available. He showed that contrast in effort and CPUE information is critical for obtaining reliable parameter estimates. Constant effort policies were frequently preferred to fixed escapement policies because average yield was about the same, but variation in yield was reduced. Finally, he recommended that adaptive management policies be implemented with the goal of learning the most about the system. Ludwig and Walters (1985) suggested that simple surplus production models of this form may often be preferred to more complicated age-structured methods using CPUE data (see chapter 5) because the surplus production models make fewer requirements of the data to produce reliable estimates.

Tsoa et al. (1985) provided a difference equation that is a generalization of the Graham-Schaefer system by using a power relationship between yield, effort, and biomass, which was given in (1.55). They also incorporated the sampling process of yield and effort from logbooks by distinguishing between total yield and logbook yield and effort. Their procedure also results in a nonlinear regression equation with logbook yield in year $t+1$ as the dependent variable, four independent variables (logbook effort in years t and $t+1$, logbook yield in year t , and total yield in year t), and five parameters

[q , α , and β in (1.55), m , and B_∞]. In application to trawl cod data, they concluded that their estimates were reasonable, although there was sensitivity to initial conditions, and convergence required many iterations. It is probably overoptimistic to attempt to obtain five parameter estimates from yield and CPUE data alone. In section 1.3.4, experimental resolution of parameters is discussed.

In a more sophisticated approach to estimating production parameters, Pella (1993) allowed for both measurement and process errors in biomass dynamics models of the type given in section 2.1. The Kalman filter provides the analytical basis for the estimation using the state space form of time series models; a step-by-step description of the process is given in that paper. As one illustration of the approach, Pella showed that reasonable estimates of population parameters were obtained using the Kalman filter in a situation where measurement error models gave unreasonable results.

2.2.8. Prager's Nonequilibrium Method

Prager (1994) reviewed the estimation techniques for production models and provided several extensions. His approach is akin to the Schnute method in section 2.2.6 and uses the time-dependent solutions for biomass in (2.9) and yield in (2.10) for the Graham-Schaefer model. By letting $\alpha_t = 4m/B_\infty - F_t$ and $\beta = 4m/B_\infty^2$ for fishing mortality, F_t , during year t , the Graham-Schaefer model (2.5) becomes

$$\dot{B}/B = \alpha_t - \beta B,$$

and equilibrium biomass in (2.7) can be written

$$B_* = B_\infty - F_t/\beta = \alpha_t/\beta.$$

By substituting B_{t+1} for $B(t)$ and B_t for B_0 in (2.9), the difference equation

$$B_{t+1} = \begin{cases} \frac{\alpha_t B_t}{\beta B_t + (\alpha_t - \beta B_t) e^{-\alpha_t}}, & \alpha_t \neq 0 \\ \frac{B_t}{\beta B_t + 1}, & \alpha_t = 0 \end{cases} \quad (2.73)$$

is obtained. The corresponding yield equation from (2.10) is

$$Y_t = \begin{cases} \frac{F_t}{\beta} \ln \left[1 + \frac{\beta B_t}{\alpha_t} (e^{\alpha_t} - 1) \right], & \alpha_t \neq 0 \\ \frac{F_t}{\beta} \ln [1 + \beta B_t], & \alpha_t = 0 \end{cases}. \quad (2.74)$$

An implicit solution for fishing mortality is obtained by solving for F_t in (2.74), which results in

$$F_t = \begin{cases} \beta Y_t / \ln \left[1 + \frac{\beta B_t}{\alpha_t} (e^{\alpha_t} - 1) \right], & \alpha_t \neq 0 \\ \beta Y_t / \ln [1 + \beta B_t], & \alpha_t = 0. \end{cases} \quad (2.75)$$

Fishing effort, E_t , is then F_t/q .

The basic data are yields $\{Y'_t\}$ and efforts $\{E'_t\}$. Parameters of the model are $\{m, B_\infty, q,$ and $B_1\}$, where B_1 is an initial condition necessary for applying the difference equation (2.73). Various objective functions can be used for estimating parameters using nonlinear least squares or likelihood techniques. If yield is assumed to have multiplicative error, then the objective function is the residual sum of squares (RSS) criterion

$$\text{RSS}_Y = \sum (\ln Y'_t - \ln Y_t)^2.$$

If effort is assumed to have multiplicative error, then the objective function is the RSS criterion

$$\text{RSS}_E = \sum (\ln E'_t - \ln E_t)^2,$$

which is equivalent to the sum of squared CPUE deviations

$$\text{RSS}_U = \sum [\ln(Y'_t/E'_t) - \ln(Y_t/E_t)]^2.$$

The difficulty in using RSS_E is in obtaining the implicit solutions for F_t in (2.75).

Several extensions to this basic model include handling missing data, incorporating more than one fishery, using auxiliary biomass estimates from a survey, allowing q to vary, bootstrapping to obtain standard errors and confidence intervals, and forecasting. Prager also discussed the issues of autocorrelation and process error in surplus production models and other extensions to production models. Application of Prager's method to other production models involves numerical integration techniques as in Rivard and Bledsoe (1978), because closed-form solutions of the yield equations rarely exist.

2.2.9. Example

Recall example 2.1 of a stock following the Graham-Schaefer system in section 2.1.1 (table 2.1, figure 2.4). By using values of B_t and Y_t from table 2.1, calculations of true $\text{ASP}_t = Y_t + \Delta B_t$ from (2.40), \bar{B}_t (approximated by the average of B_t and B_{t+1}), and $\dot{P}(\bar{B}_t)$ from (2.5) are shown in table 2.2. The closeness of ASP and $\dot{P}(\bar{B}_t)$ (figure 2.10) suggests that the rectangular approximation (2.40) in section 2.2.1 is a good one. These quantities are not directly observable but will be used in parameter estimation to determine if any bias exists in the methods.

Table 2.3 shows the calculations of observable quantities (denoted by a caret) from yield, effort, and CPUE. First, $\widehat{\bar{B}}_t$ is calculated from (2.41) by dividing CPUE by q . Resulting observed average biomass (table 2.3) differs little from true average biomass (table 2.2) after year 2. Next, biomass at the start of each year, \widehat{B}_t , is estimated from (2.42) as the average of two successive average biomasses; it is not possible to estimate biomass at the start of year 0. Observed biomass (table 2.3) differs from true biomass (table 2.1) somewhat in years when there is a change in the overall trend, which would be expected to occur from using averages. Changes in biomass and ASP are then estimated from (2.43) and (2.44); it is not possible to estimate ASP in years 0 and 29. Plots of true and observed ASP as a function of true and observed average biomass show the parabolic shape expected from the Graham-Schaefer system (figure 2.10). Observed $\widehat{\text{ASP}}$ (table 2.3) differs most from true ASP (table 2.2) in years when the trend changes. This phenomenon can be explained by comparing the time trajectory

Table 2.2. Calculations of annual surplus production, ASP_t , average biomass, \bar{B}_t , and productivity, \dot{P} , for the population scenario in table 2.1.

t	ASP_t	\bar{B}_t	\dot{P}
0	549	8421	532
1	957	5990	961
2	989	4604	994
3	929	3706	933
4	849	3077	852
5	770	2611	772
6	697	2253	698
7	631	1969	633
8	574	1739	575
9	523	1549	524
10	562	1701	565
11	690	2229	693
12	813	2853	816
13	914	3557	917
14	979	4307	981
15	998	5061	1000
16	974	5776	976
17	918	6417	920
18	844	6963	846
19	766	7408	768
20	795	7277	793
21	883	6720	882
22	930	6324	930
23	958	6034	957
24	974	5815	973
25	983	5648	983
26	989	5518	989
27	993	5416	993
28	996	5336	995
29	997	5272	997

of yield with ASP and latent productivity, \dot{P} , as a function of average biomass, \bar{B} (figure 2.11). Yield and biomass fall dramatically below the MSY level in the first 10 years due to high fishing pressure, increase beyond the MSY level when fishing pressure is drastically reduced in the second 10 years, and then decrease to the MSY level in the third 10 years when fishing mortality is at the MSY level. At the two turning points, observed ASP varies from latent productivity due to the change in yield. Thus, observations of ASP can be expected to have intrinsic variability associated with them, but no inherent bias. In contrast, observations of yield, and consequently CPUE, reflect nonequilibrium conditions and can be expected to produce anomalous results.

Parameter estimates from the various methods in sections 2.2.1–2.2.7, along with the residual sums of squares, are shown in table 2.4. Residual sums of squares can only be compared among methods when the same dependent variable is used. No attempt

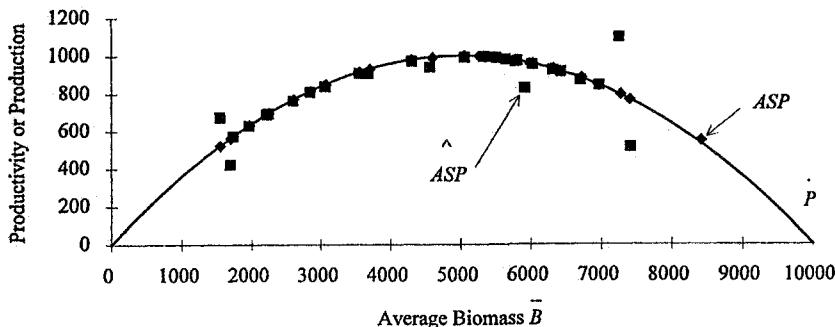


Figure 2.10. Actual ASP as a function of true average biomass, \bar{B} , and observed $\widehat{\text{ASP}}$ as a function of observed average biomass, $\widehat{\bar{B}}$, and the true parabolic Graham-Schaefer latent productivity curve, P , as a function of biomass with productivity parameters $B_\infty = 10,000$ and $m = 1000$.

is made to estimate variability, as the focus is on finding significant bias. Variability could be determined from the delta method, jackknifing, or bootstrapping.

One would expect no bias in parameter estimation from methods related to the Graham-Schaefer system. First, from model (2.45) with a constant error structure assumption and the true values of ASP and \bar{B} , estimates of all production parameters are nearly identical to the true values, indicating no bias. When observed ASP and \bar{B} are used, no appreciable bias is again detected; the residual sum of squares is higher, as expected. The use of model (2.46) with variance proportional to squared average biomass leads to the same conclusions. The resulting productivity relationship with biomass is indistinguishable from the true one (figure 2.12). Most of the subsequent results are based on the use of the proportional variance model and the true quantities because results were not appreciably different from other choices.

Of the remaining biomass-based methods, the Pella-Tomlinson model (2.48) and the Fletcher quadratic model (2.51b) are fitted by nonlinear least squares, while the Gompertz-Fox model (2.50), the Quinn-Collie threshold model (2.52b), and the recruitment adjustment model (2.53) are fitted by linear regression. The dependent variable is $\ln(\text{ASP}/\bar{B})$ for the recruitment adjustment method and ASP/\bar{B} for the other methods. As the data are generated with no time lag, average biomass in the same year is used for the recruitment adjustment method. The threshold model with ASP as the dependent variable is also fitted to illustrate the calculation of production parameters.

The Pella-Tomlinson, Fletcher quadratic, and Quinn-Collie threshold models fit the data well (figure 2.12), and production parameters are estimated with no apparent bias. The estimate of parameter n in the Pella-Tomlinson model is close to 2, the true value. The Fletcher quadratic model estimates B_m close to its true value of 5000. The threshold models estimate a threshold close to 0, the true value; as with the Graham-Schaefer, the error structure does not affect the conclusions. The Gompertz-Fox model does not fit the data well (figure 2.12) and has severely biased estimates of B_∞ and B_m . As the data are generated from the Graham-Schaefer model, that result is not surprising. The recruitment adjustment method produces estimates of m and B_m that, surprisingly, do not differ greatly from their true values; that is a consequence of a good approximation of the left side of the parabola by the Ricker curve (figure 2.12).

Table 2.3. Yield, Y_t , effort, E_t , and catch-per-unit-effort (CPUE), U_t , for each year and corresponding calculations of observed average biomass, biomass at the start of each year, and annual surplus production (ASP).

t	Y_t	E_t	U_t	\hat{B}_t	\bar{B}_t	$\widehat{\text{ASP}}_t$
0	3706	45	82	8236		
1	2662	45	59	5916	7076	828
2	2055	45	46	4567	5241	940
3	1658	45	37	3685	4126	907
4	1379	45	31	3064	3374	837
5	1171	45	26	2603	2833	763
6	1011	45	22	2247	2425	692
7	884	45	20	1965	2106	629
8	781	45	17	1736	1850	572
9	696	45	15	1546	1641	674
10	85	5	17	1692	1619	422
11	111	5	22	2220	1956	688
12	142	5	28	2847	2534	809
13	178	5	36	3553	3200	908
14	215	5	43	4307	3930	971
15	253	5	51	5065	4686	991
16	289	5	58	5783	5424	969
17	321	5	64	6425	6104	915
18	349	5	70	6971	6698	844
19	371	5	74	7416	7193	513
20	1451	20	73	7256	7336	1097
21	1341	20	67	6707	6982	871
22	1263	20	63	6316	6511	924
23	1206	20	60	6028	6172	953
24	1162	20	58	5811	5920	971
25	1129	20	56	5645	5728	981
26	1103	20	55	5516	5581	988
27	1083	20	54	5415	5465	992
28	1067	20	53	5334	5375	995
29	1054	20	53	5271	5303	

Of the effort-based methods, the Graham-Schaefer ASP model (2.55), the equilibrium approximation method of section 2.2.5, the Schnute nonequilibrium model (2.67), and the Hilborn nonequilibrium model (2.70) are used. In the equilibrium approximation method, average effort of the current and previous year [$T = 2$ in (2.63)] is arbitrarily used.

The two ad hoc methods of fitting ASP and CPUE versus fishing effort, E , fail miserably, with severely biased estimates of productivity parameters. The empirical relationship between ASP and E does not resemble the equilibrium parabola (figure 2.13) because effort at a given biomass level differs from the fishing effort that keeps the stock at equilibrium. As a consequence, ASP is higher than equilibrium values at low and high levels of effort and slightly lower at intermediate levels, which results in overestimates of m and B_∞ . Given this intrinsic bias, there is no reason to consider other ASP-effort models such as the Pella-Tomlinson.

In the method of equilibrium approximation, the observed CPUE data are fitted

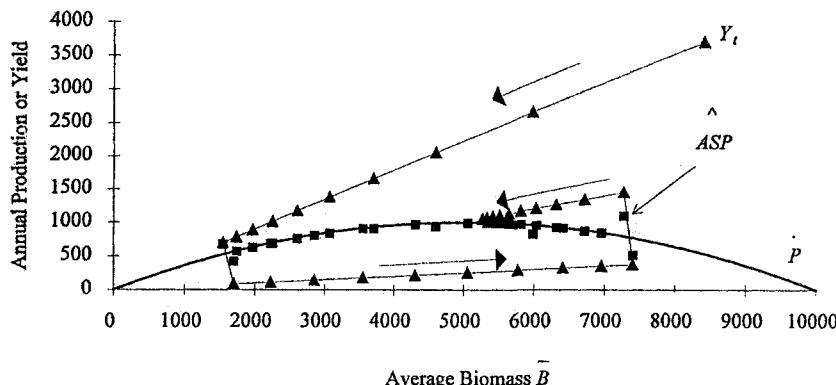


Figure 2.11. Time trajectory of yield, Y_t , as a function of average biomass, \bar{B} , and the observed \hat{ASP} and latent productivity, \hat{P} , relationships from figure 2.10.

without bias as a function of effort, but observed CPUE is higher than at equilibrium at high levels of effort due to fishing down the stock and lower than equilibrium at low levels of effort due to rebuilding the stock (figure 2.14). This results in underestimating B_∞ (corresponding to the y -intercept) and overestimating m (which is directly related to the y -intercept and inversely related to the slope).

The Schnute nonequilibrium method produces estimates closest to the true values of all of the methods considered. The Hilborn method is also satisfactory, although not as good as the Schnute method. Both of these methods have the advantage over the others that an estimate of catchability, q , is obtained in addition to the other production parameters. The Schnute estimate of q is unbiased, while the Hilborn estimate is slightly biased downward.

Taken together, these results suggest that a variety of approaches can be used to understand stock productivity. Methods concentrating on ASP perform best when related to biomass rather than effort and are preferred when CPUE data are not available. The best method to use with a given set of data involves the trade-off of greater stability of estimates when using two-parameter models such as the Graham-Schaefer and Gompertz-Fox versus the better fitting capability of the Pella-Tomlinson, Fletcher quadratic, and threshold models. When effort data are available, there is no need to consider ad hoc approaches in estimating productivity parameters because nonequilibrium methods (Schnute, Hilborn) outperform them.

2.3. RELATION OF SURPLUS PRODUCTION TO RECRUITMENT, GROWTH, AND NATURAL MORTALITY

The elemental form of the Graham-Schaefer system from (2.6) may be written

$$\dot{B} = \hat{P} - \dot{Y} = aB - bB^2 - FB, \quad (2.76)$$

where the first term provides a linear increase due to productivity, the second term damps the linear increase, and the third term provides a linear decrease due to fishing. A factor that affects the change in biomass linearly has come to be known as a density-independent factor because its per capita effect on the population is constant. In contrast, a density-dependent factor affects the change in biomass in some nonlinear fashion.

Table 2.4. Estimates of regression coefficients (a , b , c), threshold, T , maximum productivity, m , pristine biomass, B_∞ , biomass at maximum sustainable yield, \hat{B}_m , and catchability, q , where applicable, and residual sum of squares, RSS, for various production models and dependent variables.

Model ^a	Dependent variable	a	b	c	\hat{T}	\hat{m}	\hat{B}_∞	\hat{B}_m	\hat{q}	RSS
True value					0	1000	10000	5000	0.01	0
G-S	ASP	0	0.398	-0.0000396		998	10037	5018		200
G-S (obs.)	ASP	0	0.394	-0.0000392		987	10031	5016		217129
G-S	ASP/B	0.398	-0.0000397			999	10024	5012		0.0000056
G-S (obs.)	ASP/B	0.401	-0.0000405			991	9892	4946		0.020
P-T	ASP/B	<i>n</i> : 1.99	NA	NA		998	10051	5014		0.0000047
G-F	ASP/B	1.488	-0.153			948	16865	6204		0.0069506
F-Q	ASP/B	NA	NA	NA		998	10060	5013		0.0000046
QC-T	ASP/B	2.760	0.397	-0.0000395	-7	998	10039	5016		0.0000049
QC-T	ASP	5.154	0.395	-0.0000394	-13	997	10050	5018		174
Rec. adj.	ln(ASP/B)	-0.677	-0.000202			925	N/A	4948		0.232
G-S	ASP/E	160.6	-3.551			1816	16059	8029		34548
Eq. appr.	CPUE	60.2	-0.545			1664	6021	3011		8709
Schnute	ln(CPUE ratio)	0.400	-0.00401	-0.00998		1000	9997	4999	0.00998	0.0000363
Hilborn 1	Rel. CPUE ratio	0.405	-0.00437	-0.00872		1077	10634	5317	0.00872	0.0401450

^aModel notation: G-S, Graham-Schaefer; P-T, Pella-Tomlinson; G-F, Gompertz-Fox; F-Q, Fletcher quadratic; QC-T, Quinn-Collie threshold; Rec. adj., recruitment adjustment; Eq. appr., equilibrium approximation; (obs.) observed values. CPUE, catch-per-unit-effort.

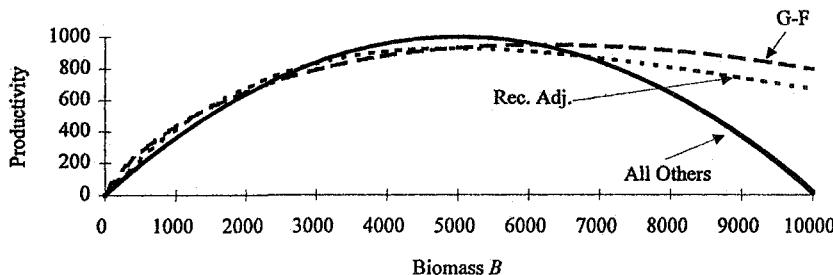


Figure 2.12. The estimated relationship between latent productivity, \hat{P} , and biomass, B , for the Graham-Schaefer, Pella-Tomlinson, Gompertz-Fox, Fletcher quadratic, Quinn-Collie threshold, and recruitment adjustment models. Parameter estimates are taken from table 2.4 for true ASP values and ASP/\bar{B} as the dependent variable. The solid line is indistinguishable from the true relationship.

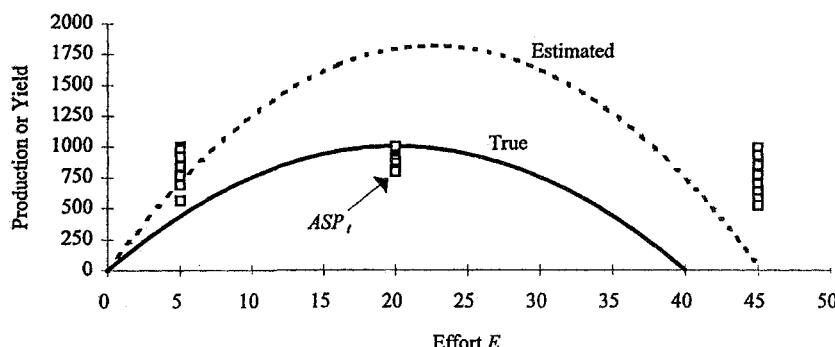


Figure 2.13. Actual values of ASP as a function of fishing effort, E , and the true and estimated relationships between equilibrium yield and fishing effort for the Graham-Schaefer ASP model (2.55). Parameter estimates from table 2.4 for the Graham-Schaefer model with ASP/E are used.

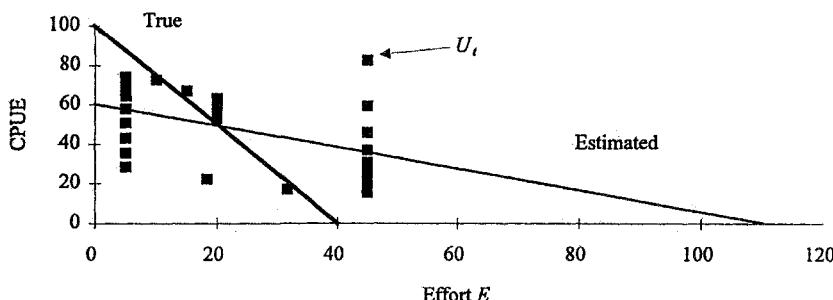


Figure 2.14. Actual values of CPUE U_t as a function of average fishing effort, \bar{E}_t , of the current and previous year and the true and estimated relationships between equilibrium CPUE and fishing effort, E , for the method of equilibrium approximation (section 2.2.5). Parameter estimates from table 2.4 for the Graham-Schaefer model with U are used.

In (2.76), latent productivity is then the combination of a density-dependent effect of productivity, modeled as a quadratic relationship, and a density-independent effect due to fishing.

The major factors affecting the growth of a population include an increase due to recruitment, R ; an increase due to growth of individuals, G ; a decrease due to natural mortality, D ; and a decrease due to fishing, Y , as suggested by Jensen (1984a). Thus, a general population model for change in biomass would include the changes in these factors, or

$$\dot{B} = \dot{R} + \dot{G} - \dot{D} - \dot{Y}. \quad (2.77)$$

One possible population model would assume that the first three factors are the product of quadratic density-dependent effects, while fishing is a density-independent effect, or

$$\begin{aligned}\dot{R} &= (r_1 + r_2 B)B \\ \dot{G} &= (g_1 + g_2 B)B \\ \dot{D} &= (d_1 + d_2 B)B \\ \dot{Y} &= FB.\end{aligned}$$

Substituting these relationships into (2.77) produces the equation

$$\dot{B} = (r_1 + g_1 - d_1)B - (r_2 + g_2 - d_2)B^2 - FB, \quad (2.78)$$

which is equivalent to the elemental form (2.76) for the Graham-Schaefer system. The first term in (2.78) collects the density-independent effects of recruitment, growth, and natural mortality, while the second term collects the density-dependent effects. A more common special case of (2.78) is for density-independent natural mortality, which sets $d_1 = M$ and $d_2 = 0$. Still, the elemental form of relationship is the Graham-Schaefer system.

The Pella-Tomlinson and Gompertz-Fox systems may be constructed in the same fashion, only with an exponent that differs from 2 in (2.78). The quadratic recruitment relation can be derived from the Ricker spawner-recruit model by taking the first two terms of a Taylor series expansion (Jensen 1984a).

Thus, surplus production models can account for density-dependent effects in growth, recruitment, and mortality when modeled with a parabolic or polynomial equation. The lack of biological realism that is frequently attributed to these models comes from the failure to account for time lags in the response of these processes (Walter 1973). The differential equation models assume an instantaneous response based on current population biomass, and the difference equation models assume a response based on population biomass in the prior year. Nevertheless, the basic concepts of equilibrium yield, surplus production, maximum sustainable yield, pristine biomass, and density dependence are focal points in later chapters.

Stock and Recruitment

The regenerative process of a population is critical to the maintenance of the population. The mathematical modeling of the process is of fundamental importance in fish population dynamics. Much effort has been directed to the study of recruitment to the population at various stages of life history. It could be argued that little is yet understood. The major issue is whether recruitment is primarily related to spawning stock or environmental conditions. Empirical relationships between spawning stock and recruitment show extreme annual variability (Larkin 1973, Ricker 1975a, Hennemuth et al. 1980, Getz and Swartzman 1981, Rothschild 1986). Yet it is clear that there must be some bounds on recruitment due to limits in early life history, such as food, spawning area, rearing area, and cannibalism.

3.1. SPAWNER-RECRUIT MODELS

For any fish population, the cycle of regeneration can be visualized as

$$\text{Eggs} \rightarrow \text{Larvae} \rightarrow \text{Juveniles} \rightarrow \text{Recruits} \rightarrow \text{Spawners} \rightarrow \text{Eggs} \rightarrow \dots \quad (3.1)$$

In the simplest model, abundance at each stage is assumed proportional to that of the previous stage. Hence, egg production, N_0 , is proportional to spawning stock, \mathcal{S} , or

$$N_0 = f\mathcal{S}, \quad (3.2)$$

where f is average net fecundity in the population. Recruitment, R , is proportional to egg production, or

$$R = \ell N_0, \quad (3.3)$$

where ℓ is early life survival from the egg stage to the time of recruitment. From (3.2) and (3.3), recruitment is also proportional to spawning stock, or

$$R = \alpha\mathcal{S}, \quad (3.4)$$

where $\alpha = \ell f$. This relationship is called “density independent” because the ratio, R/S , of recruitment to spawning stock is independent of population density as measured by spawning stock. From (3.3), population density can also be measured by egg production, N_0 . The parameter α is called the productivity or density-independent parameter. The relationship (3.4) is generally not realistic because it allows recruitment to increase without bound as a function of spawning stock, unless fecundity is density dependent.

At the opposite extreme, recruitment may be considered a random event in the sense that it is taken from a probability density function with parameters independent of the population (Hennemuth et al. 1980). Essentially, the processes connecting the different stages in (3.1) are viewed as being so complex that only probability distributions can adequately capture the variation. This concept is deduced from empirical plots of recruits and spawners but is flawed in that it does not recognize the limits of recruitment at extremely high or low spawner levels. Further, the relationship between recruits and spawners may be masked by measurement errors (section 3.2.3). A middle ground is provided by Getz and Swartzman (1981), who modeled recruitment as a Markov transition matrix, where spawners and recruits are classified into different groups representing relatively low to relatively high levels.

If expected recruitment is considered constant in (3.3), then N_0 and early life survival, ℓ , must have an inverse relationship on average, or

$$\ell \propto 1/N_0 \quad \text{for } E(R) = \text{constant}.$$

Hence, constant expected recruitment implies that early life survival is a density-dependent function of egg production, a fact not often recognized.

3.1.1. Beverton-Holt

If density-dependent effects are present at some life-history stage in (3.1), then the simple model (3.4) is unacceptable. Suppose that Z_t is the mortality at life stage t and that T is the age of recruitment. In some populations, T may be a function of population size, but this effect will not be considered. From (1.17),

$$\frac{dN}{dt} = -Z_t N \quad \text{where } N(0) = N_0.$$

Suppose that Z_t is made up of both density-independent and density-dependent effects, or

$$Z_t = a_1 + b_1 N,$$

which suggests that the population of young fish before recruitment inhibits itself through competition for food (resulting in larval starvation) or space (such as over-crowding of eggs). Then, the differential equation becomes

$$\frac{dN}{dt} = -(a_1 + b_1 N)N, \quad (3.5)$$

which is the same as differential equation (1.8) describing the logistic law, only with negative parameters. Its solution from (1.9) is

$$N(t) = \frac{N_0}{e^{a_1 t} - \frac{b_1}{a_1} N_0 + \frac{b_1}{a_1} N_0 e^{a_1 t}}.$$

With the assumption that the number of eggs, N_0 , is proportional to spawners, as in (3.2), this equation for $t = T$ becomes

$$R \equiv N(T) = \frac{S}{\frac{e^{a_1 T}}{f} + \frac{b_1}{a_1} (e^{a_1 T} - 1) S}$$

or $R = \frac{S}{\alpha^* + \beta^* S} = \frac{\alpha S}{1 + \beta S},$ (3.6)

where $\alpha = f \exp[-a_1 T]$ and $\beta = f b_1 [1 - \exp(-a_1 T)]/a_1$. This model is called the Beverton-Holt spawner-recruit curve, first derived by Beverton and Holt (1957); also see Fogarty et al. (1991). Parameterizations with (α^*, β^*) and (α, β) are both common, with the relationship between them being $\alpha^* = 1/\alpha$ and $\beta^* = \beta/\alpha$. Parameter α is still the productivity parameter, representing the number of recruits per spawner at low numbers of spawners. It is proportional to fecundity, f , as expected. Parameter β controls the level of density dependence and is proportional to both f and density-dependent mortality parameter b_1 . For small a_1 , β is nearly independent of a_1 because $[1 - \exp(-a_1 T)]/a_1 \approx T$.

This relationship is a strictly increasing function of spawners, which approaches the asymptote

$$R_p = 1/\beta^* = \alpha/\beta,$$

which is maximum recruitment (figure 3.1). The subscript p denotes “peak”; the subscript m , used later in section 3.3, will denote “maximum productivity” in accord with chapter 2. Hence the effect of density dependence in early life history is to produce a constraining effect on recruitment as spawning stock gets large.

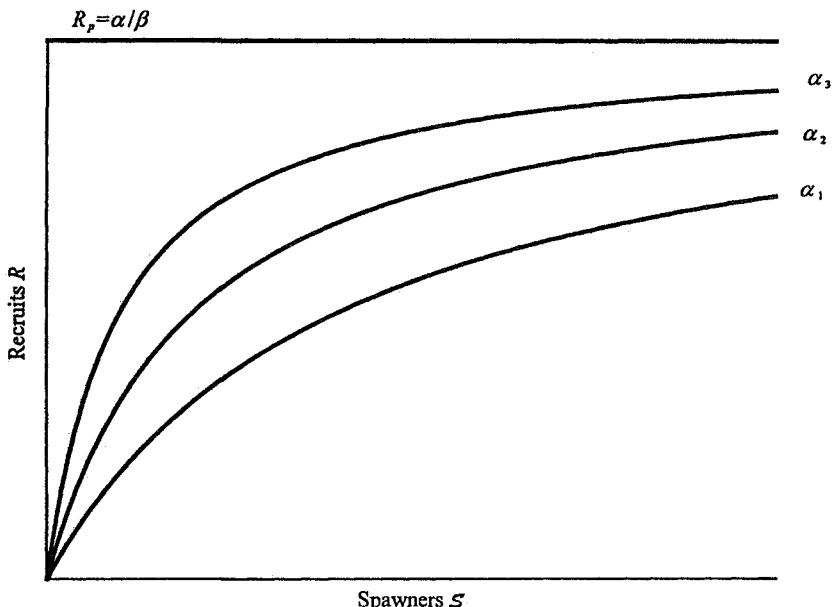


Figure 3.1. The Beverton-Holt spawner-recruit model. Three curves are shown, corresponding to three values of productivity parameter α and a constant value of $R_p = \alpha/\beta$.

Parenthetically, it is not necessary for density dependence to operate during all early life-history stages before recruitment to obtain (3.6). If density dependence operates at any one time period and the relationship between other stages is density independent, then (3.6) still results.

3.1.2. Ricker

Suppose that the same model as in section 3.1.1 is constructed, except that the spawning stock inhibits the population of young fish before recruitment (such as through cannibalism). Then Z_t is modeled with density-independent and density-dependent effects as

$$Z_t = a_2 + b_2 S,$$

and the differential equation (1.17) becomes

$$\frac{dN}{dt} = -(a_2 + b_2 S)N, \quad (3.7)$$

which is the differential equation describing the exponential decay law, if variation in S is ignored. (If not, the integral average spawning stock replaces S in the solution.) Its solution from (1.18) is

$$N(t) = N_0 e^{-(a_2 + b_2 S)t}.$$

For $t = T$ and by assuming that $N_0 = fS$ from (3.2), this equation becomes

$$R \equiv N(T) = (f e^{-a_2 T}) S e^{-b_2 T S}$$

or $R = \alpha S e^{-\beta S} = S e^{\alpha - \beta S}, \quad (3.8)$

which is called the Ricker spawner-recruit curve, first derived by Ricker (1954). As in the Beverton-Holt model, productivity parameter α is proportional to fecundity, f , and parameter β measures the level of density dependence. The second frequently used parameterization in (3.8) follows a convention set by Ricker (1975a) of substituting $\exp(\alpha)$ for α .

This relationship is dome-shaped as a function of spawners, with a maximum (peak) at the point

$$(R_p, S_p) = \left(\frac{\alpha}{\beta e}, \frac{1}{\beta} \right)$$

(figure 3.2). As $S \rightarrow \infty$, $R \rightarrow 0$. Hence the effect of a negative spawner influence in early life history is to produce an increasingly deleterious effect on recruitment as spawning stock gets large.

As with the Beverton-Holt model, it is not necessary for mortality to be affected by spawners during all early life-history stages before recruitment to obtain the Ricker relation (3.8). If the effect operates at any one time period and the relationship between other stages is density independent, then (3.8) still results.

Dome-shaped curves

For further insight into the types of spawner-recruit curves that may occur, we show that dome-shaped curves cannot result from an autonomous (only a function of the variable)

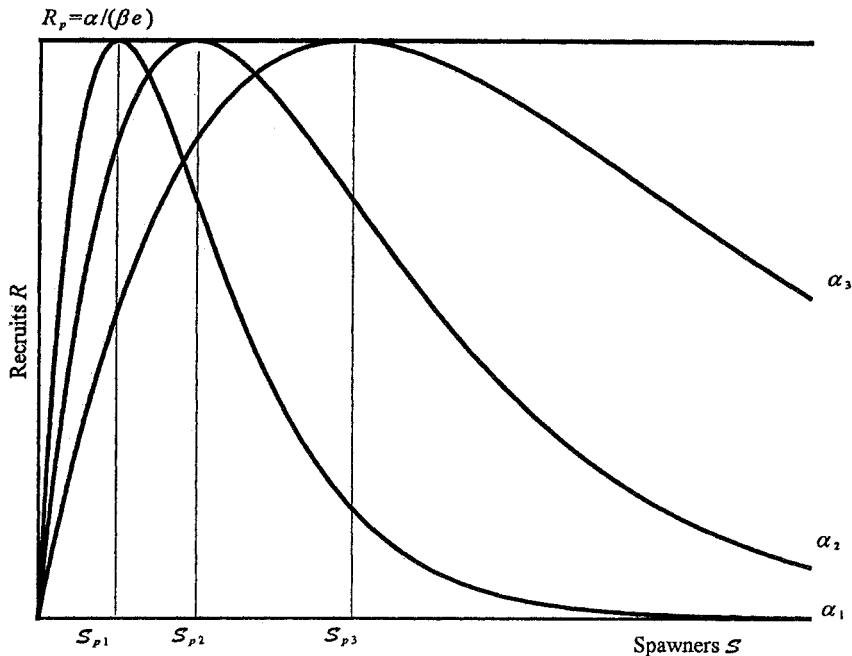


Figure 3.2. The Ricker spawner-recruit model. Three curves are shown, corresponding to three values of productivity parameter α and a constant value of density dependence parameter β .

differential equation for the mortality process. Precisely stated, let the differential equation governing the spawner-recruit function be given as

$$\frac{dN}{dt} = \mathcal{F}(N),$$

where \mathcal{F} is a continuous parametric function. The initial condition, $N(0)$, represents spawners, and the solution $N(T)$ at time T represents recruits. Suppose that the solution is applied to two initial conditions where $N_1(0) < N_2(0)$. A dome-shaped curve can only occur if $N_1(T) > N_2(T)$ for some pair of initial conditions. This result is seen graphically in figure 3.3, where $N(T)$ is the result of projecting $N(0)$ on the x -axis to the y -axis via the dome-shaped curve.

That a dome-shaped curve cannot occur when \mathcal{F} is only a function of N can be proven by the method of contradiction. Suppose that $N_1(0) < N_2(0)$ and $N_1(T) > N_2(T)$. Then by continuity of function \mathcal{F} , there must exist a value t^* such that $N_1(t^*) = N_2(t^*)$. Yet by uniqueness of a solution to a differential equation with a given initial condition (t^* in this case), it must then be true that $N_1(T) = N_2(T)$. Thus, both inequalities cannot hold.

The function \mathcal{F} is equal to $-(a_1 + b_1 N)N$ for the Beverton-Holt model from (3.5), which is only a function of N . As argued above, the resulting autonomous differential equation cannot be dome-shaped, which is indeed true for this model. The function \mathcal{F} is equal to $-(a_2 + b_2 S)N$ for the Ricker model from (3.7). The nonautonomous term $b_2 S$ allows the possibility of a dome-shaped curve.

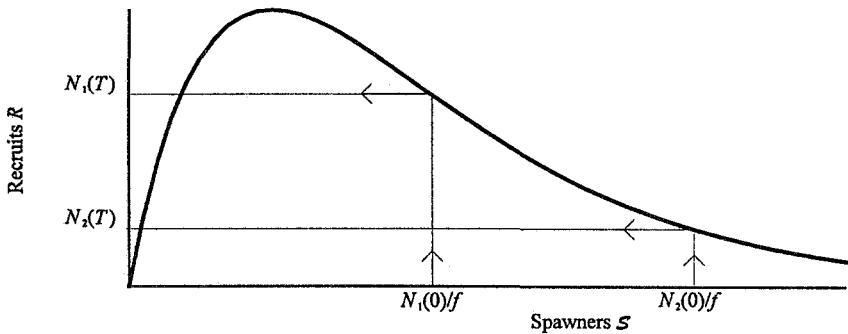


Figure 3.3. A typical dome-shaped curve, showing two initial conditions $S_1 = N_1(0)/f$ and $S_2 = N_2(0)/f$. Resulting recruitment, $R_i = N_i(T)$, is found by projecting from the x axis to the y axis. In this particular case where $S_1 < S_2$, note that $R_1 > R_2$, which can only happen for a dome-shaped curve.

Ludwig-Walters model

Another generalization of the Ricker model was proposed by Ludwig and Walters (1989) and later used by Kinas (1993). The Ludwig-Walters model can be derived by assuming that the density-dependent mortality term is a power function of spawning stock, or $Z_t = a_2 + b_2 S^\gamma$. With this assumption, the resulting spawner-recruit model is

$$R = \alpha S e^{-\beta S^\gamma} = S e^{\alpha - \beta S^\gamma}. \quad (3.9)$$

Its curve is dome-shaped like the Ricker with a peak at

$$(R_p, S_p) = \left(\alpha (\beta \gamma)^{-1/\gamma}, e^{-1/\gamma} \right).$$

In a study to determine optimal effort, Ludwig and Walters (1989) showed that a higher value of γ than the Ricker value of 1 decreases the variance in estimated optimal effort but may introduce a bias. They suggested that a robust scheme is to use $\gamma = 2$ when low estimation accuracy is suspected.

Environmental variation

A generalization of the Ricker relation occurs if it is posited that other factors also affect the survival at early life-history stages. Environmental factors are frequently thought to be important during these stages. Suppose these other variables are labeled X_1, \dots, X_p . Then Z_t can be written

$$Z_t = a + bS + c_1 X_1 + \dots + c_p X_p,$$

which leads to the generalized Ricker relation

$$R = \alpha S e^{-\beta S + \gamma_1 X_1 + \dots + \gamma_p X_p}. \quad (3.10)$$

This approach has been used by Anderson and Wilen (1985), Caputi (1988), and Quinn and Niebauer (1995), among others.

In particular, $\{X_i\}$ may be thought of as random variables and $\{\gamma_i\}$ as the corresponding influences. Letting ϵ be the linear combination $\sum \gamma_i X_i$, a stochastic version of the Ricker spawner-recruit model is

$$R = \alpha S e^{-\beta S} e^{\epsilon}. \quad (3.11)$$

If the $\{X_i\}$ are normally-distributed, then R follows the deterministic Ricker model (3.8) with lognormal error. The biological interpretation of this result is that if a combination of normally distributed, random factors affects mortality during early life history, then the variation expected about a spawner-recruit curve would be lognormally distributed (Walters and Hilborn 1976, Hennemuth et al. 1980, Peterman 1981, Walters 1986). The term ϵ is called “process error.”

In contrast, Shelton (1992) argued that the distributional shape depends on life-history characteristics of individual species and that a variety of distributional shapes would be expected. For example, the underlying distribution would be approximately normal if the survival of individuals during early life is independent (and constant).

Reish et al. (1985) used a different approach to incorporate environmental effects. The spawning stock, S , is replaced with an “effective” spawning stock, \tilde{S} , that adjusts for environmental effects, where

$$\tilde{S} = S e^{\Sigma \gamma_i X_i}.$$

Their applications included the Beverton-Holt and the gamma models, but this approach could be applied to any spawner-recruit model.

A variant of this approach is to replace only αS with $\alpha \tilde{S}$ (rather than all occurrences of S). For the Ricker model, this approach results in the same equation as (3.10), if only the density-independent part of (3.8) is modified. If environmental factors are likely to affect recruitment independently of spawning stock, the rationale for the partial replacement is established. Another variant of this approach is to define environmentally adjusted recruits as

$$\tilde{R} = R e^{-\Sigma \gamma_i X_i}.$$

The resultant values are thus “corrected” for the environment and should be more likely to exhibit a discernible spawner-recruit relationship.

Another approach for incorporating environmental data into spawner-recruit relationships is the use of generalized additive models (Hastie and Tibshirani 1990, Jacobson and MacCall 1995). If Y is a recruitment variable (e.g., R , $\ln R$, $\ln R/S$) and X is an environmental variable, the general form of such a model is

$$Y = \alpha + f(X) + g(S) + \epsilon,$$

where α is the y -intercept parameter, f and g are functions, and ϵ is a normal error term. Functions f and g can be parametric or nonparametric; the nonparametric function is a scatterplot smoother, such as “lowess.” The overall functional form of the model is determined exclusively from the data rather than imposing a particular functional form. This approach was applied to Pacific sardine by Jacobson and MacCall (1995).

3.1.3. Cushing

In principle, any mathematical model can be used for spawner-recruit relationships as long as it goes through the origin, increases monotonically at low spawning levels, and shows some level of density dependence at high spawning levels. Cushing (1971, 1973) proposed a simple two-parameter model

$$R = \alpha S^\gamma = \alpha S(S^{\gamma-1}), \quad (3.12)$$

where γ is an index of density dependence. This model will be revisited in chapter 4 in consideration of growth. To provide density dependence, γ must be different from 1. Cushing (1971) showed that the index γ was linearly related to the cube root of fecundity across a variety of fish species.

This model is not used much in practice. One principal limitation is the lack of a peak level of recruitment; recruitment continues to increase as spawning level increases (figure 3.4). In fact, there is infinite recruitment for infinite spawning stock.

3.1.4. Deriso-Schnute

A three-parameter generalization of the Beverton-Holt and Ricker models was proposed by Deriso (1980) and elaborated upon by Schnute (1985). The derivation of this model, as given by Deriso (1978), is based on a two-species generalization of the logistic law (1.8). Suppose that the mortality process of a predator year-class obeys the logistic law

$$\frac{dN}{dt} = \left[-\alpha_0 - \alpha_1 \frac{N(t)}{P(t)} \right] N(t), \quad \alpha_0, \alpha_1 > 0, \quad (3.13)$$

which has been generalized to include a dynamic resource term $P(t)$. The resource (or prey) is subject to depletion according to the model

$$\frac{dP}{dt} = \left[\beta_0 - \beta_1 \frac{N(t)}{P(t)} \right] P(t) = \beta_0 P(t) - \beta_1 N(t), \quad \beta_0, \beta_1 > 0, \quad (3.14)$$

which is a generalization of the exponential law with depletion by a predator.

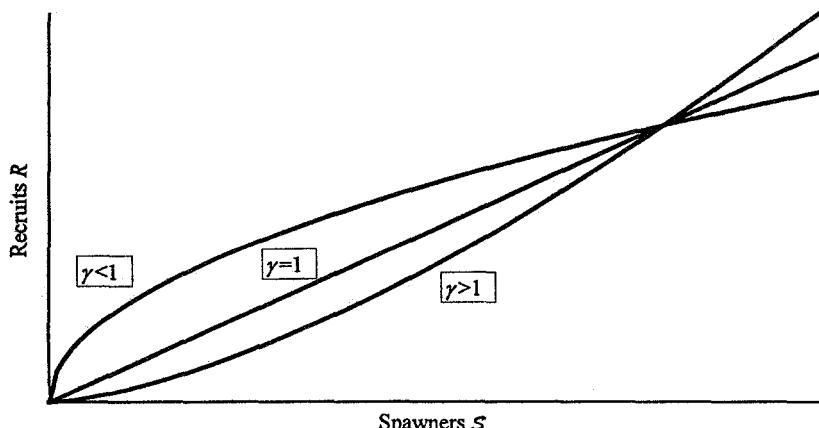


Figure 3.4. The Cushing spawner-recruit model. Three curves are shown, corresponding to values of shape parameter γ less than, equal to, and greater than 1.

Note that depletion depends only on predator abundance in this model, which corresponds to the asymptote in an Ivlev-type foraging term (Ivlev 1961), where, for all prey abundances, the predator takes a fixed number of prey (per unit time). Such a model is likely not valid when prey are scarce. More is said about this model later under the topic of compensatory mortality in section 3.1.7. Note that (3.14) implies that the prey are limited only by predation.

The solution to the above coupled system of nonlinear differential equations can be found by solving first for $X(t) = P(t)/N(t)$,

$$\text{viz., } \frac{dX}{dt} = \left(\frac{dP}{Pdt} - \frac{dN}{Ndt} \right) \frac{P(t)}{N(t)} \\ = (\alpha_1 - \beta_1) + (\alpha_0 + \beta_0)X(t) \\ = \gamma_1 + \gamma_0 X(t). \quad (3.15)$$

This linear differential equation has the solution

$$X(t) = e^{\gamma_0 t} \left[X_0 + \frac{\gamma_1}{\gamma_0} (1 - e^{-\gamma_0 t}) \right], \quad (3.16)$$

where the initial condition is $X(0) = X_0$ at time $t = 0$.

The variable $X(t)$ is now substituted in the differential equation (3.13) for $N(t)$, written as

$$\frac{dN}{dt} = \left[-\alpha_0 - \frac{\alpha_1}{X(t)} \right] N(t).$$

Noting that $dt = dX/(\gamma_1 + \gamma_0 X)$, this differential equation can be rewritten

$$\frac{dN}{N} = -\alpha_0 dt - \frac{\alpha_1}{X(\gamma_1 + \gamma_0 X)} dX,$$

which has the solution

$$N(t) = N_0 e^{-\alpha_0 t} \left[\frac{X(t)(\gamma_1 + \gamma_0 X_0)}{X_0(\gamma_1 + \gamma_0 X(t))} \right]^{1/\gamma}, \quad (3.17)$$

where $\gamma = -\gamma_1/\alpha_1$. Similarly, the differential equation (3.14) for $P(t)$ can be rewritten

$$\frac{dP}{dt} = \left[\beta_0 - \frac{\beta_1}{X(t)} \right] P(t),$$

which has the same solution as $N(t)$ in (3.17), only with P in place of N , β_0 in place of $-\alpha_0$, and $-\gamma_1/\beta_1$ in place of γ .

The solutions for $N(t)$ and $P(t)$ can now be rewritten as the pair of coupled difference equations

$$N_{t+1} = \alpha N_t \left(1 - \xi \frac{N_t}{P_t} \right)^{1/\gamma} \quad (3.18)$$

$$P_{t+1} = \beta_2 P_t \left(1 - \xi \frac{N_t}{P_t} \right)^{(1+1/\gamma)}, \quad (3.19)$$

where $a = \exp(-\alpha_0)$; $\xi = -(\gamma_1/\gamma_0)[1 - \exp(-\gamma_0)]$; and $\beta_2 = \exp(\beta_0)$. The derivation for (3.18) follows from (3.17) by setting $t = 1$ and replacing $N(t)$ with N_{t+1} , N_0 with N_t , and X_0 with P_t/N_t . The solution for $X(t)$ in (3.16) is substituted, noting that

$$\frac{\gamma_1 + \gamma_0 X(t)}{\gamma_1 + \gamma_0 X_0} = e^{\gamma_0 t}.$$

A similar derivation of (3.19) uses the solution for $P(t)$ and the definition $\gamma_1 = \alpha_1 - \beta_1$.

If the resource P_t is periodically forced back to a fixed level (i.e., $P_t = P$), then the equation (3.18) for N_{t+1} can be regarded as a spawner-recruit model. A functional form for this model from Schnute (1985) is

$$R = \alpha S (1 - \beta \gamma S)^{1/\gamma}, \quad (3.20)$$

where $\beta \gamma = \xi / P$. Schnute (1985) referred to α as the productivity parameter, β as the optimality parameter, and γ as the recruitment limitation or skewness parameter. The γ parameter provides additional flexibility and generality in shape. The Beverton-Holt and Ricker models correspond to $\gamma = -1$ and $\gamma \rightarrow 0$, respectively. In addition, as $\gamma \rightarrow -\infty$, recruitment becomes proportional to spawning stock ($R = \alpha S$), and when $\gamma = 1$, then the logistic model (see sections 1.1.2, 2.1.1) results.

The properties of this model depend on the value of γ . When $\gamma > -1$, the spawner-recruit curve has a unique maximum (peak) at

$$(R_p, S_p) = \left(\frac{\alpha}{\beta} (1 + \gamma)^{-(1+\gamma)/\gamma}, [\beta(1 + \gamma)]^{-1} \right),$$

as shown in figure 3.5. For $\gamma > 0$, there are two points at which $R = 0$: $S = 0$ and $S = (\beta \gamma)^{-1}$. The presence of the right x -intercept suggests application to a population with a fixed carrying capacity, whereby recruitment would fail completely or not even take place if the population were above that level. The spawner-recruit curve is left-skewed when $0 < \gamma < 1$, symmetric when $\gamma = 1$ and right-skewed when $\gamma > 1$.

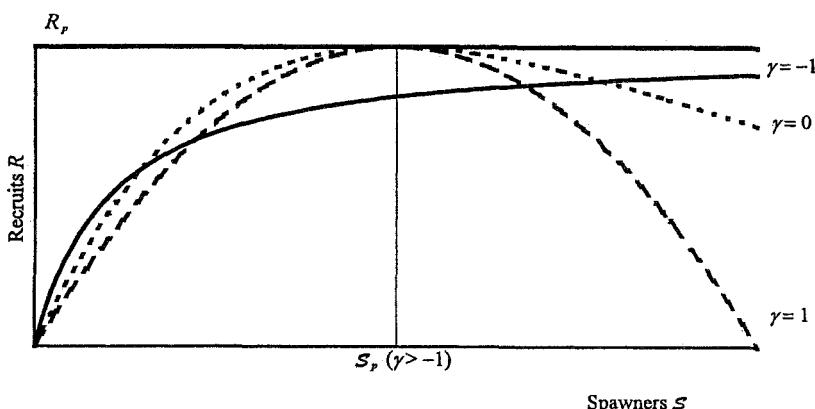


Figure 3.5. The Deriso-Schnute spawner-recruit model. Three curves are shown, corresponding to values of shape parameter γ equal to -1 (Beverton-Holt), 0 (Ricker), and 1 (logistic).

3.1.5. Shepherd

Shepherd (1982) proposed a generalization of the Beverton-Holt, Ricker, and Cushing models of the form

$$R = \frac{\alpha S}{1 + \beta S^\gamma}, \quad (3.21)$$

like the Pella-Tomlinson modification of the Graham-Schaefer model (section 2.1.2). This model has similar flexibility and generality as the Deriso-Schnute model (figure 3.6). The Beverton-Holt model is a special case of this general model when $\gamma = 1$. When $\gamma > 1$, the spawner-recruit curve is dome-shaped like the Ricker, and when $\gamma < 1$, the curve increases indefinitely like the Cushing model. When $\gamma > 1$, the unique maximum (peak) occurs at

$$(R_p, S_p) = \left(\frac{\alpha}{\beta \gamma} [\beta(\gamma - 1)]^{(\gamma-1)/\gamma}, [\beta(\gamma - 1)]^{-1/\gamma} \right),$$

as shown in figure 3.6. Shepherd's parameterization replaces β with $\kappa^{-\gamma}$, where κ is called a threshold, the spawning level at which recruitment is one-half of what it would have been under density independence. This model does not include the possibility of zero recruitment at a positive spawning level and does not contain the Ricker model as a special case.

A straightforward derivation of this model results from considering the relationship between recruitment and growth. Suppose that density dependence parameter b_1 in the Beverton-Holt model derivation (section 3.1.1) is inversely proportional to resultant growth, say $b_1 = c_1/W_T$, where W_T is size at age T of recruitment (Cushing and Horwood 1977). Further suppose that growth is a density-dependent function of the number of eggs, N_0 , say

$$W_T = d_1/N_0^{\gamma-1};$$

that is, weight at recruitment is inversely related to a power of egg (or larval) abundance. Hence, $b_1 = (c_1/d_1)N_0^{\gamma-1}$, and substituting into (3.5) yields

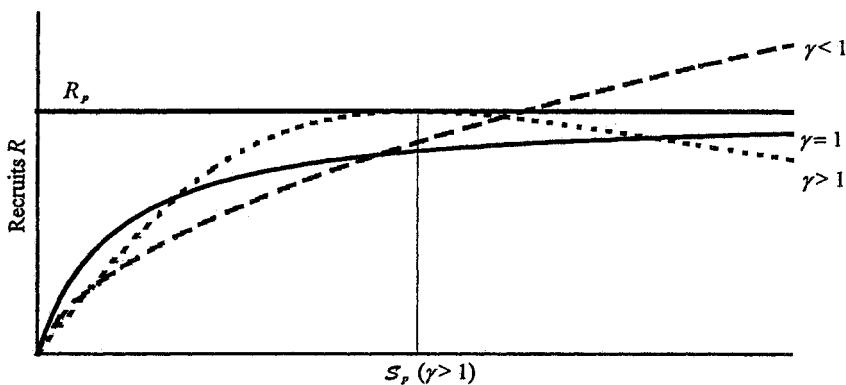


Figure 3.6. The Shepherd spawner-recruit model. Three curves are shown, corresponding to values of shape parameter γ less than 1 (having no asymptote), equal to 1 (Beverton-Holt), and greater than 1 (dome-shaped).

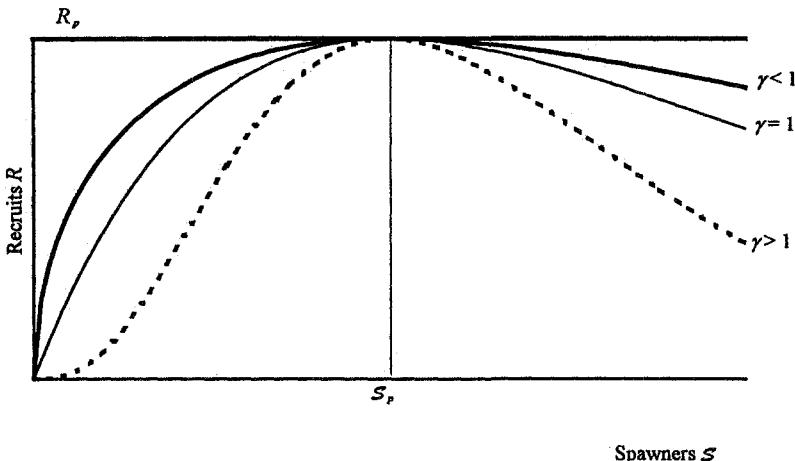


Figure 3.7. The gamma spawner-recruit model. Three curves are shown, corresponding to values of shape parameter γ less than 1 (nearly asymptotic), equal to 1 (Ricker), and greater than 1 (depensatory).

$$R \equiv N(T) = \frac{S}{\frac{e^{a_1 T}}{f} + \frac{c_1}{a_1 d_1} f^{\gamma-1} (e^{a_1 T} - 1) S^\gamma}$$

or $R = \frac{S}{\alpha^* + \beta^* S^\gamma} = \frac{\alpha S}{1 + \beta S^\gamma}.$

3.1.6. Gamma

Reish et al. (1985) proposed a generalization of the Ricker and Cushing models of the form

$$R = \alpha S^\gamma e^{-\beta S} = \alpha S (S^{\gamma-1} e^{-\beta S}), \quad (3.22)$$

which is an unnormalized gamma function. This model has similar flexibility and generality as the Deriso-Schnute model (figure 3.7), although the asymptotic behavior of the Beverton-Holt model is not completely captured. When $\gamma > 0$, the spawner-recruit curve is dome-shaped like the Ricker, and the Ricker is a special case when $\gamma = 1$. The Cushing model results when $\beta = 0$. Behavior similar to the Beverton-Holt model occurs as γ approaches 0, according to Reish et al. (1985). The case when $\gamma \leq 0$ does not correspond to a valid spawner-recruit model because it does not go through the origin.

When $\gamma > 0$ and $\beta > 0$, a unique maximum (peak) occurs at

$$(R_p, S_p) = \left(\alpha \left(\frac{\gamma}{\beta} \right)^\gamma e^{-\gamma}, \frac{\gamma}{\beta} \right),$$

as shown in figure 3.7. This model does not contain the Beverton-Holt model as a special case.

3.1.7. *Miscellany*

The derivations of the Beverton-Holt and Ricker models in this chapter are not the only ones. Chapman (1973) developed these and other models from assumptions about spawning area and niches. One of his alternative models turns out to be a special case of the von Bertalanffy growth model (section 4.2) of the form

$$R = \alpha[1 - \exp(-\beta S)]. \quad (3.23)$$

This model has similar characteristics to the Beverton-Holt model and is derived by assuming that spawning areas overlap in a similar manner as randomly placed bombs cover a target area. This model was earlier derived by McNeil (1964) in two ways, using a differential equation approach and using the Poisson distribution. Cushing (1973) developed alternative models from considerations of critical periods and growth. Cushing and Horwood (1977) developed a model that explicitly incorporated weight into the derivation.

Alternative parameterizations of these models can also be found. In this book, we parameterize spawner-recruit models in terms of productivity parameter α . The level of peak recruitment and corresponding spawning stock (R_p, S_p) has also been used (Clark 1991). Ricker (1971, 1975a) reparameterized spawner-recruit models in relation to the level where recruitment replaces the spawning population $[(R_r, S_r)$, where $R_r = S_r$, see section 3.3] or to the maximum productivity level, or equivalently the level producing maximum sustainable yield $[(R_m, S_m)$, see section 3.3]. Kimura (1988) gave a parameterization of spawner-recruit models for an arbitrary position (R_1, S_1) on a spawner-recruit curve. Schnute and Kronlund (1996) reparameterized spawner-recruit parameters in terms of management parameters related to optimal harvesting.

When spawning stock is measured by egg production, the ratio R/S represents early life survival, and, conversely, $1 - R/S$ represents early life mortality. All of the major spawner-recruit models contain “compensatory” mortality, which is defined to be early life mortality that increases (or survival that decreases) with increasing spawner abundance. Compensatory mortality occurs for spawning levels that satisfy the condition

$$\frac{d(R/S)}{dS} < 0. \quad (3.24)$$

The Ricker, Beverton-Holt, Cushing, Deriso-Schnute, and Shepherd models are compensatory for values of S from 0 up to at least S_p (given sufficient constraints on the parameters to make them valid spawner-recruit models). “Overcompensation” refers to a decrease in recruitment with increasing spawning level; it occurs when the slope of the spawner-recruit curve is negative; hence when

$$dR/dS < 0. \quad (3.25)$$

Overcompensation implies a dome-shaped spawner-recruit curve, such as the Ricker and some cases of the Deriso-Schnute, Shepherd, and gamma models. A “pure compensation” model is one for which compensation, but not overcompensation, occurs at all spawning levels, such as the Beverton-Holt.

The opposite type of mortality is called “depensatory” mortality, where early life mortality decreases (or survival increases) with increasing spawning abundance. Its condition is

$$\frac{d(R/S)}{dS} > 0. \quad (3.26)$$

“Critical depensation” refers to the situation where at low spawning levels, recruitment is insufficient to replace spawning stock. This concept is discussed further in section 3.3.

Of the models considered in section 3.1, only the gamma model (section 3.1.6) with $\gamma > 1$ has depensation. In figure 3.7, the upward-curving portion of the curve for low levels of spawners $\gamma > 1$ is evidence of depensation. Analytically, it can be shown by using (3.26), by taking the derivative of equation (3.22) divided by S and showing that it is positive when $S < (\gamma - 1)/\beta$.

Other depensation models can also be constructed. Indeed, the solution (3.19) to the prey model in section 3.1.4 contains depensatory mortality [$d(P_{t+1}/P_t)/dP_t > 0$] for sufficiently large prey abundance and a predator population periodically forced to a constant ($N_t = N$). The mechanism for depensation in that model is common to examples in the literature (e.g., Clark 1974, Larkin and McDonald 1968, and Deriso 1978), involving a predation rate that is either constant or declines nonlinearly with decreasing prey abundance.

Thompson (1993) generalized the Beverton-Holt model to include depensation as

$$R = \frac{\alpha S^\gamma}{1 + \beta S^\gamma}. \quad (3.27)$$

Myers et al. (1995) used (3.27) with data from 128 fish stocks from around the world and found it was difficult to detect depensation. Liermann and Hilborn (1997) reanalyzed these data from a Bayesian perspective using (3.27) and reached a similar conclusion. However, they suggested that depensatory models be included routinely in analyses because the distribution of depensation estimates was very broad. An application of (3.27) to Gulf of Maine cod (*Gadus morhua*) data suggested that depensation was a strong possibility (National Research Council 1998b).

A four-parameter generalization of the Ricker model, given by

$$R = \alpha S e^{\beta S - \delta S^\gamma},$$

is depensatory when $S^{\gamma-1} < \beta/(\gamma\delta)$. If used with semelparous populations (section 2.3), this model exhibits pure depensation (no critical depensation). Collie and Spencer (1993) constructed a logistic population model (section 1.2) combined with a Holling type III predation equation, given by

$$\frac{dP}{dt} = rP \left(1 - \frac{P}{K}\right) - \frac{cP^2}{d^2 + P^2}, \quad (3.28)$$

where r , K , c , and d are parameters. As (3.28) does not seem to have a closed-form solution, numerical integration techniques were used to show that this model exhibits depensation.

3.2. PARAMETER ESTIMATION

Suppose that for a group of year-classes indexed by t , a time series $\{R_t, S_t\}$ of recruitment and corresponding spawning level is available, where recruitment can be expressed in units of numbers or biomass. In many cases, recruitment refers to some reference age, r , so that t is treated as a time (rather than year-class) index and R_{t+r} replaces R_t . In other cases, such as for sockeye salmon, recruitment occurs over a number of years, so that a year-class index is necessary. We use the former notation for the most part, except where temporal dynamics are explicitly considered. Spawning level may be measured as the number of spawners, biomass of spawners, number of eggs, or some other measure of spawning potential. For example, pink salmon on the west coast of the United States have a two-year life cycle. For some stocks, escapement is sampled or enumerated in a given year to represent spawning level. Recruitment is then measured as the number of pink salmon returning two years later, the combination of harvested fish and escapement. In contrast, many marine species are represented by several ages. Age-structured methods (chapter 8) can be used to determine population abundance for a given age and time. Spawning biomass can be determined as the product of abundance, average weight, and maturity, summed over ages for a given year, t , and recruitment can be determined as the abundance at starting age r at time $t + r$.

3.2.1. Linear Regression Approach

Parameter estimation for spawner-recruit models has traditionally involved the use of standard linear regression techniques with linearized forms of the models (e.g., Ricker 1975a). This practice imposes a particular error structure on the model, which may not be appropriate for the data set to be analyzed. A better practice is to consider modeling the error structure as an integral part of the process, not as an afterthought (Schnute 1991). At any rate, the use of linear and nonlinear regression techniques involves several assumptions that should be carefully examined by investigators.

For the Beverton-Holt spawner-recruit curve, (3.6) can be recast as

$$\frac{1}{R} = \beta^* + \alpha^* \frac{1}{S} \quad (3.29)$$

or as

$$\frac{S}{R} = \alpha^* + \beta^* S. \quad (3.30)$$

Traditionally, (3.29) or (3.30) has been considered of the form of a linear regression, $Y = \beta_0 + \beta_1 X + \epsilon$, to obtain parameter estimates $\hat{\beta}_0$ and $\hat{\beta}_1$, where ϵ is an additive error term. The necessary assumptions of the linear regression method are (1) the data Y are identically and independently distributed with constant variance, (2) the independent variables X are measured without error, and (3) for valid confidence statements, the underlying distribution is normal. If X is subject to measurement error, then the regression estimates are biased (Fuller 1987). In one application, Reish et al. (1985) found no violations of these assumptions for the first form (3.29), suggesting that the distribution of $1/R$ is approximately normal with constant variance. In the second form (3.30), the variable S appears in both the dependent variable Y and the independent variable X . A consequence of this presence is that a significant positive regression coefficient, $\hat{\beta}_1$, could be expected, even if there is no spawner-recruit relationship. This

can be verified by generating variates $1/R$ from a uniform distribution and associating them with random variates, S , generated from another distribution. Ricker (1973, 1975a) suggested using arithmetic mean (AM) and geometric mean (GM) regression to account for these errors, an approach that has generated considerable debate (Jolicouer 1975, Ricker 1975b, 1982; Sprent and Dolby 1980, Schnute 1984). We consider measurement errors in section 3.2.3.

The simple linear regression model may still be inadequate after accounting for measurement errors because strong recruitments may cause increases in future spawning levels (Walters 1985, 1990), which then affect subsequent recruitments. The resulting bias may be much larger than the bias caused by measurement errors in recruitment and spawning stock, particularly if the errors are autocorrelated (Armstrong and Shelton 1988, Caputi 1988). We address autocorrelated errors in section 3.2.4.

The standard linear regression estimates are

$$\begin{aligned}\hat{\beta}_0 &= \bar{Y} - \hat{\beta}_1 \bar{X} \\ \hat{\beta}_1 &= \sum(X - \bar{X})(Y - \bar{Y}) / \sum(X - \bar{X})^2,\end{aligned}$$

which are easily obtained from computer spreadsheets or statistical packages. For (3.29), $\hat{\beta}^* = \hat{\beta}_0$ and $\hat{\alpha}^* = \hat{\beta}_1$. For (3.30), $\hat{\beta}^* = \hat{\beta}_1$ and $\hat{\alpha}^* = \hat{\beta}_0$. For either form, the corresponding estimates of productivity parameter α and density dependence parameter β are $\hat{\alpha} = 1/\hat{\alpha}^*$ and $\hat{\beta} = \hat{\beta}^*/\hat{\alpha}^*$. Variance estimates can be obtained using the delta method (Seber 1982), the jackknife method, or the bootstrap method (Efron 1982).

The analogous linear relationship for the Ricker model from (3.8) is

$$\ln \frac{R}{S} = \ln \alpha - \beta S = a - \beta S. \quad (3.31)$$

By treating this as a linear regression model of the form $Y = \beta_0 + \beta_1 X + \epsilon$, estimates $\hat{\alpha} = \hat{\beta}_0$ and $\hat{\beta} = -\hat{\beta}_1$ can be obtained. The median-unbiased estimate of α_1 is $\hat{\alpha} = \exp(\hat{a})$. A nearly unbiased estimate is $\hat{\alpha}_2 = \exp(\hat{a} + \hat{\sigma}^2/2)$.

Quite often, the statistical significance of the declining right-hand limb in the Ricker model is tested by determining whether β is equal to 0 with the use of standard regression or correlation techniques. If measurement errors for spawning stock are small and there are data points on the right-hand limb, there is no reason this test cannot be made.

However, if spawning stock is subject to large measurement errors or treated as a random variable, this test might be misleading. In (3.31), the variable S appears in both the dependent variable Y and independent variable X . Consequently, a significant negative regression coefficient, $\hat{\beta}_1$, can be expected, even if there is no declining right-hand limb in the spawner-recruit relationship. This can be illustrated by generating variates, R , from a uniform distribution and associating them with random variates, S , generated from another distribution (Eberhardt 1970). Eberhardt showed that one would expect a negative correlation of about -0.7 between $\ln(R/S)$ and S when recruit and spawner data are drawn from independent distributions. Indeed, the correlation between $Y_t = \ln(R_t/S_t)$ and S_t is

$$\rho_{Y,S} = \frac{-\sigma_S}{\sqrt{[\exp(\sigma_S^2) - 1](1 + \sigma_R^2/\sigma_S^2)}}, \quad (3.32)$$

where R_t and S_t are generated from independent lognormal distributions with medians R and S and scale parameters σ_R^2 and σ_S^2 . [The standard deviation of $\ln R_t$ is σ_R , which is also approximately equal to the coefficient of variation (CV) of R_t .] This correlation is always negative and approaches 0 as σ_S^2 approaches 0. Graphs of $\rho_{Y,S}$ from (3.32) are shown in figure 3.8 as a function of σ_S for typical values of σ_R of 0.1, 0.25, 0.5, and 1. Depending on the relative magnitude of spawner and recruit variabilities, $\rho_{Y,S}$ can range from 0 to -1 . It appears largest for variabilities of approximately the same magnitude. A sample of data would have an expected correlation as shown in figure 3.8. For example, if a random sample was taken from the two lognormal distributions with CVs of 0.5 and 0.25 for recruits and spawners, respectively, the expected correlation is -0.44 . From a standard statistics textbook, a sample correlation with this value for any sample size >20 is significant at the .05 level, even if there were no dome-shaped relationship between spawners and recruits. Furthermore, if a sample of just 10 data points is available (as is often the case), a sample correlation between -0.63 and -1 is statistically significant. Any pair of CVs in figure 3.8 producing an expected correlation in that range would often produce a sample correlation in excess of this value as well. The main conclusion is that a test of significance of the declining right-hand limb of spawner-recruit models with the Ricker model using correlation or regression techniques can lead to erroneous conclusions.

The above remarks do not pertain to the more general issue of statistical significance of density-dependent mortality, in contrast to the interpretation of such results by Eberhardt (1970). Indeed, a complete absence of dependence of recruits on spawners, as used to generate figure 3.8, is a qualitative description of the asymptotic portion of a Beverton-Holt spawner-recruit model (3.6). That asymptotic portion of the model, illustrated by the flat portion of the curves on the right in figure 3.1, contains strong negative density-dependent mortality, but not a declining right-hand limb. As mentioned in section 3.1, a different type of density dependence is present when R is assumed to be independent of S . Standard bivariate analysis techniques can be used to explore this form of density dependence.

Other factors such as environmental variables are incorporated into the generalized

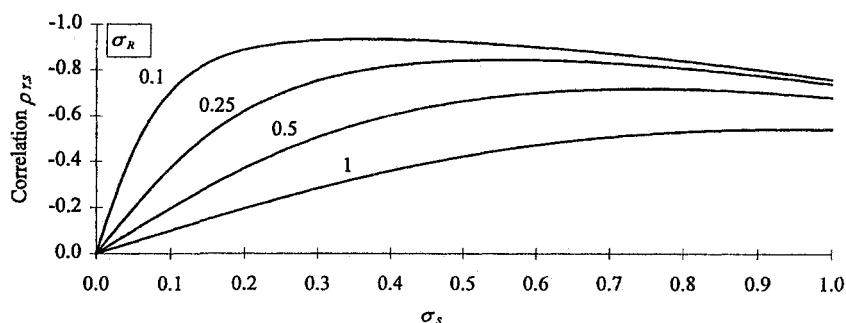


Figure 3.8. Expected correlation between $\ln(R_t/S_t)$ and S_t as a function of the coefficient of variation in S_t , where R_t and S_t are from independent lognormal distributions. Four curves are shown, corresponding to different values (0.1, 0.25, 0.5, 1) of the coefficient of variation in R_t .

Ricker model in (3.10). Multiple linear regression can be used with the recasting of (3.10) as

$$\ln \frac{R}{S} = a - \beta S + \gamma_1 X_1 + \cdots + \gamma_p X_p. \quad (3.33)$$

When performing the linear regression (3.31) or (3.33), one must carefully observe the sign of the coefficient for the variable S . It should be negative if the model and data assumptions are reasonable.

The analogous linear relationship for the Cushing model from (3.12) is

$$\ln R = a + \gamma \ln S, \quad (3.34)$$

where $a = \ln \alpha$ (Walters and Ludwig 1981). Under the same linear regression assumptions, estimates \hat{a} and $\hat{\gamma}$ can be obtained. The median-unbiased and nearly unbiased estimates of α were given below (3.31). The variable S does not appear in the dependent variable, suggesting that no spurious correlations should occur.

The gamma model can also be linearized by taking logarithms of (3.22), resulting in

$$\ln R = a + \gamma \ln S - \beta S, \quad (3.35)$$

which may be considered of the form of a multiple linear regression with dependent variable $\ln R$ and independent variables $\ln S$ and S .

Neither the Deriso-Schnute nor the Shepherd models can be linearized due to the presence of exponent γ . Nonlinear techniques in the next section must be used.

3.2.2. Nonlinear Regression Approach

In this section, spawning level is still assumed to be measured without error. However, recruitment is assumed to follow a spawner-recruit model with an error distribution. Let a spawner-recruit relationship be generally written

$$R = G(\mathcal{F}(S), \epsilon), \quad (3.36)$$

where $\mathcal{F}(S)$ is one of the deterministic spawner-recruit models in section 3.1 and ϵ is a random measurement error from some statistical distribution. Two special cases of (3.36) are additive error and multiplicative error models

$$R = \mathcal{F}(S) + \epsilon \quad (3.37)$$

$$\text{and} \quad R = \mathcal{F}(S) e^\epsilon, \quad (3.38)$$

respectively, where ϵ is assumed to have expected value 0 and constant variance σ^2 . The multiplicative error model (3.38) can be transformed into an additive error model by taking logarithms:

$$\ln R = \ln \mathcal{F}(S) + \epsilon. \quad (3.39)$$

The theory of least squares and nonlinear regression can be used to obtain parameter estimates (Draper and Smith 1981, Gallant 1987, Bates and Watts 1988, Seber and Wild 1989). Most statistical packages have this capability, and computer spreadsheets have solvers for optimizing objective functions. Closed-form solutions cannot be obtained in most cases, which means that numerical methods must be used.

For the Beverton-Holt model, the additive and multiplicative models used in nonlinear regression are

$$R = \frac{\alpha S}{1 + \beta S} + \epsilon \quad (3.40)$$

$$\text{and} \quad \ln R = a + \ln S - \ln(1 + \beta S) + \epsilon, \quad (3.41)$$

where $a = \ln \alpha$. The additive model has the dependent variable R , the independent variable S , and two parameters to estimate (disregarding the nuisance parameter σ^2). The multiplicative model has the dependent variable $\ln R$, the independent variable S , and two parameters to estimate. The multiplicative model could also be written in terms of the variable $\ln S$ by writing $S = \exp(\ln S)$.

For the Ricker model, the additive and multiplicative models used in nonlinear regression are

$$R = \alpha S e^{-\beta S} + \epsilon \quad (3.42)$$

$$\text{and} \quad \ln R = a + \ln S - \beta S + \epsilon. \quad (3.43)$$

The multiplicative model is in the form of a linear regression except for the offset term $\ln S$. The least squares solution is identical to performing a regression of $\ln R/S$ versus S .

Similar equations can be written for the Cushing, Deriso-Schnute, Shepherd, and gamma models by using (3.37) and (3.38). The important consideration is to choose an error structure based on the likely distribution of the data (Carroll and Ruppert 1984). In section 3.1.2, the lognormal model resulted from a combination of independent mortality processes, suggesting its use as the default distribution. It generally fits the error structure of actual data sets fairly well (e.g., Quinn and Collie 1990, Quinn et al. 1990).

Example 3.1. Southeast Alaska pink salmon

Spawner and recruit data for pink salmon (*Oncorhynchus gorbuscha*) are available for 1960–1989. Pink salmon are anadromous with a two-year life cycle, wherein all salmon return in the summer two years after spawning in the summer and fall. An escapement index obtained by aerial surveys of selected streams is converted into an absolute escapement estimate, S_t , which is acknowledged to be inaccurate. Harvest, C_t , is accurate because it is monitored by a fish ticket program. The number of recruits is the sum of escapement and harvest ($R_t = S_t + C_t$). Estimates of spawners, harvest, and recruits are shown in table 3.1, with recruits in year $t + 2$ shown on the same line as spawners and harvest in year t , so that values on one line refer to the same year-class. Figure 3.9 shows the empirical relationship between recruits and spawners. Recruitment and the variation in recruitment appear to increase as a function of spawning levels up to 5 million. One additional point occurs at a spawning level of 8.8 million.

The increasing variation suggests a multiplicative error structure, so the six spawner-recruit relationships of section 3.1 are fitted with $\ln R$ as the dependent variable. A nonlinear regression package is used to obtain parameter estimates for consistency, even when linear regression could be used. (Nonlinear regression produces the same estimates as linear regression as long as the same error structure is assumed). In

Table 3.1. Harvest, escapement, and return of northern South-east Alaska pink salmon (thousands of fish), 1960–1991, and average sea surface temperature (SST) between June and November off Sitka, Alaska, 1960–1990.

Year, t	Harvest, C (year t)	Escapement, S (year t)	Return, R (year $t+2$)	SST (year $t+1$)
1958			2678	
1959			10459	11.23
1960	1260	1418	2446	11.63
1961	7624	2835	14934	11.46
1962	489	1957	10031	12.33
1963	10901	4033	8050	11.62
1964	7281	2750	7884	11.05
1965	5159	2891	4430	11.11
1966	4786	3098	13086	11.69
1967	2429	2001	6051	11.50
1968	9871	3215	7801	11.08
1969	3608	2443	5846	10.39
1970	5240	2561	6101	10.81
1971	3012	2834	4175	10.59
1972	3242	2859	2541	10.35
1973	1880	2295	2194	11.07
1974	661	1880	1512	10.26
1975	615	1579	6704	11.20
1976	139	1373	5742	11.81
1977	2521	4183	8809	11.32
1978	2758	2984	4062	11.86
1979	3750	5059	9277	11.36
1980	1393	2669	15452	12.38
1981	5328	3949	10343	11.22
1982	11233	4219	8950	12.22
1983	6053	4290	30011	11.74
1984	4974	3976	3999	10.41
1985	21212	8799	9917	11.51
1986	1143	2856	4906	11.78
1987	5628	4289	18215	11.81
1988	2014	2892	9461	12.26
1989	13638	4577	23359	12.30
1990	5659	3802		
1991	18112	5247		

Returns are the sum of harvest and escapement and in the table are lagged two years behind for proper brood year correspondence. SST is lagged one year behind to correspond to when pink salmon are in the ocean.

addition, a model with constant logarithmic recruitment ($\ln R = a + \epsilon$) and a model for density independence ($\ln R = a + \ln S + \epsilon$) from (3.4) are fitted.

Parameter estimates, standard errors, correlations among the parameter estimates, residual sums of squares, and the coefficients of determination, R^2 , are shown in table 3.2. Unlike many nonlinear regression models, R^2 is a useful measure because each spawner-recruit model has a constant a as a parameter. The measure R^2 represents the additional variability explained in the data over a model with just the constant a . Figure 3.9 shows a plot of predicted recruits versus spawners.

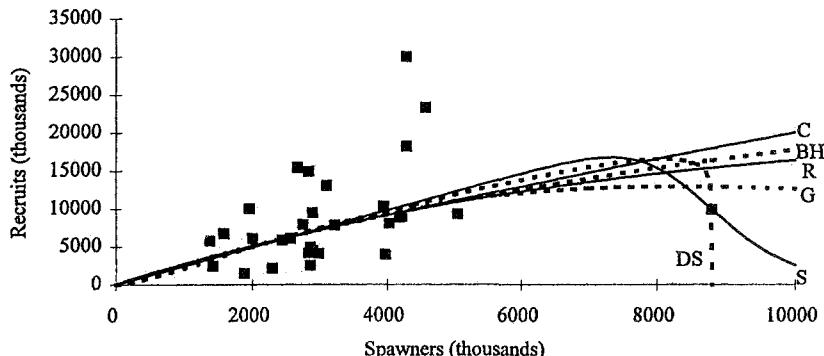


Figure 3.9. Observed recruits and spawners (squares) for pink salmon in northern Southeast Alaska and fitted spawner-recruit curves for the Bevertton-Holt (BH), Ricker (R), Cushing (C), Deriso-Schnute (DS), Shepherd (S), and gamma (G) models.

The two-parameter models converge rapidly to final solutions. It is more troublesome to fit the three-parameter models; solutions can be obtained only by trial and error with different starting values. For the Deriso-Schnute model, a reparameterization is necessary to obtain final estimates because there is a tendency of the fit to produce a right x -intercept smaller than the largest observed size of 8.8 million. The only solution is to constrain the right x -intercept to 8.8 million because higher values inflate the residual sum of squares. This is accomplished by replacing $\beta\gamma$ in (3.20) with $1/[8800 + \exp(\delta)]$, where δ is the replacement parameter and the exponent constrains δ to be non-negative.

The constant log-recruitment model is the simplest model that can be fitted to the data. The density-independent model fits better than the constant model and has a statistically significant coefficient, suggesting that recruitment increases as spawning level increases. For any of the six density-dependent spawner-recruit models, standard errors for estimates of parameters other than the constant a are large compared to the estimates themselves; thus, few estimates are statistically significant from 0. Correlations among parameter estimates tend to be close to -1 or 1 , suggesting that several combinations of parameters could explain the data well. The residual sums of squares for the two-parameter models are consistently higher than for the three-parameter models, although the difference is not statistically significant (by using the method given later in section 4.5). The amount of variation in $\ln R$ explained is only 25–28%, whereas the density-independent model explains 24%. In figure 3.9, the data point at 8.8 million is strongly influential, having the most effect on the Deriso-Schnute, Shepherd, and gamma curves. The other models show almost no density dependence; their curves continue to rise with little suppression of increase. All in all, the evidence of a convincing density-dependent spawner-recruit relationship is not present in these data. The best model based on these analyses is the density-independent model. Additional observations above 5 million spawners are needed to clarify the relationship if one exists.

One further approach is to attempt to explain some of the variation in recruitment by considering environmental variables. In table 3.1, average sea surface temperature data off Sitka, Alaska are shown (Zebdi 1991). The data are lagged so that the timing

Table 3.2. Parameter estimates, standard errors, correlations, residual sum of squares (RSS), and coefficient of determination, R^2 , for each spawner-recruit model fit to the Southeast Alaska pink salmon data.

Model	Parameter			RSS	R^2	
	α	β or δ	γ			
Constant	Estimate	8.868		13.96	0%	
	Standard error	0.127				
Density independent	Estimate	0.869		10.63	24%	
	Standard error	0.111				
Beverton-Holt	Estimate	1.042	5.92E-05	10.47	25%	
	Standard error	0.346	1.24E-04			
	Correlation					
	Matrix β	0.95				
Ricker	Estimate	1.047	5.52E-05	10.45	25%	
	Standard error	0.278	7.90E-05			
	Correlation					
	Matrix β	0.92				
Cushing	Estimate	2.012		8.57E-01	10.53	25%
	Standard error	2.270		2.84E-01		
	Correlation					
	Matrix γ	-1.00				
Deriso-Schnute	Estimate	0.931	-3.90E+01	11.684	10.09	28%
	Standard error	0.123	0.00E+00	9.860		
	Correlation					
	Matrix δ	ND				
Shepherd	Estimate	0.895	1.60E-61	15.431	10.05	28%
	Standard error	0.118	8.62E-58	461.000		
	Correlation					
	Matrix β	-0.27				
Gamma	Estimate	-2.141	1.73E-04	1.446	10.35	26%
	Standard error	6.490	2.53E-04	0.907		
	Correlation					
	Matrix β	-0.94				
Generalized Ricker (Environment)	Estimate	-6.114	9.07E-05	0.638	6.05	57%
	Standard error	1.630	6.17E-05	0.144		
	Correlation					
	Matrix β	-0.01				
	Estimate	-0.99		0.13		
	Standard error					

ND, estimate could not be determined.

agrees with when pink salmon are found in the sea (roughly in the next year after spawning). The generalized Ricker model (3.10) is fitted with $\ln R$ as the dependent variable as before by using nonlinear regression. Results of parameter estimation are shown in table 3.2. The density-dependent parameter estimate is still not statistically significant ($P = 0.14$), but its lower P value suggests a stronger relationship than previously. The environmental coefficient is highly significant ($P < .001$), suggesting that the marine environment may be important in pink salmon dynamics or that sea surface temperature is correlated with another variable. One possible interpretation of this result is that density dependence may be lurking under the mask of environmental variation. Analyzing both effects simultaneously then allows both to emerge from the data.

Plots of residuals as a function of time and of spawners in figure 3.10 show the better fit of the generalized Ricker compared to standard Ricker. The lack of pattern in the residuals suggests that heteroscedasticity is not present and that the log transformation is a reasonable one. Plotting observed recruits and predicted recruits from the generalized Ricker model shows the ability of the generalized model to show scatter (figure 3.11), as sea surface temperature is different each year. Also shown in the plot are Ricker curves that correspond to the median, first quartile, and third quartile of the empirical sea surface temperature distribution, obtained by substituting those values into the predictive equation. Thus the generalized Ricker curve may be thought of as a family of different Ricker spawner-recruit curves. The member of the family that is operative depends on the sea surface temperature in the first year after spawning. The area between the first and third quartiles in figure 3.11 is the predicted area where the spawner-recruit values will occur 50% of the time. ■

3.2.3. Measurement Error Approach

Neither of the two approaches given thus far is appropriate in the situation where recruitment and spawning level are both measured with error. The topic of measurement error models (or errors-in-variables models) has received much attention in the statistical literature; an excellent compendium can be found in the book by Fuller (1987). Much of the basic underlying theory was derived by Kendall and Stuart (1979). The presence of measurement errors can mask a true underlying spawner-recruit relationship (Walters and Ludwig 1981) and cause the normal regression coefficients to be biased (Fuller 1987).

One caveat to the measurement error approaches is that the presence of substantial measurement errors can sufficiently mask the underlying nonlinear relationship between recruitment and spawning stock to the point that there is essentially no information left to estimate the relationship. Thus, the application of measurement error models may not be a panacea for inaccurate data collection. Another caveat is that it is unlikely that process error is negligible in spawner-recruit relationships, given the large variability found in most empirical relationships and the likely role of the environment in affecting recruitment. Although a combined measurement/process error model has been constructed for spawner-recruit relationships in a special situation (see "Identical errors," below), an accepted general approach has not appeared to date. When underlying relationships are linear, the Kalman filter is useful for obtaining estimates (see Sullivan 1992, Pella 1993). Most spawner-recruit relationships, however, can seldom be appropriately linearized, so when substantial measurement and process errors are present, the best way to proceed is currently unknown; but see sections 5.4.3–5.4.4.

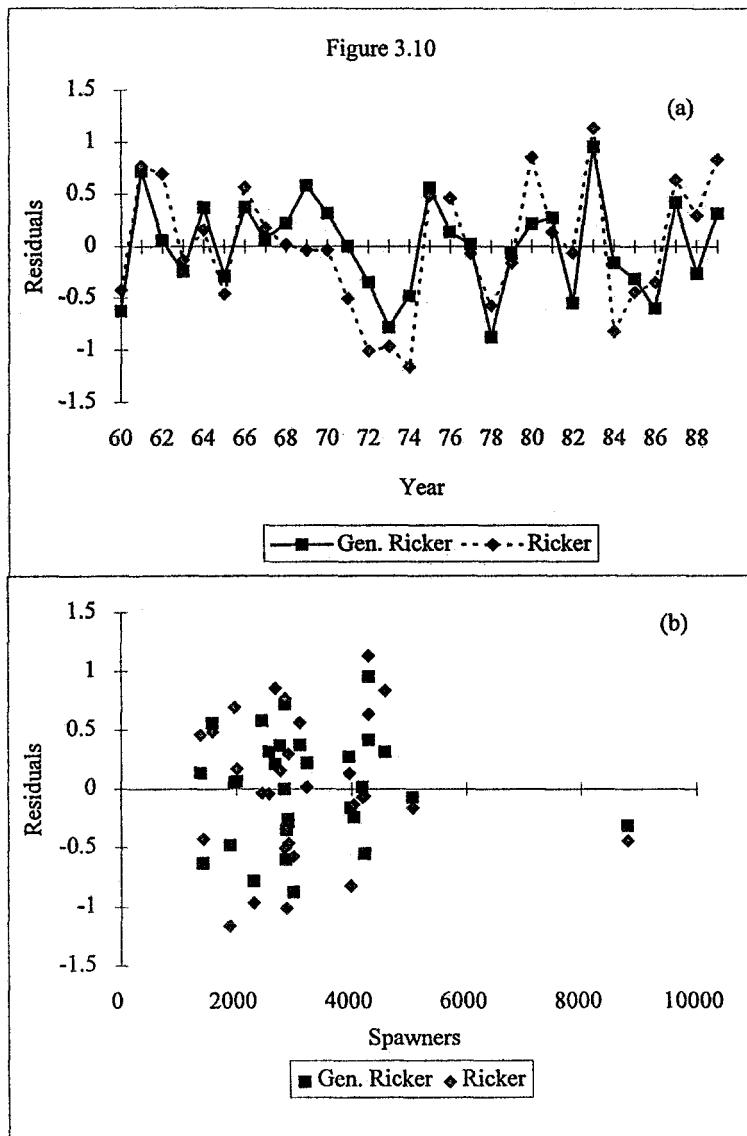


Figure 3.10. Residuals from fits of the Ricker and generalized Ricker spawner-recruit curves to northern Southeast Alaska pink salmon data as a function of time (a) and spawners (b).

Independent errors

The first situation considered is when recruitment is measured independently of spawning level. If the true underlying relationship is linear—

$$y_t = \beta_0 + \beta_1 x_t$$

—but unobservable, the functional measurement error model from Fuller (1987) is

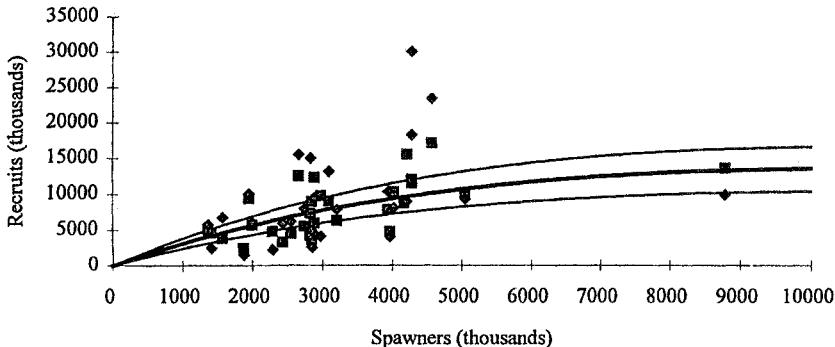


Figure 3.11. Observed recruits (squares) and predicted recruits (diamonds) from the generalized Ricker fit to northern Southeast Alaska pink salmon data. The spawner-recruit curve corresponding to median sea surface temperature is the bold line, and the other two lines correspond to the first and third quartiles of sea surface temperature.

$$\begin{aligned} Y_t &= y_t + e_t \\ X_t &= x_t + u_t, \end{aligned} \quad (3.44)$$

where e_t and u_t are uncorrelated, normal random variables with expected value 0 and variances σ_e^2 and σ_u^2 , respectively. This results in the linear model

$$Y_t = \beta_0 + \beta_1 X_t + v_t,$$

where the residuals $v_t = e_t - \beta_1 u_t$ are correlated with the observed X_t , unlike the normal regression setup.

Unbiased parameter estimates are obtained by Fuller (1987) in two cases: (1) σ_u^2 is known, or (2) the ratio of variances $\delta = \sigma_e^2/\sigma_u^2$ is known. For the first case, the estimators are

$$\begin{aligned} \hat{\beta}_1 &= \frac{m_{XY}}{m_{XX} - \sigma_u^2} = \frac{\frac{1}{n-1} \sum (X_t - \bar{X})(Y_t - \bar{Y})}{\frac{1}{n-1} \sum (X_t - \bar{X})^2 - \sigma_u^2}, \\ \hat{\beta}_0 &= \bar{Y} - \hat{\beta}_1 \bar{X}, \\ \hat{\sigma}_e^2 &= m_{YY} - \hat{\beta}_1 m_{XY}, \\ \hat{\sigma}_v^2 &= \hat{\sigma}_e^2 + \hat{\beta}_1^2 \sigma_u^2 = \frac{1}{n-1} \sum \hat{v}_t^2, \\ \text{and} \quad \hat{\sigma}_{uv} &= -\hat{\beta}_1 \sigma_u^2. \end{aligned} \quad (3.45)$$

Estimates of the residuals \hat{v}_t and variables \hat{x}_t and \hat{y}_t corrected for measurement error are

$$\begin{aligned} \hat{v}_t &= Y_t - (\hat{\beta}_0 + \hat{\beta}_1 X_t), \\ \hat{x}_t &= X_t - \frac{\hat{\sigma}_{uv}}{\hat{\sigma}_v^2} \hat{v}_t, \\ \text{and} \quad \hat{y}_t &= \hat{\beta}_0 + \hat{\beta}_1 \hat{x}_t. \end{aligned}$$

Table 3.3. Estimates of parameters for the Cushing spawner-recruit model with measurement error as a function of the standard deviation (σ_u) of the independent variable $X = \ln S$.

σ_u	0	0.05	0.1	0.15	0.2	0.25	0.3	0.32
γ	0.857	0.871	0.914	0.997	1.141	1.402	1.948	2.361
a	2.012	1.903	1.557	0.896	-0.260	-2.350	-6.710	-10.021
$\hat{\sigma}_e^2$	0.343	0.341	0.334	0.321	0.298	0.256	0.168	0.102
$\hat{\sigma}_v^2$	0.343	0.343	0.343	0.343	0.350	0.379	0.510	0.673
$\hat{\sigma}_{uv}$	0.000	-0.002	-0.009	-0.022	-0.046	-0.088	-0.175	-0.242
$\hat{\sigma}_{uv}/\hat{\sigma}_v^2$	0	-0.006	-0.027	-0.065	-0.130	-0.231	-0.344	-0.359
$\hat{\sigma}_e^2/\sigma_u^2$	∞	136	33.4	14.3	7.45	4.09	1.87	0.993

A model check can be performed by plotting \hat{v}_t versus \hat{x}_t ; no trend in these estimated residuals should occur.

Example 3.2. Cushing measurement error

For the Southeast Alaska pink salmon data set in example 3.1, the amount of error in the spawner data is not known. Nevertheless, it is instructive to examine the effects of such error on parameter estimates. For the Cushing spawner-recruit model (3.34), the above theory applies with variables $Y_t = \ln R_t$ and $X_t = \ln S_t$ and parameters $\beta_0 = a$ and $\beta_1 = \gamma$. Table 3.3 shows parameter estimates applied to these data as a function of the standard deviation (σ_u) of measurement error of the independent variable.

Estimates of γ and a vary dramatically as a function of measurement error. As the γ parameter of the Cushing model increases, density dependence decreases until at $\gamma = 1$ a density-independent relationship is reached. In this example, the effect of measurement error is to decrease density dependence. The estimated variance $\hat{\sigma}_e^2$ in $\ln R$ decreases as the amount of measurement error increases. As expected, the estimated variance in the residuals $\hat{\sigma}_v^2$ and the resulting correction factor in the independent variable $(\hat{\sigma}_{uv}/\hat{\sigma}_v^2)$ increases in magnitude as well.

Plots of the observed dependent and independent variables and their respective estimates of the unobserved variables are shown in figure 3.12 for the situation where both measurement errors are about equal ($\sigma_u = 0.32$). The previous estimated line without measurement error considered is shown as well. By treating the data as having errors in both variables, the slope of the line increases. This results because no longer is only variation in the y direction minimized, but variation in the x direction is considered as well. Note that predicted values involve correcting x values as well as y values, as shown by the arrows moving from the observed data to the predicted data. Thus, measurement error has a big effect on parameter estimates in this example.

One caveat to this analysis is that no process error is assumed in this approach. Thus, if another observation occurred at a particular spawning level, the model assumes that the same recruitment would take place. The previous analysis that uncovered a significant relationship with an environmental variable suggests that this assumption may be invalid. ■

In the second case where the ratio of variances δ is known, a different estimate of β_1 occurs:

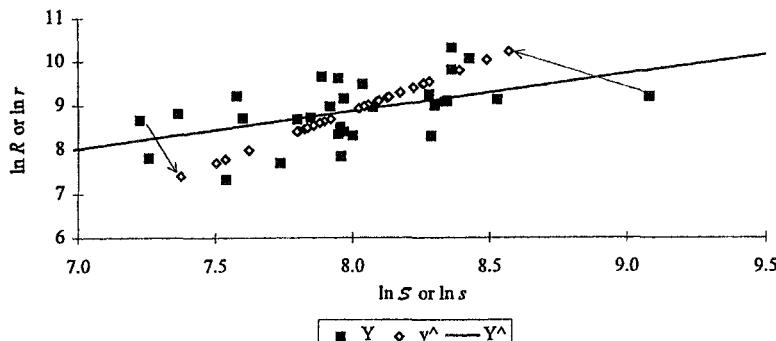


Figure 3.12. Predicted recruits versus predicted spawners (diamonds) for the Cushing measurement error model with the pink salmon data. Results are shown for $\sigma_u = 0.32$, which is where the estimated variance ratio $\hat{\sigma}_e^2/\sigma_u^2$ is near 1 (see table 3.3). Also shown are observed recruits versus observed spawners and the nonmeasurement error line previously estimated. The arrows show the movement of observed data to the predicted line.

$$\hat{\beta}_1 = \frac{m_{YY} - \delta m_{XX} + \sqrt{(m_{YY} - \delta m_{XX})^2 + 4\delta m_{XY}^2}}{2m_{XY}},$$

where m_{YY} is the analogous estimated variance of the Y 's. The other equations remain the same, except that an estimate of σ_u^2 is needed, which is given by

$$\hat{\sigma}_u^2 = \frac{m_{YY} + \delta m_{XX} - \sqrt{(m_{YY} - \delta m_{XX})^2 + 4\delta m_{XY}^2}}{2\delta}.$$

These linear methods work only with spawner-recruit models that can be expressed as linear models with some function of recruitment as the dependent variable and some function of spawning level as the single independent variable, which only includes the first form of the Beverton-Holt (3.29) and the Cushing (3.34). Even then, it must be assumed that the transformed data follow the normal distribution.

For other models, nonlinear measurement error models can be constructed (Fuller 1987). Essentially, this approach involves the use of nonlinear least squares and dummy variables for both recruitment and spawning level. For n data points, there are $2n$ observations of recruitment and spawning level. The number of parameters to be estimated is the number of parameters in the spawner-recruit model plus n parameters for the unobserved x 's. In this approach, the ratio of variances should be known, so that the recruitment portion of the data receives proper weight in the estimation process in relation to the spawning level data.

Example 3.3. Ricker measurement error

For the Southeast Alaska pink salmon data set (example 3.1) with $n = 30$ observations, a nonlinear least squares procedure can be used to estimate parameters for the Ricker spawner-recruit model with measurement error as follows. As in example 3.2, it is assumed that $\ln R$ and $\ln S$ follow independent, normal distributions. Parameters of the model are α , β , and the unobserved log spawning levels $\{\kappa_t = \ln s_t, t = 1, \dots, n\}$. The model for the n observations of log recruitment is

$$Y_t \equiv \ln R_t = a + \kappa_t - \beta \exp(\kappa_t) + e_t, \quad t = 1, \dots, n.$$

The model for the n observations of log spawners is

$$\ln S_t = \kappa_t + u_t, \quad t = 1, \dots, n,$$

where e_t and u_t are defined as before.

It is assumed that the ratio of variances is known. The constant δ is defined as the ratio of the variances of $\ln R$ and $\ln S$ (i.e., $\delta = \sigma_e^2/\sigma_u^2$). As most nonlinear least squares routines do not have the capability of modeling heterogeneous variance, the observations $\ln S_t$ are replaced by $\sqrt{\delta} \ln S_t$, and the model for $\ln S_t$ is replaced by

$$Y_{t+n} \equiv \sqrt{\delta} \ln S_t = \sqrt{\delta} \kappa_t + e_{t+n}, \quad t = 1, \dots, n.$$

This model can then be used in a nonlinear least squares routine with the dependent variable Y_t . The residual degrees of freedom, f , is the total number of observations $2n$ minus the number of estimated parameters $n + 2$, or $f = n - 2$. An estimate of σ_e^2 is the residual mean square $\hat{\sigma}_e^2 = \sum_{t=1}^{2n} (Y_t - \hat{Y}_t)^2/f$, and an estimate of σ_u^2 is $\hat{\sigma}_u^2 = \hat{\sigma}_e^2/\delta$.

Results of parameter estimation for the pink salmon data are shown in table 3.4 for a value of $\delta = 16$. Thus, the coefficient of variation in $\ln R$ is assumed to be four times that of $\ln S$. Larger amounts of measurement error than this (smaller values of δ) result in unrealistically negative estimates of β . The effect of measurement error is to reduce the estimate of β from the nonmeasurement error case (table 3.2) by more than half and to reduce its statistical significance as well. The estimate of a changed little. Estimates of the unobserved $\kappa_t = \ln s_t$ do not vary much from their observed counterparts $\ln S_t$. The residual sum of squares is slightly lower than before; it includes variation in $\ln S$ as well as $\ln R$.

Plots of the observed dependent and independent variables and their respective estimates of the unobserved variables are shown in figure 3.13. The previous estimated line without measurement error considered is shown. Over the range of observed data, there is little difference in the relationships due to the small amount of measurement error assumed in $\ln S$.

The major impact of measurement error in this model is to weaken the amount of density dependence estimated. Given that strong variations in parameter estimates occur with other choices of δ , this analysis is in agreement with the analysis using the Cushing model that measurement error needs to be considered in estimation of spawner-recruit relationships. ■

A different approach can be used when measurement errors are non-normal. It is not necessary to assume that σ_u^2 or δ is known, as all parameters are estimable (Schnute 1984, Fuller 1987). In this case, likelihood equations are constructed and then maximized to obtain parameter estimates. An example of this approach is found in Schnute (1984).

The method of grouping (Wald 1940, Ricker 1975a) can also be used. In this approach, the observations are divided into two groups. A consistent estimator of β occurs when the grouping is independent of the errors and when the limit of the minimum of the means of the unobserved independent variables is greater than 0.

Table 3.4. Parameter estimation for the Ricker spawner-recruit model with measurement error using nonlinear least squares.

Parameter	Estimate		SE
	α	0.95	
	β	2.62E-05	
i	$\kappa_i = \ln s_i$	SE $_i$	ln r_i
1	7.24	0.15	8.15
2	7.99	0.15	8.87
3	7.62	0.15	8.52
4	8.29	0.15	9.14
5	7.93	0.15	8.81
6	7.94	0.15	8.82
7	8.07	0.15	8.94
8	7.61	0.15	8.51
9	8.08	0.15	8.95
10	7.80	0.15	8.69
11	7.85	0.15	8.73
12	7.92	0.15	8.80
13	7.90	0.15	8.79
14	7.69	0.15	8.58
15	7.48	0.15	8.38
16	7.39	0.15	8.31
17	7.25	0.15	8.17
18	8.33	0.15	9.18
19	7.97	0.15	8.85
20	8.52	0.15	9.34
21	7.94	0.15	8.82
22	8.29	0.15	9.14
23	8.34	0.15	9.19
24	8.42	0.15	9.26
25	8.24	0.15	9.10
26	9.05	0.15	9.78
27	7.94	0.15	8.82
28	8.40	0.15	9.23
29	7.99	0.15	8.86
30	8.47	0.15	9.30
RSS	9.97		
$\hat{\sigma}_e^2$	0.356		
$\hat{\sigma}_u^2$	0.0223		

The ratio δ of the variances of log recruits to log spawners is set to 16. Included are parameter estimates, standard errors, residual sum of squares (RSS), estimates of unobserved log spawners and log recruits, and observations of log spawners and log recruits.

Identical errors

The second situation considered is when recruitment and spawning level have the same errors. An example of this situation is where recruitment is the combination of spawning level and harvest, such as for Pacific salmon. Maximum likelihood estimators were derived for the Cushing and Ricker models for the cases when the variance associated with measurement error is known (Walters and Ludwig 1981) and when the ratio of

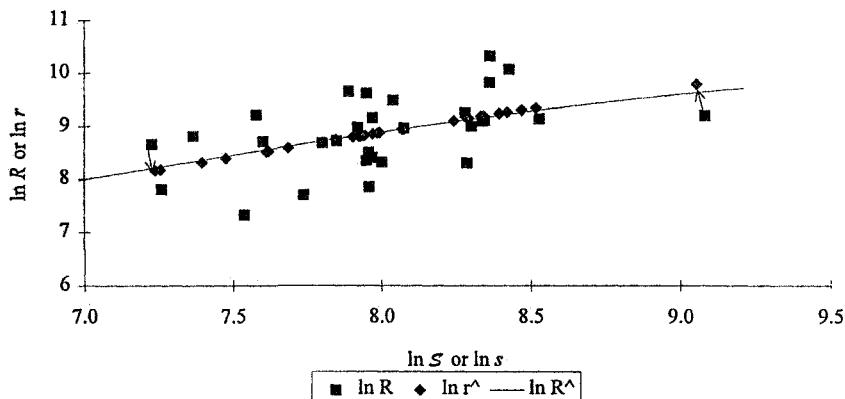


Figure 3.13. Predicted recruits versus predicted spawners (diamonds) for the Ricker measurement error model using nonlinear least squares with the pink salmon data. Also shown are observed recruits versus observed spawners and the nonmeasurement error line previously estimated. The arrows show the movement of observed data to the predicted line; each value of $\ln S_t$ is corrected to the estimate κ_t .

variances is known (Ludwig and Walters 1981). Our treatment follows their derivations but is slightly more general. Here the t index refers to time, so that a given error is correctly attributed to a given recruitment and spawning level.

Consider one of the linear versions of spawner-recruit models developed in section 3.2.1 in which the dependent variable y is only a function of recruits and the independent variable x is only a function of spawning level. Suppose that the true underlying relationship is linear with process error w_t :

$$y_t^* = y_t + w_t = \beta_0 + \beta_1 x_{t-1} + w_t,$$

where y_t is the deterministic linear relationship, x_{t-1} refers to the spawning level of the previous generation, and w_t is normally distributed with expected value 0 and variance σ_w^2 . Further suppose that y^* and x are subject to the same measurement error, such that

$$Y_t = y_t^* + u_t \quad \text{and} \quad X_t = x_t + u_t,$$

where u_t is normally distributed with expected value 0 and variance σ_u^2 . Then

$$Y_t = \beta_0 + \beta_1 x_{t-1} + e_t = y_t + e_t, \quad (3.46)$$

where $e_t = w_t + u_t$. This model is analogous to the measurement error model (3.44), except that u_t and e_t are correlated. Essentially the same estimates result as (3.45), except that Walters and Ludwig (1981) derive consistent estimators based on n rather than on $n - 1$ in the formula for $\hat{\beta}_1$. This approach works for the Cushing model with $y = \ln r$ and $x = \ln s$.

For the Ricker model with process error,

$$y_t^* \equiv \ln(r_t/s_{t-1}) = a - \beta s_{t-1} + w_t = y_t + w_t,$$

let

$$\ln R_t = \ln r_t + u_t, \quad \ln S_t = \ln s_t + u_t, \quad \text{and} \quad Y_t = \ln(R_t/S_{t-1}).$$

This situation corresponds to (3.46) with $x_t = s_t$, $Y_t = y_t + e_t$, and $e_t = w_t + u_t - u_{t-1}$, where once again u_t and e_t are correlated. An additional complication is that the error in X is multiplicative [$X_t = x_t \exp(u_t)$], so that this does not quite fit the measurement error model (3.44). However, Walters and Ludwig show that consistent estimators of $\beta_1 = -\beta$ and $\beta_0 = a$ are

$$\begin{aligned}\beta_1^* = -\beta^* &= \frac{(C_{XY} + \bar{X}\sigma_u^2)B^3}{[C_{XX} - \bar{X}^2(B^2 - 1)]} \\ \beta_0^* = a^* &= \bar{Y} - \beta_1^* \frac{\bar{X}}{B},\end{aligned}$$

where $B = \exp(\frac{1}{2}\sigma_u^2)$, a bias correction term for \bar{X} , and $C_{XY} = \frac{1}{n} \sum (X - \bar{X})(Y - \bar{Y})$. They also derive a formula for the bias in $\hat{\beta}_1$ from an ordinary linear regression, in which the bias can be either negative or positive. Unfortunately, they do not present a formula for estimated spawner abundance adjusted for measurement error.

Example 3.4. Identical Ricker measurement error

For the Southeast Alaska pink salmon data (example 3.1), corrected estimates a^* and β^* are computed as a function of the standard deviation, σ_u , for $\ln S$ (equivalent to the CV for S) and plotted in figure 3.14. The corrected estimates take on any positive or negative values depending on the amount of measurement error. There is an interesting discontinuity at a measurement error of about 0.41, which occurs when the denominator of the formula for β^* goes to 0. Similar to the previous analysis with independent errors, the estimate of β is unrealistically negative for a large enough measurement error. Unlike the previous analysis, for smaller amounts of measurement error, the estimate of amount of density dependence increases. This suggests that the choice of error structure is important in constructing measurement error models. ■

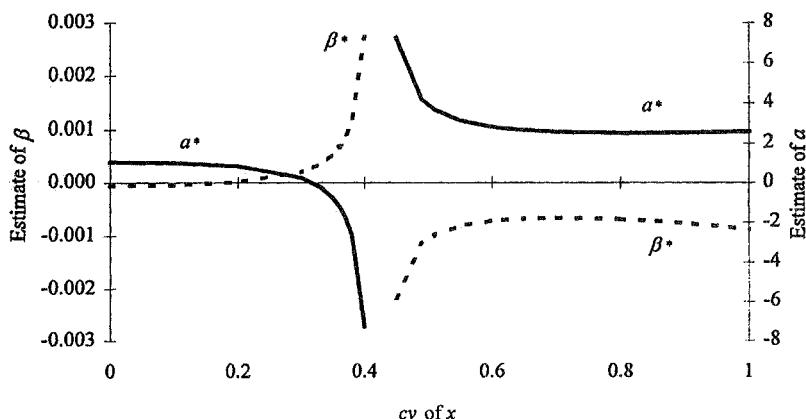


Figure 3.14. Corrected estimates a^* and β^* as a function of the standard deviation, σ_u , for the Ricker measurement error model of Ludwig and Walters applied to the pink salmon data.

Ludwig and Walters (1981) elaborated upon this approach by assuming that only the ratio of variances of measurement to process error is known. No closed-form solutions exist, but an iterative maximum likelihood procedure is used to obtain estimates. There are $n + 3$ parameters $\{a, \beta, \sigma_w^2, u_1, \dots, u_n\}$ for $2n + 1$ observations (R_0 is not used). In their examples, the density dependence parameter β was usually overestimated, and the correction for measurement error did not always work unless there was good contrast in the spawning level data. They concluded that "a great deal of recent historical data is going to remain less than useless" (Ludwig and Walters 1981, p. 716) unless variation in measurement error is accounted for, a point which still remains true.

3.2.4. Autocorrelated Errors

A generalized spawner-recruit model that relaxes the assumption that data are uncorrelated has emerged. If environmental effects on spawner-recruit relationships are large, then succeeding observations of recruitment may be correlated: good years are followed by good years, bad years by bad years (Quinn et al. 1990). This phenomenon of autocorrelation can be modeled by returning to the process error model (3.11) in the more general form

$$R_t = \mathcal{F}(S_{t-r}) \exp(\epsilon_t),$$

where r is the lag between spawning and recruitment, and measurement error is ignored. On a log scale,

$$\ln R_t = \ln \mathcal{F}(S_{t-r}) + \epsilon_t. \quad (3.47)$$

The errors are assumed to be autocorrelated, which can be written as the p th order autoregressive process

$$\epsilon_t = a_t + \phi_1 \epsilon_{t-1} + \dots + \phi_p \epsilon_{t-p}. \quad (3.48)$$

If the autocorrelations are ignored, then biased estimates result. The solution is to perform linear or nonlinear time series analysis, on which a large literature exists (Box and Jenkins 1976, Gallant 1987, Bates and Watts 1988, Seber and Wild 1989). A straightforward way to accomplish this is to minimize the residual sum of squares with respect to spawner-recruit and autoregressive parameters simultaneously; one uses (3.48) starting with datum $p + 1$.

An iterative procedure is to perform the linear regression approach, perform time series analysis on the residuals, and then to correct the dependent variable by substituting (3.48) into (3.47) (Seber and Wild 1989). An example of this approach is found in Collie et al. (1990). Anderson and Wilen (1985) provide a two-stage least squares procedure to estimate parameters. Walters (1990) provides an analytical approach to correct for bias caused by using least squares estimates.

3.3. DYNAMICS FOR SEMELPAROUS POPULATIONS

In a semelparous population, each member surviving to maturity makes a single reproductive contribution. We treat the simplest situation in which that contribution is made at the constant age of maturity, r . In contrast, an iteroparous population has members that make multiple reproductive contributions from the age of maturity to some later age when they die. The dynamics of the constant-maturity semelparous population depend only on the spawner-recruit relationship and are derived in this section. The dynamics

of an iteroparous (or age-structured) population require investigations of growth, maturity, and mortality considered in later chapters. Some semelparous populations such as sockeye salmon (*Oncorhynchus nerka*) return at different ages. Analysis of such a population is often accomplished by pooling returns from the same brood year and then fitting a spawner-recruit relationship (e.g., Adkison et al. 1996). For a complete analysis of dynamics, consideration of the proportion returning each year is required.

In chapter 1, we considered differential equation models of the form

$$\frac{dx}{dt} = G(x) = r(x)x, \quad (3.49)$$

where $G(x)$ is the population rate of change and $r(x) = G(x)/x$ is the relative or per capita rate. Clark (1976a) defined a pure compensation model as one in which $r(x)$ decreases as a function of x up to the carrying capacity, K , such as the logistic. A depensation model occurs when $r(x)$ increases for small values of x . A critical depensation model occurs when $G(x) < 0$ for small values of $x < K_0$, where the term K_0 represents the minimum viable population size or threshold level. These models are illustrated in figure 3.15. It is not possible to get an overcompensation model like the Ricker from the autonomous differential equation (3.49), as shown in section 3.1.2. Inclusion of the fishing mortality term $-Fx$ in (3.49) results in a surplus production model. Its behavior is straightforward: the population moves toward an equilibrium level (possibly 0) determined by the amount of harvest.

In terms of spawner-recruit models, analogous difference equations govern population dynamics in succeeding generations:

$$S_{t+r} \equiv R_{t+r} = \mathcal{F}(S_t) \quad (3.50)$$

in the absence of harvesting, and

$$S_{t+r} \equiv R_{t+r} - C_{t+r} = \mathcal{F}(S_t) - C_{t+r} \quad (3.51)$$

for harvest level C_t in year t . The behavior of difference equations is often more complicated than that of differential equations. In the absence of harvesting, four different

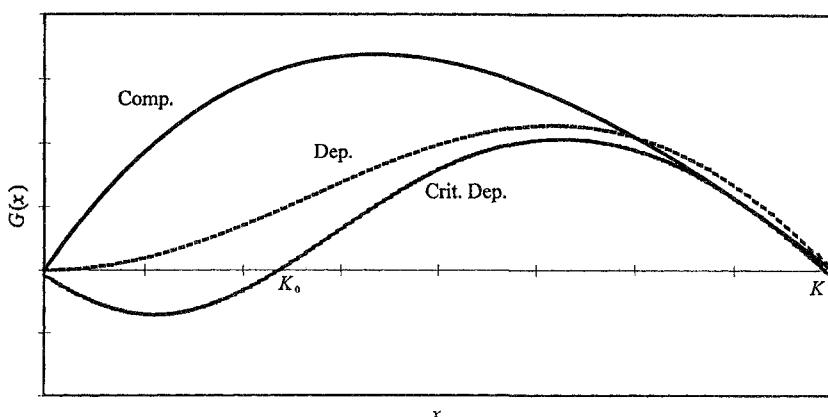


Figure 3.15. Population growth function $G(x)$ as a function of population size x for three situations: compensation (Comp.), depensation (Dep.), and critical depensation (Crit. Dep.).

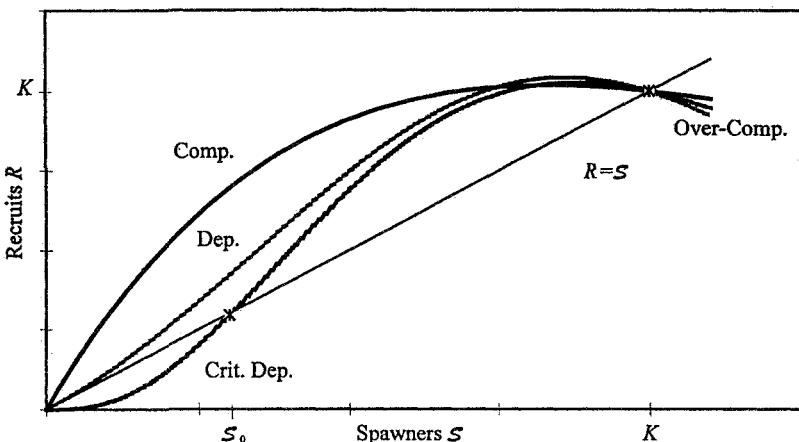


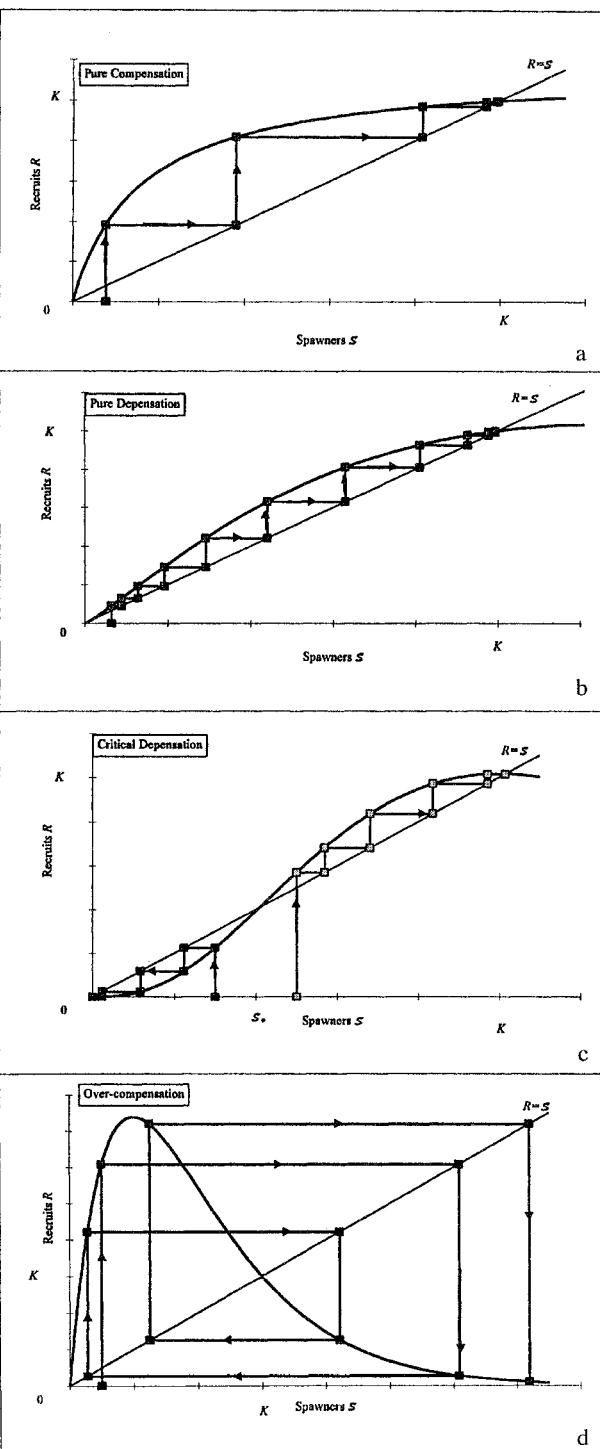
Figure 3.16. Generalized spawner-recruit functions $R(S)$ as a function of spawning level, S , showing compensation (Comp.), depensation (Dep.), critical depensation (Crit. Dep.), and overcompensation (Over-Comp.).

possibilities can be described: compensation, depensation, critical depensation, and overcompensation (figure 3.16), as discussed in section 3.1.7. The definitions for these phenomena are equivalent to those for the differential equation model (3.49) with $R - S$ replacing $G(x)$ in the definitions. Thus, compensation occurs when R/S decreases as a function of S , depensation occurs when R/S increases as a function of S ; and critical depensation occurs when, for small values of S less than the threshold S_0 , the resulting level of recruitment is lower than the spawning level ($R - S < 0$ or $R < S$). Overcompensation occurs when R decreases as S increases. Pure compensation and pure depensation models are those without overcompensation and critical depensation, respectively.

The dynamics of the population can be followed by mapping subsequent generations across the replacement line $R = S$, as shown in figure 3.17. Compensation and depensation result in monotonic convergence of the population to carrying capacity, $K = S_r$, where r refers to replacement. Critical depensation introduces an unstable point, S_0 , below which the population goes to 0. Overcompensation can lead to monotonic convergence, periodic oscillations, or apparently random behavior, as shown below.

Fish schooling is one mechanism that can lead to depensation (Brock and Rifenburgh 1960, Clark 1976a). Schooling is an effective survival technique for many fishes. When prey group together, predators cannot find them as easily. As mortality is then related to the volume of a school, relative mortality is concave downward (Clark 1976a). Either depensation or critical depensation can occur depending on parameter values.

An equilibrium point, K , occurs when $\mathcal{F}(K) = K$, where subscripts are dropped from (3.50). This point is stable if $S \rightarrow K$ as $t \rightarrow \infty$ for S_1 sufficiently near K . Clark (1976a) proved that K is a stable equilibrium point if $-1 \leq \mathcal{F}'(K) < 1$ and unstable if $|\mathcal{F}'(K)| > 1$. The results are ambiguous if $\mathcal{F}'(K) = 1$. As an example, consider the Ricker model normalized at the equilibrium point $K = 1$: $\mathcal{F}(S) = S \exp[a(1 - S)]$.



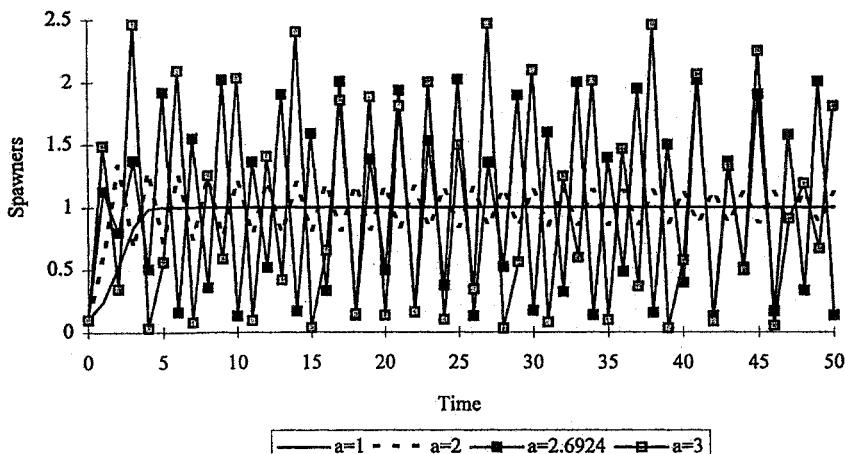


Figure 3.18. Time trajectories of spawners for the Ricker spawner-recruit model for four values of productivity parameter a (1, 2, 2.6924, and 3).

The derivative is $\mathcal{F}'(1) = 1 - a$. Hence $K = 1$ is stable when $0 < a \leq 2$. Clark further showed that there is an increasing sequence of a 's starting at $a = 2$ for which limit cycles occur. The sequence converges to 2.6924. For a greater than this value, there exists limit cycles of every period 2, 3, 4, ... along with an uncountable number of a 's for which the system does not fall into a cycle (i.e., exhibits seemingly random behavior). Hence, overcompensation can give rise to chaotic behavior when productivity $\alpha = \exp(a)$ is high. Figure 3.18 shows temporal behavior of this model for four values of a . For $a = 1$, the population converges to the equilibrium value of 1. For $a = 2$, a limit cycle of period 2 is evident, and for $a = a^*$, a limit cycle of period 8 is suggested. For $a = 3$, no apparent limit cycle is evident, although there is a tendency for certain population sizes to reoccur, while others seem to never occur. Botsford (1981a) also considered the nature of equilibria in spawner-recruit models. Fagen and Smoker (1989) examined chaotic dynamics in application of the Ricker model to salmon hatcheries.

Jensen (1987) defined chaos as irregular, unpredictable behavior of deterministic, nonlinear systems, which can arise from simple systems with only one or two parameters. His example of a logistic map, $x_{t+1} = a'x_t(1 - x_t)$, with one parameter (normalized at $K = 1$) gives rise to similar behavior as the Ricker model. For $a' < 1$, the population goes extinct eventually. If $a' > 4$, then the maximum population can exceed 1, which can result in extinction in two steps. For $1 < a' < 3$, almost all populations converge to a fixed point. When $3 < a' < 4$, the equilibrium point becomes unstable, which results in limit cycles of any period and random behavior depending on the exact value of a' . Period-doubling bifurcations occur when $3.5 < a' < 4$.

Figure 3.17. Time trajectories of recruitment, R , and spawning level, S , for four situations: (a) pure compensation, (b) pure depensation, (c) critical depensation, and (d) overcompensation. The lines show the population trajectories from an initial spawning level. In the first two cases, a stable equilibrium point, $R_r = S_r = K$, is reached. For critical depensation, a stable equilibrium point, $R_r = S_r = K$, is reached if initial spawning level is above threshold S_0 , and extinction occurs if not. Parameter S_0 is an unstable equilibrium point. For overcompensation, this population apparently exhibits a limit cycle or chaotic behavior.

In the presence of harvesting, the maximum harvest at equilibrium can be found by dropping subscripts from (3.51) and rearranging to give

$$C = \mathcal{F}(\mathcal{S}) - \mathcal{S}. \quad (3.52)$$

Hence the maximum sustainable catch (MSC) occurs when

$$\mathcal{F}'(\mathcal{S}) = 1,$$

which corresponds to the largest vertical difference between the spawner-recruit curve, $R = \mathcal{F}(\mathcal{S})$, and the replacement line, $R = \mathcal{S}$ (figure 3.19; also see example below). The difference between recruitment and spawning stock ($R - \mathcal{S}$) can also be thought of as the production to the stock that would occur if it were not harvested. Thus, spawner-recruit models for semelparous populations are analogous to surplus production models in chapter 2, with production in place of productivity and the spawning stock in place of biomass. The major difference between them is the time lag between spawning and recruitment. In light of this analogy, the subscript m will be used for the following productivity parameters.

For the Beverton-Holt model (3.6), MSC occurs when

$$\alpha^* = (\alpha^* + \beta^* \mathcal{S}_m)^2 \quad \text{or} \quad \alpha = (1 + \beta \mathcal{S}_m)^2,$$

or when $\mathcal{S}_m = (\sqrt{\alpha^*} - \alpha^*)/\beta^*$ or $\mathcal{S}_m = (\sqrt{\alpha} - 1)/\beta$. For the Ricker model (3.8), MSC occurs when

$$(1 - \beta \mathcal{S}_m)e^{\alpha - \beta \mathcal{S}_m} = 1 \quad \text{or} \quad \alpha(1 - \beta \mathcal{S}_m)e^{-\beta \mathcal{S}_m} = 1,$$

either of which is a transcendental equation that cannot be solved directly for \mathcal{S}_m . Numerical methods or trial-and-error can be used. For any spawner-recruit model given

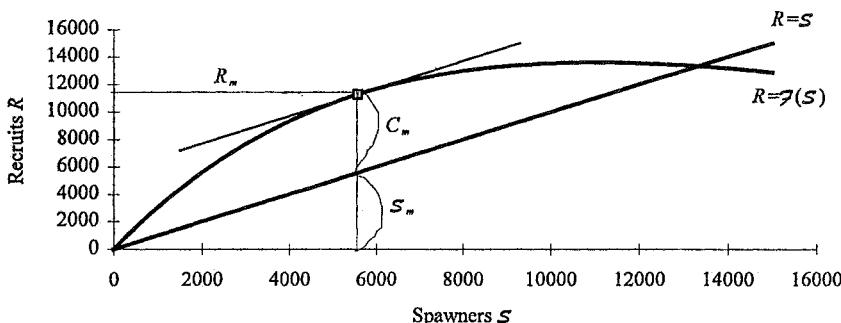


Figure 3.19. Estimated production relationship for northern Southeast Alaska pink salmon by using the generalized Ricker spawner-recruit model (3.10) with median sea surface temperature. The level (R_m, \mathcal{S}_m) at which maximum sustainable catch (MSC) occurs corresponds to the point on the spawner-recruit curve, $R = \mathcal{F}(\mathcal{S})$, which is the tangent to the replacement line, $R = \mathcal{S}$. The distance between R_m and the line $R = \mathcal{S}$ at that point is the MSC. Note that the value R_m differs from maximum recruitment and the recruitment that balances spawning level, which occurs at the intersection of the spawner-recruit curve with the replacement line. The intersection of the spawner-recruit curve and the replacement line is denoted (R_r, \mathcal{S}_r) , where $R_r = \mathcal{S}_r$.

spawning level S_m at MSC, recruitment at MSC is $R_m = \mathcal{F}(S_m)$ and MSC from (3.52) is $m = R_m - S_m$. Converting MSC to a harvest rate results in maximum sustainable exploitation rate, $\mu_m = m/R_m$. For the Ricker model, a good approximation of μ_m is given by $\mu_m \approx \ln \alpha(0.5 - 0.07 \ln \alpha)$ (Hilborn and Walters 1992).

If recruitment, spawning stock, and harvest are expressed in terms of biomass, then maximum sustainable yield (MSY) is used instead of MSC (Ricker 1954, 1971, 1975a). Ricker (1971) gives several other “critical statistics” from the Beverton-Holt and Ricker models. Similar calculations can be done for other spawner-recruit models.

Example 3.5. Maximum sustainable catch for Southeast Alaska pink salmon
 For the pink salmon data (example 3.1), the best relationship found was the generalized Ricker. This model suggests that recruitment is a function of the environment as well as a function of spawning stock. The approach used here is to calculate MSC by using three values of the environmental variable, representing the first three quartiles of the sea surface temperature (SST) distribution. Essentially, this results in three different Ricker relationships with the a parameter recast as $\tilde{a} = a + \gamma \text{ SST}$ and the same value of β . Details of the calculations of MSC parameter estimates are given in table 3.5. As SST increases, the productivity parameter \tilde{a} also increases, reflecting the positive effect of SST. As a consequence, spawners, recruitment, MSC, and exploitation rate all increase as a function of SST.

The estimated exploitation rate is least variable of the parameters, suggesting that a reasonable management strategy would be to provide a harvest rate in the range between the first and third quartiles. The actual management strategy used by the Alaska Department of Fish and Game is a fixed escapement policy where no fishing is allowed unless a certain level of escapement is obtained and all remaining fish above that level can be caught. The range of escapements estimated to provide MSC is also not too variable, suggesting that a reasonable policy is to keep escapement in the range between the first and third quartiles. However, because the spawner-recruit relationship is quite uncertain, it would also be wise to allow higher escapements in some years to better nail down the relationship. This latter policy, called adaptive management, has received much attention (Walters 1986, Hilborn and Walters 1992). The subject of optimal harvesting policies receives greater attention in chapter 11. ■

Table 3.5. Estimates of spawners, S_m , recruits, R_m , catch, C_m , and exploitation rate, μ_m , at maximum sustainable levels given sea surface temperature (SST) at the three quartiles of its distribution.

	1st Quartile	Median	3rd Quartile
SST	11.069	11.479	11.798
$\tilde{a} = a + \gamma \text{ SST}$	0.948	1.210	1.413
$\alpha = \exp(\tilde{a})$	2.580	3.353	4.110
S_m	4562	5574	6282
R_m	7782	11271	14604
$C_m = \text{MSC}$	3220	5697	8321
μ_m	0.414	0.505	0.570

The assumed underlying spawner-recruit model is the generalized Ricker with parameter estimates taken from table 3.2: $a = -6.114$; $\beta = 9.07E-05$; $\gamma = 0.638$.

3.4. BAYESIAN CONSIDERATIONS

An alternative to maximum likelihood estimation of parameters for a spawner-recruit model is to follow the Bayesian approach. Such an approach is characterized by the viewpoint that any unknown quantity, say, θ , is an uncertain element for which one can assign a probability density, say, $p(\theta)$, to express the probability of a particular value of θ among the set of all possible values of θ , say, Θ . The unknown quantity represented by θ can be a parameter in a particular model or any other quantity of interest, such as abundance in the most recent year. From the Bayesian perspective, the objective of estimation is to calculate the probability density function associated with each unknown quantity in a model. From such a calculation one can then quantify the probability of an underlying model (including specific parameter values). A further set of calculations is often completed to examine the utility (such as long-term yield) of a specific action (such as a given amount of exploitation) if θ turns out to be the true value for the unknown parameter. Because the probabilities $p(\theta)$ were calculated, one is then in a position to calculate the expected utility, which is the average utility across Θ weighted by the probabilities $p(\theta)$. More on the use of utility functions is given in chapter 11.

The Bayesian approach described here begins with a set of prior probabilities for each unknown parameter, denoted $\pi(\theta)$. The prior density describes what is known about θ prior to, or in the absence of, actual data observations. Given a set of observed data on spawners and recruits, say $\{\mathcal{S}, \mathcal{R}\}$, Bayes Theorem is used to calculate the so-called posterior probability density of θ , as follows:

$$p(\theta|\mathcal{S}, \mathcal{R}) \propto P(\mathcal{S}, \mathcal{R}|\theta)\pi(\theta) \quad (3.53)$$

where $P(\mathcal{S}, \mathcal{R}|\theta)$ is the likelihood of all observations on spawners and recruits given a specific set of parameter values for a specified spawner-recruit model. The proportionality constant for (3.53) is obtained by ensuring that the p 's sum to 1, which may require a numerical approximation scheme such as the ones described below. The structure above can accommodate models where observations are measured without error, but it is also valid when the observations contain measurement error. This second case, which includes the more general mixed measurement error–process error problem, is dealt with in chapter 5.

When the posterior distribution is sought for a single quantity, such as MSY, it becomes necessary to compute a marginal distribution. There are several methods to do this, and most involve some type of numerical approximation. A straightforward approach is the sampling, importance resampling (SIR) scheme of Rubin (1987). The procedure is as follows:

1. Draw n random samples $\theta_1 \dots \theta_n$ from the prior density $\pi(\theta)$, where θ is a multidimensional vector in general.
2. Assign weights $w_1 \dots w_n$, the “importance weights,” to each θ_i proportional to the likelihood of the observations, $w_i \propto P(\mathcal{S}, \mathcal{R}|\theta_i)$.
3. Resample m values $\theta_1^* \dots \theta_m^*$ with replacement from the random samples in step 1 with probabilities proportional to the weights calculated in step 2.
4. Calculate the corresponding output of interest, say $\mu_1 \dots \mu_m$, for each of the θ_i in step 3. These are samples from the marginal distribution of μ and can be used for inference.

In an application of a Leslie matrix model (see chapter 7) to bowhead whales, Givens et al. (1993) reported that a sample of $n = 200,000$ and $m = 5000$ produced satisfactory results. Other “importance” functions can be used (Gelman et al. 1995) and are often more efficient (M. Adkison, 1997, personal communication). The approach favored by Kinas (1993, 1996) for calculating marginal distributions is the adaptive importance sampling procedure, which numerically approximates the integral of the posterior distribution $p(\theta|S, R)$ by approximation with an adaptive linear combination of multivariate normal (or Student) distributions. A third approach is Gibbs sampling (Casella and George 1992, Gelman et al. 1995), which may be easier to apply. Another approach called the Metropolis algorithm is described in chapter 5.

Example 3.6. Skeena River sockeye salmon—Bayesian estimation

Kinas (1993) analyzed data on Pacific sockeye salmon (*Oncorhynchus nerka*) of the Skeena River from a Bayesian perspective, which can be compared to the maximum likelihood estimates obtained by Hilborn and Walters (1992). Kinas (1993) applied two spawner-recruit models to the data: the Beverton-Holt model (3.41) and the Ricker model (3.43), both with a multiplicative lognormal error structure. The likelihood function for the logarithmic data is a product of normal density functions, so the log likelihood function for the Beverton-Holt model is

$$\ln P(S, R|\alpha, \beta) = -\frac{n}{2} \ln(2\pi\sigma^2) - \frac{1}{2\sigma^2} \sum_{t=1}^n \left(\ln \frac{R_t}{S_t} - \ln \frac{\alpha}{1 + \beta S_t} \right)^2,$$

where σ^2 is the variance of the log-normal errors, the ϵ 's of (3.41). The log likelihood function for the Ricker model follows analogously.

Kinas (1993) selected prior density functions to be Student distributions for parameters α and β with means and variances chosen to correspond to the coarse features of the observed data. Because the observed data were examined for the choice of parameters in the prior distributions, the posterior density plots (figure 3.20) have variances that are probably biased low. The prior density function for σ^2 was apparently arbitrarily chosen to be an inverse gamma distribution with chosen mean and variance. Specification of prior density distributions is difficult, but sensitivity analyses can be made to examine the effect that different distributions have on conclusions of the analysis. For this example, we show only one set of results based on one set of prior density functions.

Based on examination of fitted lines from the two models to the Skeena River sockeye data, Kinas (1993) could not tell from the fits which model was better; Hilborn and Walters (1992) reached a similar conclusion. Although the fitted lines look similar, plots of the posterior probability distributions look different for equilibrium spawners and exploitation at the level of MSY (figure 3.20). The Ricker model produced estimates of exploitation in the range of 0.5 to 0.6 versus estimates in the range of 0.4 to 0.5 for the Beverton-Holt model. Kinas (1993) suggested that spawning levels above those in the historical data may be required to tell which of the two models is better. ■

Geiger and Koenings (1991) also used a Bayesian model, but in this case to determine optimum escapement levels, rather than to estimate parameters. They selected discrete sets of values for α and β , and chose prior probabilities for α and β from lake and smolt characteristics and the beliefs of fisheries managers. The likelihood function

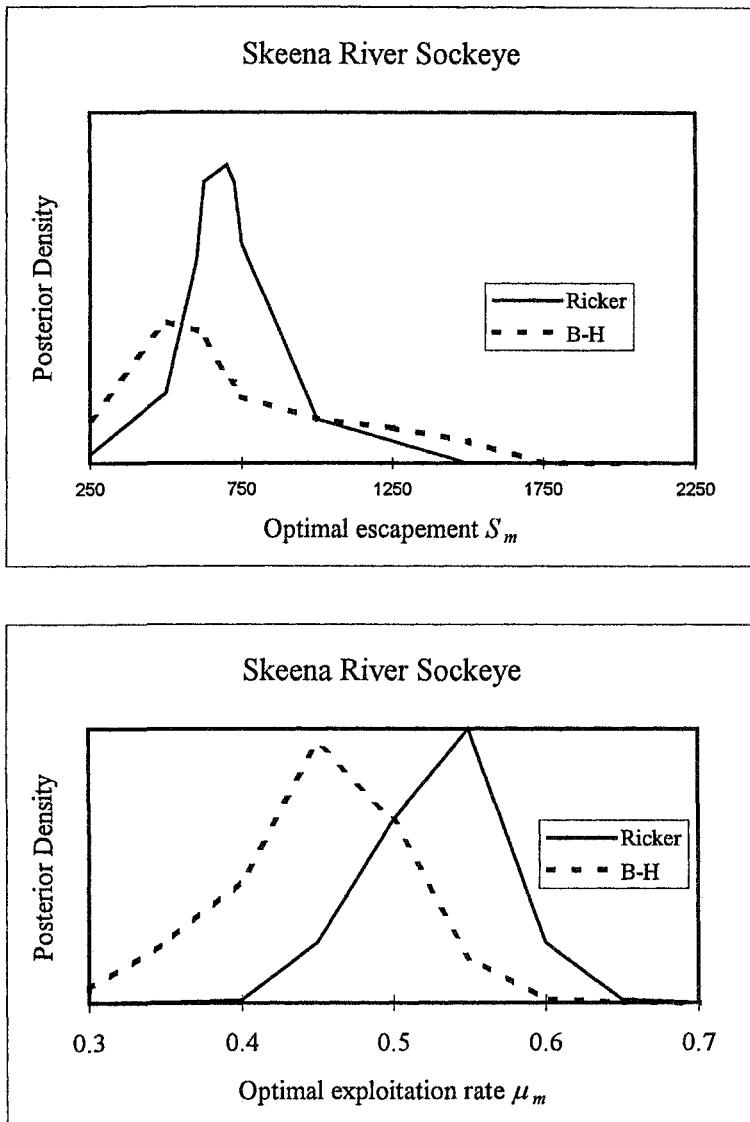


Figure 3.20. Approximate posterior probability densities for spawners, S_m , and exploitation fraction, μ_m , at the level of maximum sustainable yield, m . (Dashed line) Beverton-Holt; (Solid line) Ricker. (Redrawn from Kinas 1993, figure 4.5 c,d.)

was assumed to be a Student's t distribution. From the posterior probability distribution for α and β , they found the optimum escapement level that yielded the smallest expected loss in future expected yield. The optimum escapement level was different from the level that resulted from the highest posterior probability. Thus, the model that appears to fit the prior information and data best need not be the model that results in the optimal decision.

Adkison and Peterman (1996) examined the Bayesian approach in the spawner-

recruit setting in greater detail by looking at the implementation process. They showed that overly precise results and undue confidence in decisions arising from the approach can occur if the range of models is too limited, the data are contradictory, or the prior distributions do not correctly specify the original uncertainty. Although their analysis showed that care must be taken in implementing the Bayesian approach, they also noted that it is superior to many deterministic analyses.

Growth and Fecundity

The process of how an individual changes over time in length, weight, age, and reproductive characteristics is rooted in physiological processes far beyond the scope of this book. An individual obtains energy from food, and that energy may be converted into growth, reproductive development, or activity. According to von Bertalanffy (1938), growth is the net result of two opposing processes, catabolism and anabolism. Anabolic processes involve the synthesis of protein, while catabolic processes degrade it. As outlined by Pauly (1981), catabolism occurs in all living cells and results in breaking down body substances; it is therefore proportional to the mass and weight of an individual. Anabolism is the process of building up body substances and is proportional to respiratory rate. Respiratory rate, in turn, is usually proportional to surface area. Such general principles lead to differential equations for growth processes that are generally applicable to several species, including fish.

The variety of patterns for the relationship between growth variables (length, weight, age, etc.) is large. Physiologically, this may be explained in terms of an individual partitioning energy into different categories. One individual may defer growth to pursue activity and channel energy into reproduction. Thus, the strategy of an individual is critical in determining the form of a relationship between growth and time. However, for simplicity, we limit ourselves mainly to forms that are based on empirical relationships, differential equations, or difference equations.

Relationships between weight and length (section 4.1) and between size and age (sections 4.2 and 4.3) receive major attention. Models use constant parameters to describe mean growth of individuals in a population. Mark–recapture information is frequently used to determine growth parameters; the corresponding models are presented in section 4.4. Methods for comparing growth models are also frequently needed (section 4.5). Also, the relationship between otolith measurements and the aforementioned variables is treated in section 4.6, because there is great interest in using characteristics of otoliths (as well as other body structures) to predict the length, weight, and age of several fish species. Variation in growth has important implications in modeling, as shown in section 4.7. In contrast to sections 4.1–4.4, some of these models allow variation in parameters to describe growth of individuals in a population. In our treatment of fe-

cundity (section 4.8), we examine the common models for reproductive characteristics such as fecundity, maturity, and sex ratio, which leads to determination of population statistics. The general approach used in this chapter is to derive an underlying model, explain its essential features, and present appropriate parameter estimation procedures. A general discussion of model fitting and choice of appropriate models is in section 4.5.1. In our development, we primarily use Greek letters to denote parameters of the models, but when parameters have units corresponding to measurements of size or age, we follow the historical convention of using Roman letters.

4.1. WEIGHT-LENGTH MODELS

Growth is necessarily a three-dimensional process, with length, width, and depth of an individual all changing over time. Certain constraints govern the growth process as well. An individual generally does not shrink in length, and an individual of a particular species is limited as to its maximum size. However, within limits, there is a great variety of patterns that could occur. Our goal is to describe such patterns with mathematical models.

The simplest assumption that can be made is that length, width, and depth of an individual change in proportion to one another, a phenomenon described as *isometric* growth. The surface area of an organism is then proportional to the square of any of the one-dimensional measurements, and the volume of an organism will be proportional to the cube. If the specific gravity of an organism does not change as a function of these dimensions, weight is proportional to the cube of length.

If L represents length (or any of the one-dimensional measurements) and W represents weight, the isometric relationship between length and weight is

$$W = \alpha L^3, \quad (4.1)$$

where α is a parameter to be determined from data. In fishes, the cubic relationship does not fit the data in many cases, indicating some violation of the above assumptions. A two-parameter generalization of (4.1) provides a reasonable fit in most cases; namely,

$$W = \alpha L^\beta. \quad (4.2)$$

This model is known as the *allometric* growth model, which assumes that growth of one dimension is proportional to some power of the other(s). More complicated models for the length-weight relationship have not been necessary for most fish species.

Several examples of the isometric and allometric growth curves are shown in figure 4.1. Parameter α is often referred to as a condition factor because two fish with different weights at the same length and with the same parameter β have correspondingly different α values. Parameter β is a measure of curvature. The weight-length relationship is linear if $\beta = 1$, quadratic if $\beta = 2$, cubic if $\beta = 3$, etc.

Estimation

The appropriate estimation of parameters of the allometric or isometric growth models depends on the error structure chosen for the data. An additive error structure is appropriate when the variability in growth is assumed to be constant as a function of the independent variable. A multiplicative error structure is appropriate when variability

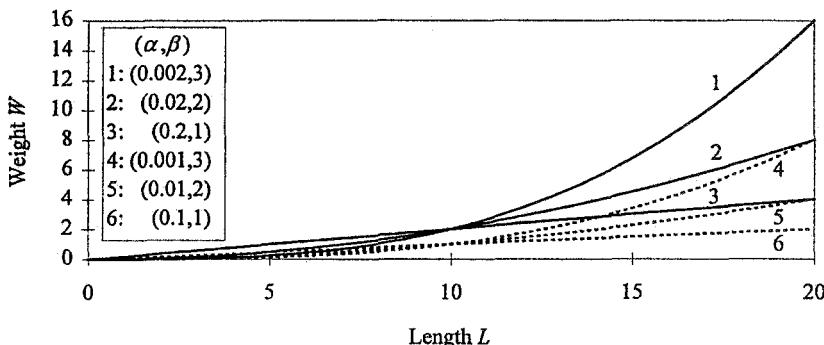


Figure 4.1. The relationship of weight W versus length L for the allometric and isometric ($\beta = 3$) growth models.

in growth increases as a function of the independent variable. Suppose that a set of data $\{W_i, L_i\}$ for $i = 1, \dots, n$ is collected. In all cases below, ϵ_i is a random error term with mean 0 and constant variance σ^2 ; the residual mean squared error from the estimation procedure is an estimate of σ^2 .

For the allometric model with an additive error structure, the data can be modeled as

$$W_i = \alpha L_i^\beta + \epsilon_i. \quad (4.3)$$

Estimates of α and β are obtained from nonlinear least squares with W_i as the dependent variable and L_i as the independent variable.

The isometric model with an additive error structure follows from (4.3) with $\beta = 3$. It is not appropriate to set β equal to 3 and then use the estimate of α from the allometric procedure; α must be reestimated. The estimate of α is obtained from linear regression through the origin with W_i as the dependent variable and L_i^3 as the independent variable.

For the allometric model with a multiplicative error structure, the data can be modeled as

$$W_i = \alpha L_i^\beta e^{\epsilon_i}, \quad (4.4)$$

where ϵ_i is a random error term with mean 0 and constant variance σ^2 . By taking logarithms of this equation,

$$\ln W_i = \ln \alpha + \beta \ln L_i + \epsilon_i, \quad (4.5)$$

which is the form of a linear regression equation with $\ln W_i$ as the dependent variable and $\ln L_i$ as the independent variable. A median-unbiased estimate of α is obtained by exponentiation, or $\hat{\alpha} = \exp(\ln \alpha)$. The estimated standard error of $\hat{\alpha}$ from the delta method (Seber 1982, p. 7–9) is $\text{SE}(\hat{\alpha}) = \hat{\alpha} \text{SE}(\ln \alpha)$.

The isometric model with a multiplicative error structure follows from (4.4) or (4.5) with $\beta = 3$. Rearranging (4.5) with $\beta = 3$,

$$\ln W_i - 3 \ln L_i = \ln \alpha + \epsilon_i. \quad (4.6)$$

The estimate of $\ln \alpha$ using linear least squares is just the mean of the left-hand side of (4.6), or $\widehat{\ln \alpha} = \overline{\ln W} - 3 \overline{\ln L}$.

Table 4.1. Simulated growth data for Atka mackerel in the Bering Sea.

Length(cm)	Weight (dg)			Length(cm)	Weight (dg)		
	Observed	Predicted			Observed	Predicted	
20	7.6	5.1	6.9	36	83.3	31.4	51.8
21	10.0	8.7	8.2	37	38.7	58.9	56.9
22	9.1	15.4	9.6	38	82.8	95.5	62.4
23	7.5	9.9	11.1	39	45.0	75.0	68.2
24	9.8	11.2	12.9	40	104.2	101.3	74.4
25	13.1	12.9	14.8	41	54.6	64.7	80.9
26	14.5	21.8	17.0	42	73.6	59.3	87.9
27	18.3	29.0	19.3	43	146.3	64.0	95.3
28	30.1	17.5	21.9	44	114.2	127.8	103.1
29	23.2	39.0	24.7	45	112.2	132.8	111.4
30	21.5	35.6	27.7	46	76.9	104.8	120.1
31	21.3	44.4	31.0	47	148.9	102.6	129.3
32	33.3	47.6	34.6	48	186.2	88.1	139.0
33	39.1	58.5	38.4	49	213.8	154.5	149.1
34	35.2	32.7	42.6	50	249.4	134.7	159.8
35	54.8	29.8	47.0				

^aSSQ is the sum of squared deviations about the mean.

The main considerations in fitting the allometric and isometric models are that the correct error structure is chosen and that the resultant fit of the model to the data should not indicate any lack of fit. Substantial bias in $\hat{\alpha}$, which is dependent on sample size, may occur when using the log transformation procedure (Hayes et al. 1995). The additive error approach appears to be more robust.

Generally, the allometric model is fitted first to a set of weight-length data, and then a test of the null hypothesis $H_0 : \beta = 3$ is made by examining whether the confidence interval for β contains the value 3. If it does, then one may accept the null hypothesis depending on consideration of the power of the test. If accepted, then the isometric model is then fitted. The only major advantage of using the isometric growth model is that certain calculations of yield per recruit are simplified (see chapter 6).

Example 4.1. Atka mackerel in the Bering Sea

The reported growth curve for Atka mackerel in the Bering Sea is an allometric model with $\alpha = 0.000270$ and $\beta = 3.393$ (Ronholt and Kimura 1986). Data were simulated from this growth model by using multiplicative errors with ϵ_i generated from a uniform distribution between -0.5 and 0.5. Two observations were generated from each length class between 20 and 50 cm (table 4.1). The data clearly show the increase in variance about the allometric curve as length increases (figure 4.2). The raw data are used in the analysis. Some researchers might be tempted to average the data for each length interval, but this would underestimate the true variability about the growth curve.

Linear regression results, shown in table 4.2, include estimates of $\ln \alpha$, α , and β , standard errors, confidence intervals, and other summary statistics. Predicted estimates of weight shown in figure 4.2 show that the least squares procedure provides a reasonable fit to the data. The isometric growth model is not appropriate for these data because the 95% confidence interval does not contain the value 3. However, confidence intervals must be treated with caution for these data because the error structure is not normally distributed. ■

4.2. LVB GROWTH MODEL

4.2.1. Length–Age

This class of models has been the most studied and most used of all length-age models for fishes because of its utility in other models (see chapter 6, for example) and its empirical success in describing growth. The principle underlying its success is that the growth rate of fishes tends to slow down as they get older. In this section, length, L , is modeled as a function of age, t . However, this model may be appropriate for other size variables Y as well; section 4.2.2 shows its use with weight, W .

The simplest model that can be written for the case of decreasing growth with age is a differential equation with a linearly decreasing growth rate, or

$$\frac{dL}{dt} = \omega - \kappa L, \quad \omega > 0, \kappa > 0, \quad (4.7)$$

with initial condition $L(t_0) = L_0$. This parameterization is from Gallucci and Quinn (1979). Equation (4.7) is a linear nonhomogeneous differential equation with two parameters and an initial condition. Hence three constants are necessary to specify the solution. The parameter ω , the growth rate at the initial time t_0 , is useful for comparing populations (Gallucci and Quinn 1979, Appeldoorn 1982). The parameter κ (often represented by the Roman letter K) is a growth parameter, with units of t^{-1} . It is also a useful descriptor of a population and appears to be related to natural mortality in many populations (section 8.3). This differential growth equation specifies an initial growth rate ω , which decreases linearly as a function of length to 0 at length $\omega/\kappa = L_\infty$, which is the asymptotic length. Substituting into (4.7), the equivalent differential equation is

$$\frac{dL}{dt} = \kappa(L_\infty - L), \quad \kappa > 0, L_\infty > 0. \quad (4.8)$$

With initial condition $L(t_0) = L_0$, the solution to differential equation (4.8), given in Gallucci and Quinn (1979), is

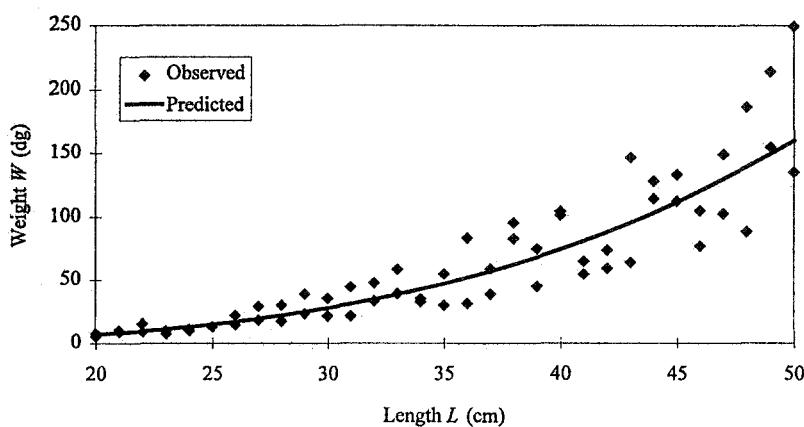


Figure 4.2. Observed and predicted weight versus length for the Atka mackerel example.

Table 4.2. Regression statistics for the Atka mackerel example.

Statistic of interest	Value
$\widehat{\ln \alpha} \pm 1 \text{ SE}$	-8.342 ± 0.499
95% CI for $\ln \alpha$	($-9.340, -7.344$)
$\widehat{\beta} \pm 1 \text{ SE}$	3.429 ± 0.141
95% CI for β	($3.147, 3.712$)
$\widehat{\alpha} = \exp(\widehat{\ln \alpha})$	0.000238
95% CI for α	($0.000088, 0.000647$)
n	62
$\widehat{\sigma}$	0.299
R^2	0.908
$t_{60,0.025}$	2.000
Mean of $\ln L$	3.521
SSQ ^a of $\ln L$	4.467785

^aSSQ is the sum of squared deviations about the mean.

$$L(t) = L_\infty \left[1 - e^{-\kappa(t-t_0)} \right] + L_0 e^{-\kappa(t-t_0)}.$$

Generally, one chooses $L_0 = 0$ and interprets t_0 as the age when an individual would have been of length 0 had this growth model been operative at all ages. This results in the "LVB" growth model

$$L(t) = L_\infty \left[1 - e^{-\kappa(t-t_0)} \right], \quad (4.9)$$

after Ludwig von Bertalanffy, who first developed this model for human growth processes (von Bertalanffy 1938). Use of this particular model is generally restricted to older ages of an individual because growth in early life stages does not usually follow this growth process.

A graph of the solution (4.9) is shown in figure 4.3, indicating the role of the model parameters. Parameter t_0 is a location parameter, indicating the x -intercept of the curve. Parameter κ is a curvature parameter, governing the speed with which the curve approaches the horizontal asymptote L_∞ . There is an intrinsic inverse relationship between κ and L_∞ when attempting to fit a set of data because an increase in the asymptote will cause a decrease in the curvature of the resulting curve (Knight 1968, Gallucci and Quinn 1979). Note that the curve for the LVB model contains no inflection point. We follow Ricker's (1975a) convention of calling κ the Brody growth parameter, after one of the model's first developers (Brody 1927, 1945), and parameter $\rho = \exp(-\kappa)$ the Ford growth parameter, after a researcher who developed a graphical estimation method, explained below.

The LVB model (4.9) can be recast as a difference equation. As derived by Gulland (1983), the increment of growth from time t to time $t + \tau$ is

$$\Delta L(t) \equiv L(t + \tau) - L(t) = [L_\infty - L(t)] (1 - e^{-\kappa\tau}), \quad (4.10)$$

which implies that the growth increment, $\Delta L(t)$, is a linear function of $L(t)$ with slope $-(1 - e^{-\kappa\tau})$ and y -intercept $L_\infty(1 - e^{-\kappa\tau})$. In particular, for $\tau = 1$, the annual growth

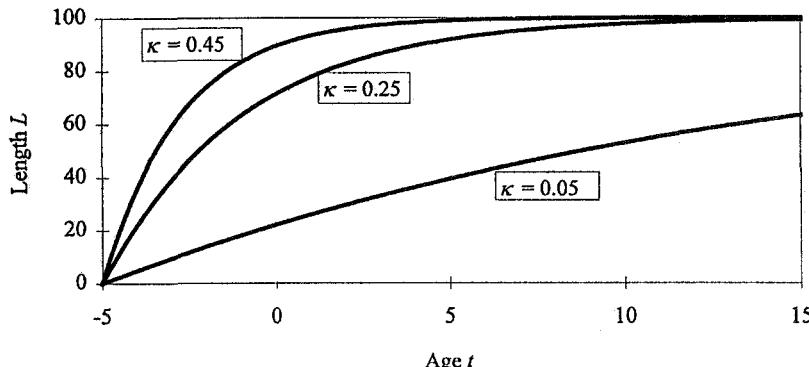


Figure 4.3. LVB curves for $L_{\infty} = 100$, $t_0 = -5$, and three values of κ : 0.05, 0.25, and 0.45.

increment can be plotted against starting length, and the LVB model is appropriate when the plot resembles a straight line. The plot of $\Delta L(t)$ versus $L(t)$ is called a Walford plot (Walford 1946). From inspection of (4.10), a plot of $L(t+1)$ versus $L(t)$ is also a straight line with the same y -intercept and slope $e^{-\kappa t}$, and the 45° straight line $L(t+1) = L(t)$ will intersect the plot at L_{∞} . This plot is called a Ford plot (Ford 1933). These plots are useful when measurements are collected on an individual over two or more time periods, such as with a mark-recapture experiment (see section 4.4). If one collects measurements on several individuals, it is tempting to average the measurements for each age and to construct these plots. Indeed, early methods of estimation consisted of these graphical methods. However, such averaging results in destroying information on variability in growth and does not use the growth information as well as techniques described in the next section.

Brody (1945) observed that the relationship of size, weight, and population size of many domestic animals and humans is sigmoidal (S-shaped). He modeled growth in two phases with a dividing line at a point t_x . His six-parameter model expressed in terms of length at age can be written (after Ricker 1975a) as

$$L(t) = \begin{cases} \alpha e^{\kappa' t}, & \text{for } t < t_x \\ \beta - \gamma e^{-\kappa t}, & \text{for } t \geq t_x \end{cases}$$

In the first equation, parameter α is the length at age 0, and parameter κ' is an instantaneous growth parameter. The second equation is equivalent to the LVB model with $\beta = L_{\infty}$ and $\gamma = L_{\infty} \exp(\kappa t_0)$, though the parameter t_0 has little meaning in this situation because the first equation describes growth before time t_x . If $L_x = L(t_x)$, the condition $\beta = \alpha \exp(\kappa' t_x) + \gamma \exp(-\kappa t_x)$ must hold for the two curves to match up at the point (L_x, t_x) . Given this condition and a value for t_x , a growth curve with four independent parameters (α , κ' , κ , and γ) results. For the curve to be continuous, the derivatives of the two equations evaluated at t_x must also be equal, which results in the additional condition $\alpha \kappa' \exp(\kappa' t_x) = \kappa \gamma \exp(-\kappa t_x)$. An alternative parameterization of the Brody growth model can be written in terms of κ' , L_x , κ , and L_{∞} by letting $\alpha = L_x \exp(-\kappa' t_x)$, $\beta = L_{\infty}$, and $\gamma = (L_{\infty} - L_x) \exp(\kappa t_x)$. The Brody model can be useful, especially when it is necessary to link data sets from early and adult life stages which might be collected on different time scales and from different studies. In

section 4.2, other sigmoidal growth models are constructed without this partitioning at time t_x and are easier to use.

Estimation

Classical methods of fitting the LVB model used linearized equations such as (4.10) and are summarized by Ricker (1975a) and Gulland (1983). But these approaches are awkward to use and have several problems. The error structure of the data is not explicitly defined, and estimates of precision for the parameter estimates are difficult to obtain. These classical methods are obsolete with the advent of modern computer approaches (Gallucci and Quinn 1979; Vaughan and Kanciruk 1992) and will not be considered further.

Suppose that a set of data $\{L_i, t_i\}$ for $i = 1, \dots, n$ is collected. Most frequently, data are collected from several individuals in a population. The growth model is then used to describe mean growth of individuals from that population, and model parameters should be interpreted as means as well. For example, L_∞ is then the mean asymptotic length, and t_0 is the hypothetical age when mean length is 0. The use of growth models when individuals have separate growth parameters is described in section 4.7.

The appropriate estimation of parameters of the LVB growth model depends on the error structure for the data. An additive error structure is appropriate when the variability in growth is assumed to be constant as a function of the independent variable. A multiplicative error structure is appropriate when variability in growth increases as a function of the independent variable.

For an additive error structure, the data are modeled as

$$L_i = L_\infty \left[1 - e^{-\kappa(t_i - t_0)} \right] + \epsilon_i, \quad (4.11)$$

where ϵ_i is a random error term with mean 0 and constant variance σ^2 . Estimates of L_∞ , κ , and t_0 are obtained from nonlinear least squares with L_i as the dependent variable and t_i as the independent variable.

For a multiplicative error structure, the data are modeled as

$$L_i = L_\infty \left[1 - e^{-\kappa(t_i - t_0)} \right] e^{\epsilon_i}, \quad (4.12)$$

where ϵ_i is a random error term with mean 0 and constant variance σ^2 . Taking logarithms of this equation,

$$\ln L_i = \ln L_\infty + \ln \left[1 - e^{-\kappa(t_i - t_0)} \right] + \epsilon_i. \quad (4.13)$$

Estimates of $\ln L_\infty$, κ , and t_0 are obtained from nonlinear least squares with $\ln L_i$ as the dependent variable and t_i as the independent variable.

Example 4.2. Rougheye rockfish in southeastern Alaska

Summarized data of length and age of rougheye rockfish from Nelson and Quinn (1987) are shown in table 4.3. The data show no appreciable increase in variance about the LVB curve as age increases (figure 4.4), which can be confirmed by constructing residual plots after fitting the model. Thus, an additive model is used in the analysis. We use the

Table 4.3. Rougheye rockfish length–age data from Nelson and Quinn (1987).

Age (years)	Average length (cm)	n	SD (cm)	Age (years)	Average length (cm)	n	SD (cm)
2	18.0	1		38	46.5	4	2.5
3	14.5	6	4.9	40	47.9	8	4.9
4	17.9	19	2.2	41	49.3	3	2.5
5	20.6	31	2.1	42	48.0	7	2.1
6	21.9	27	2.1	43	49.0	3	2.0
7	23.4	20	2.3	44	50.0	7	2.2
8	25.2	11	2.5	45	51.3	10	5.9
9	27.2	19	2.0	46	52.0	1	
10	29.6	12	3.0	47	48.9	9	2.7
11	30.7	13	2.9	49	48.7	3	2.5
12	32.4	12	3.7	50	48.6	7	2.8
13	33.0	4	2.3	52	51.5	2	0.7
14	32.8	8	2.9	53	52.0	4	11.4
15	35.0	11	4.1	54	50.0	1	
16	36.3	7	2.4	55	52.7	3	8.0
17	37.2	12	5.1	56	59.0	1	
18	36.2	10	4.4	57	52.0	5	3.9
19	38.8	5	1.8	58	50.0	1	
20	37.7	9	5.4	59	50.0	1	
21	40.6	7	3.1	60	51.0	4	1.4
22	40.9	14	4.3	61	50.0	1	
23	38.9	14	4.6	62	52.0	3	1.0
24	40.0	13	2.4	63	50.0	1	
25	41.9	15	3.9	64	59.0	2	9.9
26	42.7	15	5.5	65	55.0	2	1.4
27	42.6	9	6.4	66	52.5	2	2.1
28	45.5	8	4.0	67	50.0	2	0.0
29	40.9	8	4.6	68	54.0	1	
30	44.6	13	4.4	70	59.5	2	13.4
31	46.6	11	3.6	72	51.0	2	1.4
32	44.9	9	6.3	75	51.0	1	
33	47.2	9	4.6	77	60.0	2	12.7
34	48.3	16	5.1	80	74.0	1	
35	45.4	13	4.5	82	49.0	1	
36	48.8	10	3.4	85	57.0	1	
37	46.5	14	4.0	95	60.5	2	16.3
				All	38.1	545	11.8

raw data in the analysis, which can be approximated by others by generating normal random variates from the means and standard deviations in table 4.3.

Nonlinear least squares results, shown in table 4.4, include estimates of L_∞ , κ , and t_0 , standard errors, confidence intervals, estimated correlations, and summary statistics. Confidence intervals are quite narrow for all parameters because the number of observations is large and the range of ages is wide. However, the large negative correlations suggest that many combinations of parameters could produce a similar fit. Predicted estimates of length shown in figure 4.4 show that the least squares procedure provides a reasonable fit to the data. A useful interpretation of $\hat{\sigma}$ is that the length of an

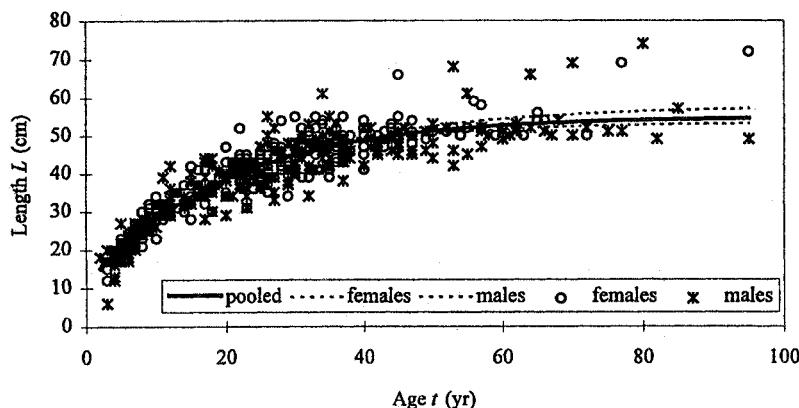


Figure 4.4. Observed and predicted length versus age for rougheye rockfish.

individual fish is normally distributed about the LVB curve with a standard deviation of 4.13 cm. ■

Alternative parameterizations of the LVB model may lead to more statistically stable parameter estimates. Gallucci and Quinn (1979) suggested that reparameterizing the LVB model with the parameter set $\{\omega, \kappa, t_0\}$ was desirable because of the negative correlation of estimates of L_∞ and κ , but positive correlation may result (Kingsley et al. 1980).

The concept of expected value parameterizations was introduced by Ross (1970) to provide efficient maximum likelihood estimation for nonlinear models, where at

Table 4.4. Nonlinear least squares statistics for the rougheye rockfish example.

Statistic of interest	Value
$\hat{L}_\infty \pm 1 \text{ SE}$	54.9 ± 0.8
95% CI for L_∞	(53.4, 56.4)
$\hat{\kappa} \pm 1 \text{ SE}$	0.0492 ± 0.0026
95% CI for κ	(0.0441, 0.0544)
$\hat{t}_0 \pm 1 \text{ SE}$	-4.53 ± 0.52
95% CI for t_0	(-5.55, -3.53)
Correlations	
$(\hat{L}_\infty, \hat{\kappa})$	-0.905
$(\hat{L}_\infty, \hat{t}_0)$	-0.678
$(\hat{\kappa}, \hat{t}_0)$	0.889
n	545
Residual df	542
Residual sum of squares	9284
Residual mean square ($\hat{\sigma}^2$)	17.13
$\hat{\sigma}$	4.13
R^2	0.877
$t_{542, 0.025}$	1.96

least some of the parameters are expected values of the dependent variable at various values of the independent variable. Ratkowsky (1986) applied this concept to the LVB growth model and a set of n observations by introducing parameters l_1 for length at the youngest age, τ_1 , in the data, l_2 for length at the oldest age, τ_2 , in the data, and the Ford growth parameter $\rho = \exp(-\kappa)$. This reparameterization of the LVB model is given by

$$L(t) = l_1 + (l_2 - l_1) \frac{1 - \tilde{\rho}^{m-1}}{1 - \tilde{\rho}^{n-1}} \quad (4.14)$$

where $m = 1 + (n - 1) \frac{t - \tau_1}{\tau_2 - \tau_1}$ and $\tilde{\rho} = \rho^{(\tau_2 - \tau_1)/(n-1)}$.

Ratkowsky showed that the parameterization $\{l_1, l_2, \tilde{\rho}\}$ is superior to many other parameterizations by using a measure of nonlinearity. The rationale for including sample size in the model was not given but may have been motivated by variance considerations. A simpler parameterization for single values at equally spaced ages was developed by Schnute and Fournier (1980). It contains the number of ages in the equation and was developed for use in length frequency analysis (section 8.1.1).

Francis (1988a) extended the expected value parameterization to all three parameters and let τ_1 and τ_2 represent arbitrary ages as long as $\tau_2 > \tau_1$. By letting τ_m be the half-way point $(\tau_1 + \tau_2)/2$ and l_m its corresponding length, his parameterization of the LVB model is

$$L(t) = l_1 + \frac{(l_2 - l_1)}{1 - r^2} \left[1 - r^{2(t - \tau_1)/(\tau_2 - \tau_1)} \right] \quad (4.15)$$

where $r = (l_2 - l_m)/(l_m - l_1)$.

Francis's parameterization $\{l_1, l_2, l_m\}$ is the complete expected value parameterization of the LVB model.

Cerrato (1990) provided an analogous but simpler reparameterization to Ratkowsky's, which can be written

$$L(t) = l_1 + (l_2 - l_1) \frac{1 - \rho^{t - \tau_1}}{1 - \rho^{\tau_2 - \tau_1}}. \quad (4.16)$$

Cerrato's parameterization $\{l_1, l_2, \rho\}$ avoids sample size n found in (4.14), a useful development. This parameterization is similar to that for the Schnute growth model, a generalization of the LVB model, found in section 4.3.5.

Using a measure of nonlinearity and simulation, Cerrato found that either (4.15) or (4.16) provided good estimates in terms of low curvature, nearly unbiased estimates, and normally distributed residuals. Surprisingly, (4.16) was better than (4.15) in some cases, considering that the latter is the complete expected value parameterization. Another important result from Cerrato's study was that choosing τ_2 as the oldest age, as in Ratkowsky's approach and as is done in many studies, is sometimes a poor choice in terms of parameter effects curvature. It is often better to choose an intermediate age. The same concept may apply to choosing τ_1 as the starting age, although there is often less variability in that section of the curve.

4.2.2. Difference Equation for Weight–Age

The relationship of weight, W , to age, t , is frequently sigmoidal, with the fastest growth in weight occurring at intermediate ages. If the ages of interest are beyond the inflection point in growth, then the weight–age relationship could perhaps be acceptably described by the LVB model. Deriso (1980) constructed a useful difference equation form of the LVB model. Rather than specifying a continuous curve, he used a single value for each annual interval. From (4.10), the annual increment of growth is a linear function with slope $1 - e^{-\kappa} = 1 - \rho$. Thus the Ford growth parameter ρ represents the relative change in growth for each age. Denoting W_r as the weight of a fish at recruitment age r , it can be shown that subsequent ages can be written as

$$W_t = W_r \frac{1 - \rho^{t-r+1}}{1 - \rho}, \quad t = r, r + 1, \dots \quad (4.17)$$

Deriso's application of this growth model is in section 5.2.

Schnute (1985) generalized Deriso's version of the LVB model by relating parameters back to the original LVB equation (4.9). From (4.10) it can be shown that the relationship between successive growth increments can be written as the difference equation

$$W_{t+1} - W_t = \rho (W_t - W_{t-1}),$$

which shows that annual growth increments decrease by the factor ρ . As a result, Schnute showed that Deriso's treatment effectively assumed that the prerecruitment weight, W_{r-1} , was equal to 0, which was no problem because Deriso was only interested in postrecruitment processes. Nevertheless, Schnute introduced a parameter for prerecruitment weight, W_{r-1} , and developed an equation analogous to the LVB model:

$$W_t = W_{r-1} + (W_r - W_{r-1}) \frac{1 - \rho^{t-r+1}}{1 - \rho}, \quad t = r, r + 1, \dots \quad (4.18)$$

The relationship between the parameters of (4.9) and (4.18) is:

$$\begin{aligned} L_\infty &= \frac{W_r - \rho W_{r-1}}{1 - \rho} \\ \kappa &= -\ln(\rho) \\ t_0 &= r - 1 - \frac{1}{\ln(\rho)} \ln \left(\frac{W_r - W_{r-1}}{W_r - \rho W_{r-1}} \right). \end{aligned}$$

Both the Deriso and Schnute formulations are limited to modeling populations where growth in weight can be reasonably modeled by the LVB model. Their use has been motivated by mathematical convenience in developing uncomplicated production models. Unless growth is well-modeled by this form, the models in the next sections are likely to be of greater utility.

4.2.3. Combining Weight–Length and Length–Age Models

A straightforward way to construct a weight–age model is to combine the isometric or allometric weight–length model (section 4.1) with the LVB length–age model (section 4.2). By writing

$$W \equiv W(L)$$

and $L \equiv L(t),$

a weight–age relationship can easily be constructed by forming

$$W(t) \equiv W [L(t)], \quad (4.19)$$

using any pair of functions $[W(L), L(t)]$. Combining the allometric weight–length equation (4.2) with the von Bertalanffy length–age equation (4.9) results in

$$W(t) = W_\infty [1 - e^{-\kappa(t-t_0)}]^\beta, \quad (4.20)$$

where W_∞ is the asymptotic weight of a fish ($= \alpha L_\infty^\beta$).

Further understanding of this type of weight–age model can be deduced from the differential equation for weight with respect to age. The allometric relationship will be derived, with the isometric relationship as a special case. By taking the derivative of (4.19) with respect to age, t , and substituting (4.2),

$$\begin{aligned} \frac{dW}{dt} &= \frac{dW}{dL} \frac{dL}{dt} = \alpha \beta L^{\beta-1} \frac{dL}{dt} \\ &= \alpha \beta L^{\beta-1} (\omega - \kappa L) \quad \text{from (4.7)} \\ &= \eta_1 W^{(\beta-1)/\beta} - \eta_2 W, \end{aligned} \quad (4.21)$$

where $\eta_1 = \alpha^{1/\beta} \beta \omega$, and $\eta_2 = \beta \kappa$. Thus the instantaneous rate of change for weight is a difference of two terms in (4.21), one of which is proportional to $L^{\beta-1}$ [or $W^{(\beta-1)/\beta}$], and the other to L^β (or W). The initial condition for this differential equation in analogy to the LVB model is $W(t_0) = 0$, a consequence of $L(t_0) = 0$ and the allometric relationship (4.2).

For the isometric case ($\beta = 3$), the first term in (4.21) is proportional to L^2 , which is proportional to surface area. Thus this term represents the metabolic process of anabolism, which was described in the introduction to this chapter. The second term is proportional to L^3 , which is proportional to volume and weight under suitable assumptions mentioned earlier. Thus this term represents the process of catabolism. The two terms should have the same role in describing anabolism and catabolism in the allometric model, but do not lend themselves to the intuitive geometric interpretation of the isometric case. Still, one could infer that in the allometric case, anabolism is proportional to a power $[(\beta - 1)/\beta]$ of weight and catabolism is directly proportional to weight.

Properties of this model are more complicated than those of the LVB length model. The differential equation (4.21) is applicable under parameter choices that result in a nonnegative growth rate. This criterion is satisfied under the conditions that $\alpha > 0$, $\beta > 0$, $\omega > 0$, and $\kappa > 0$. As a result, $\eta_1 > 0$ and $\eta_2 > 0$. A further constraint needed is $\beta > 1$, in order that the differential equation is well-behaved and decreases monotonically. It can then be shown that only a single maximum occurs past the value 0—namely, the value W_∞ at $t = \infty$. The location of the inflection point W_I can be found by setting the second derivative of (4.19) to 0. From (4.21),

$$\frac{d^2W}{dt^2} = \left(\frac{\beta - 1}{\beta} \eta_1 W^{-1/\beta} - \eta_2 \right) \frac{dW}{dt} = 0,$$

or $W_I = \left(\frac{\eta_1}{\eta_2} \frac{\beta - 1}{\beta} \right)^{\beta}.$

By substituting the original parameters for η_1 and η_2 and recalling $\omega = \kappa L_\infty$, the inflection point W_I is

$$W_I = W_\infty \left(\frac{\beta - 1}{\beta} \right)^\beta. \quad (4.22)$$

In particular, the isometric inflection point occurs at $\frac{8}{27} W_\infty$. By equating (4.20) and (4.22), it can easily be shown that the age, t_I , at which the inflection point occurs is

$$1 - e^{-\kappa(t-t_0)} = 1 - \frac{1}{\beta}$$

or $t_I = t_0 + \ln(\beta)/\kappa,$

where $\beta > 1$. Finally, the maximum growth rate, μ , can be found by substituting (4.22) into (4.21) or by differentiating (4.20) directly to obtain

$$\mu = \kappa W_\infty \left(\frac{\beta - 1}{\beta} \right)^{\beta-1}.$$

The combination of an increasing function rising to an asymptote, a single maximum, and an inflection point leads to a sigmoidal curve, as shown in figure 4.5 for three values of β . Increasing the parameter β increases the curvilinearity of the S-shaped curve. This general model is specified by three parameters, η_1 , η_2 , and β , in the differential equation, plus the initial condition parameter, t_0 , for a total of four parameters. A four-parameter model has the flexibility to model a wide variety of phenomena, and, indeed, growth in fishes frequently follows a sigmoidal pattern. One indication of this flexibility is the variable inflection point as a function of β . Further consideration of this model is described in section 4.3.4 in an alternative parameterization.

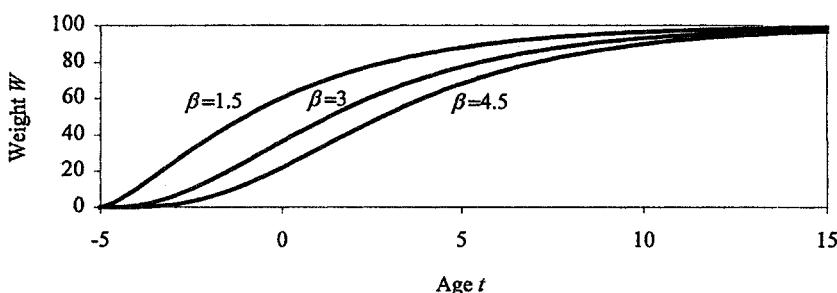


Figure 4.5. LVB allometric curves for $W_\infty = 100$, $\kappa = 0.25$, $t_0 = -5$, and three values of β : 1.5, 3 (isometric), and 4.5.

Estimation

Estimation of parameters of the LVB growth models in weight is analogous to estimation of LVB parameters for length. An error structure for the data must be selected, and the estimation is accomplished through nonlinear least squares. Suppose that a set of data $\{W_i, t_i\}$ for $i = 1, \dots, n$ is collected. For an additive error structure, the data are modeled as

$$W_i = W_\infty [1 - e^{-\kappa(t_i - t_0)}]^\beta + \epsilon_i$$

where ϵ_i is a random error term with mean 0 and constant variance σ^2 . Estimates of W_∞ , κ , t_0 , and β can be obtained from nonlinear least squares with W_i as the dependent variable and t_i as the independent variable.

For a multiplicative error structure, the data are modeled as

$$\ln W_i = \ln W_\infty + \beta \ln [1 - e^{-\kappa(t_i - t_0)}] + \epsilon_i,$$

and parameter estimates can be obtained from nonlinear least squares with $\ln W_i$ as the dependent variable. The estimate $\ln \hat{W}_\infty$ is exponentiated to obtain the estimate \hat{W}_∞ .

In practice, it is often difficult to obtain statistically stable estimates of all four parameters. With only one independent variable, the equation is potentially overparameterized. This is evidenced by high negative and positive correlations among parameter estimates and difficulties in obtaining convergence of the nonlinear least squares procedure. This difficulty can be resolved most easily by obtaining β from auxiliary sources, such as a weight-length curve fit (section 4.1) and using it in the nonlinear procedure as a fixed value.

Alternatively, estimates of parameters L_∞ , κ , t_0 , α , and β can be obtained from weight-length and length-age analyses, and the estimate of W_∞ can be calculated from the allometric equation (4.2). However, this approach assumes that mean weight at a given age is the same as the mean weight at the mean length for that age (R.I.C.C. Francis, personal communication, 1994), which may not be true if there is much individual variation in growth.

A third error structure is often used as well. If an estimate of β is available, then the weight data can be transformed as $X_i = W_i^{1/\beta}$. The data X_i are then assumed to follow the LVB curve for length with an additive error structure

$$X_i = X_\infty [1 - e^{-\kappa(t_i - t_0)}] + \epsilon_i,$$

where $X_\infty = W_\infty^{1/\beta}$. Parameter estimates can then be obtained using computer programs that fit the LVB model for length. The estimate of W_∞ is then obtained from X_∞ . Note that the transformed data are assumed to have an additive structure, rather than the original data.

Example 4.3. Pacific halibut

Weight-age data of female Pacific halibut are shown in table 4.5 from a longline survey in southeastern Alaska in 1985 (IPHC 1985). Variability is apparently higher for older ages, suggesting a multiplicative error structure. Attempts to fit four-parameter LVB models with additive and multiplicative error structures were unsuccessful in obtaining a unique solution or convergence of the iterative least squares procedure. Due to a high negative correlation between t_0 and β , nearly the same residual sum of squares

Table 4.5. Pacific halibut weight-age data of females, southeastern Alaska, 1985 longline survey.

Age (years)	Weight (kg)	Age (years)	Weight (kg)	Age (years)	Weight (kg)
4	1.7	12	18.2	20	44.8
5	2.0	13	21.6	21	52.6
6	3.9	14	25.4	22	49.1
7	4.2	15	28.8	23	56.7
8	6.4	16	30.9	24	58.6
9	7.6	17	35.6	28	54.1
10	10.9	18	37.9		
11	14.9	19	34.7		

is obtained from a variety of combinations of these two parameters. The estimate of β tends to $+\infty$, and the estimate of t_0 tends to $-\infty$.

From other studies β was estimated as 3.24 (Quinn et al. 1983a). Fitting three-parameter LVB models with this value for β is much more successful. Parameter estimates and confidence intervals for models with an additive error structure, a multiplicative error structure, and an additive data structure on the transformed data (X_i) are given in table 4.6, along with other summary statistics of the nonlinear least squares fits. Parameter estimates are substantially different depending on the error structure. Estimated correlations among estimates are fairly high, suggesting that many combinations of parameter estimates can be fit to the data with essentially the same goodness of fit. Indeed, all models provide a good fit to the data over the range of data (figure 4.6), but model predictions of weight beyond the range of data differ substantially between models. The multiplicative and transformed models meet the assumptions of homoscedasticity better than the additive model. Procedures for choosing the best model are discussed more fully in section 4.5. ■

4.3. SIZE-AGE MODELS

In this section, a variety of potential growth models is presented. To show their applicability for any kind of size data (length, weight, width, etc.), we denote the size variable of interest as Y rather than as L or W .

4.3.1. Allometric Model

For certain fish species, the change in size may not be well represented by models of the LVB form. One example of a different growth pattern is for Pacific halibut length data (McCaughran 1981). No asymptote is apparent in the growth pattern for this species; an alternative model is the allometric model (section 4.1), previously used for the weight-length relationship. For size-age, the form of the model is

$$Y = \alpha t^\beta. \quad (4.23)$$

Parameter estimation follows exactly as in section 4.1, or according to McCaughran (1981) for mark-recapture data (see section 4.4.2).

4.3.2. Ad hoc Models

For some purposes, a growth model may be of interest simply to fit the data closely or to perform basic statistical tests. A linear or polynomial model may be sufficient

Table 4.6. Parameter estimates of female Pacific halibut from the LVB weight-age model for different error structures: additive (A), multiplicative (M), and transformed (T).

	Error Structure		
	A (W_∞) ^a	M ($\ln W_\infty$)	T (X_∞)
Asymptote ± 1 SE	73.7 ± 7.5	4.92 ± 0.24	4.17 ± 0.19
95% CI for Asymptote	(58.1, 89.3)	(4.42, 5.41)	(3.77, 4.58)
\hat{W}_∞	73.7	136.5	102.4
95% CI for W_∞	(58.1, 89.3)	(83.1, 223.6)	(73.7, 138.4)
$\hat{\kappa} \pm 1$ SE	0.111 ± 0.018	0.058 ± 0.009	0.073 ± 0.009
95% CI for κ	(0.074, 0.148)	(0.039, 0.771)	(0.054, 0.092)
$\hat{t}_0 \pm 1$ SE	2.54 ± 1.11	-0.78 ± 0.48	0.07 ± 0.51
95% CI for t_0	(0.22, 4.86)	(-1.78, 0.22)	(-1.01, 1.14)
Correlations			
(Asymptote, $\hat{\kappa}$)	-0.945	-0.982	-0.970
(Asymptote, \hat{t}_0)	-0.784	-0.836	-0.788
($\hat{\kappa}$, \hat{t}_0)	0.931	0.914	0.895
n	22	22	22
Residual df	19	19	19
Residual sum of squares	180.4	0.3182	0.1578
Residual mean square ($\hat{\sigma}^2$)	9.496	0.01675	0.008304
$\hat{\sigma}$	3.082	0.1294	0.0911
R^2	0.977	0.988	0.987

^aAsymptote used in parentheses.

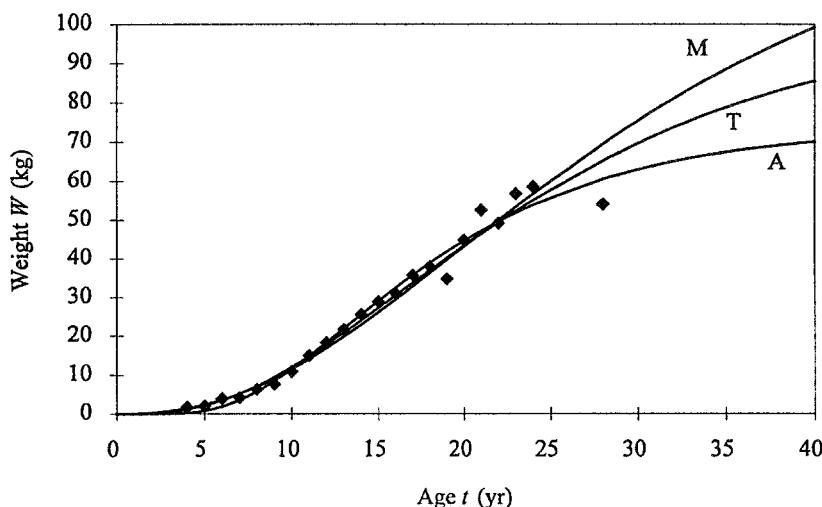


Figure 4.6. Observed and predicted values of Pacific halibut weight versus age for three error structures: A, additive; M, multiplicative; T, transformed.

to describe growth or some transformation of growth (Rao 1958, Roff 1980). Such a model may be written

$$F[Y(t)] = \alpha_0 + \alpha_1 t + \alpha_2 t^2 + \dots, \quad (4.24)$$

where $F(\cdot)$ indicates the transformation (logarithmic, square root, none, etc.) to be used and $\{\alpha_i\}$ is the set of model parameters. Roff contended that the LVB curve should be retired from use because the biological parameters are seldom useful in interpreting growth. One major limitation of polynomial fitting is that the resulting growth curve need not be monotonically nondecreasing nor have an upper asymptote, which could violate biological principles. Polynomial coefficients can often have large variances and covariances, which makes comparison of growth curves more difficult. As a result, Roff's suggestion that the LVB be retired model has generally been disregarded.

4.3.3. Gompertz Growth Model

The Gompertz growth curve is an alternative sigmoidal growth curve described by the differential equation

$$\frac{dY}{dt} = \lambda e^{-\kappa t} Y, \quad \lambda > 0, \kappa > 0, \quad (4.25)$$

with initial condition $Y(0) = Y_0$. Unlike the LVB models for length and weight, the Gompertz curve does not permit the assignment of Y_0 to 0, because then (4.25) would be identically equal to 0. To obtain a parameterization in terms of t_0 , the parameter λ can be reparameterized as $\exp(\kappa t_0)$.

In (4.25), the rate of change per unit of weight dY/Ydt declines exponentially as a function of age. The solution of (4.25) is

$$Y(t) = Y_0 \exp \left[\frac{\lambda}{\kappa} (1 - e^{-\kappa t}) \right]. \quad (4.26)$$

As $t \rightarrow \infty$, $Y(t)$ clearly approaches the asymptote

$$Y_\infty = Y_0 \exp \left(\frac{\lambda}{\kappa} \right),$$

Thus (4.26) can be rewritten in terms of the asymptote Y_∞ as

$$Y(t) = Y_\infty \exp \left(-\frac{\lambda}{\kappa} e^{-\kappa t} \right) = Y_\infty \exp \left[-\frac{1}{\kappa} e^{-\kappa(t-t_0)} \right]. \quad (4.27)$$

In either parameterization, the Gompertz is a three-parameter model. For this model, the inflection point occurs when

$$\frac{d^2Y}{dt^2} = \lambda e^{-\kappa t} \frac{dY}{dt} - \lambda \kappa Y e^{-\kappa t} = 0,$$

$$\text{or} \quad (\lambda^2 Y e^{-\kappa t} - \lambda \kappa Y) e^{-\kappa t} = 0$$

$$\text{or} \quad t_I = \frac{1}{\kappa} \ln \left(\frac{\lambda}{\kappa} \right) = t_0 + \frac{1}{\kappa} \ln \left(\frac{1}{\kappa} \right).$$

By substituting t_I for t in (4.26) and (4.27), the inflection point can easily be shown to be

$$Y_I = Y_0 \exp\left(\frac{\lambda}{\kappa} - 1\right) = \frac{Y_\infty}{e}.$$

Thus the inflection point is determined by a single parameter, Y_∞ , and is less flexible than the four-parameter allometric LVB curve (4.20), which has an inflection point determined by two parameters. The maximum growth rate, μ , which occurs at the inflection point, is found by substituting the formulae for t_I and Y_I into (4.25), which results in

$$\mu = \kappa \frac{Y_\infty}{e} = \kappa Y_I.$$

A frequently-presented alternative formulation of the differential equation (4.25) can be obtained that is only a function of Y . From (4.27),

$$\ln \frac{Y(t)}{Y_\infty} = -\frac{\lambda}{\kappa} e^{-\kappa t},$$

so that (4.25) can be reformulated as

$$\begin{aligned} \frac{dY}{dt} + \kappa Y \ln \frac{Y}{Y_\infty} &= 0, \\ \text{or } \frac{dY}{dt} + e\mu \frac{Y}{Y_\infty} \ln \frac{Y}{Y_\infty} &= 0, \end{aligned}$$

a first-order homogeneous nonlinear differential equation. Thus the Gompertz growth curve for individuals is identical to the Gompertz-Fox model for biomass derived in section 2.1.3. In both cases, the underlying differential equation results in a monotonically increasing, sigmoidal curve with an upper asymptote, which is conceptually appropriate both for mean growth of individuals and for growth of populations.

Estimation

Estimation of parameters can be accomplished in a variety of ways. If the variability of growth about the curve is constant, then (4.27) can be fitted directly using nonlinear least squares. If the variability is increasing, a multiplicative error structure may be assumed. In this case, one can take logarithms of (4.27) and add an error term to obtain

$$\ln Y_i = \ln Y_\infty - \frac{\lambda}{\kappa} e^{-\kappa t_i} + \epsilon_i, \quad (4.28)$$

which can be viewed as a nonlinear regression equation for the estimation of $\ln Y_\infty$, λ , and κ .

Example 4.4. Pacific halibut

With the data set from example 4.3 (table 4.5), a Gompertz growth curve is fitted by assuming a multiplicative error structure and using (4.28). Parameter estimates and summary statistics from the nonlinear least squares procedure are shown in table 4.7. Confidence intervals about parameters are fairly small. The residual sum of squares for the Gompertz model is smaller than for the comparable LVB model M in table 4.6,

Table 4.7. Nonlinear least squares statistics for the Gompertz growth model for the Pacific halibut example.

Statistic of interest	Value
$\widehat{\ln W_\infty} \pm 1 \text{ SE}$	4.39 ± 0.10
95% CI for $\ln W_\infty$	(4.18, 4.59)
\widehat{W}_∞	80.6
95% CI for W_∞	(65.4, 98.5)
$\widehat{\lambda} \pm 1 \text{ SE}$	0.763 ± 0.071
95% CI for λ	(0.615, 0.912)
$\widehat{\kappa} \pm 1 \text{ SE}$	0.119 ± 0.008
95% CI for κ	(0.101, 0.136)
Correlations	
$(\ln W_\infty, \widehat{\lambda})$	0.829
$(\ln W_\infty, \widehat{\kappa})$	-0.922
$(\widehat{\lambda}, \widehat{\kappa})$	-0.975
n	22
Residual DF	19
Residual sum of squares	0.2076
Residual mean square ($\hat{\sigma}^2$)	0.01093
$\hat{\sigma}$	0.1045
R^2	0.992

showing that the Gompertz model is a better model for this data set. Predicted weight versus age forms an S-shaped Gompertz curve that satisfactorily fits the data (figure 4.7). ■

4.3.4. Verhulst and Richards Growth Models

The general Verhulst growth law is governed by the differential equation

$$\frac{dY}{dt} + c_1 Y + \phi(Y) = 0,$$

(Fletcher 1975) where $\phi(Y)$ is a general nonlinear term. Solutions of this equation are monotonic and bounded and exhibit a single inflection point (Fletcher 1975). When the nonlinear term is chosen to be

$$\phi(Y) = c_2 Y^n,$$

the growth law is called the Richards (1959) growth law, although several others have also been associated with this differential equation. Comparing the resultant differential equation

$$\frac{dY}{dt} + c_1 Y + c_2 Y^n = 0$$

with (4.21), it is apparent that the Richards growth law is equivalent to the LVB allometric growth model for weight with

$$c_1 = \eta_2, \quad c_2 = -\eta_1, \quad \text{and } n = (\beta - 1)/\beta.$$

Fletcher analytically recasted the Richards growth model in terms of parameters designed to give the most analytical meaning. The differential equation is rewritten

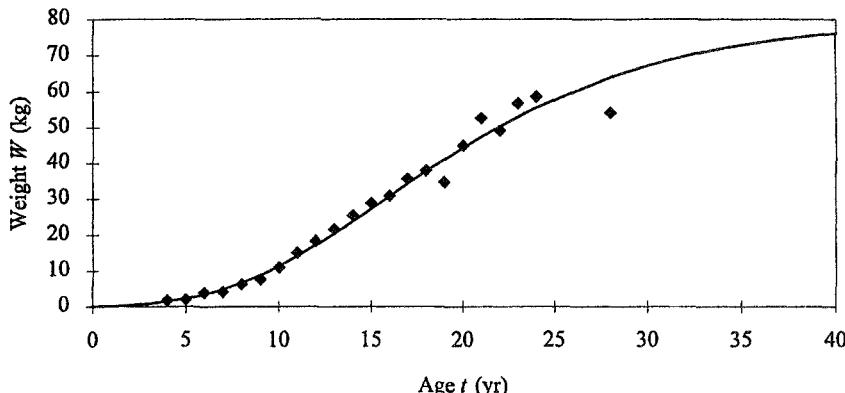


Figure 4.7. Observed and predicted weight from the Gompertz growth model versus age for the Pacific halibut example.

$$\frac{dY}{dt} - \gamma\mu \left(\frac{Y}{r}\right) + \gamma\mu \left(\frac{Y}{r}\right)^n = 0, \quad (4.29)$$

where $\gamma = n^{n/(n-1)} / (1-n)$. The parameter r is asymptotic size, and μ is the maximum growth rate. The value of Y at the inflection point is $p = n^{1/(1-n)} r$; μ is the slope at that point. There is a direct correspondence between this model for growth of individuals and the Pella-Tomlinson model for growth of populations in section 2.1.2. The solution of (4.29) is

$$Y(t)^{1-n} = r^{1-n} + C_0 \exp \left[-\mu n^{n/(n-1)} t/r \right], \quad n \neq 1$$

and $\ln Y(t) = \exp(C_0 - \epsilon\mu t/r)$, $n = 1$.

where C_0 is a constant found by substituting the initial condition, such as $Y(t_0) = 0$ into the equation (Fletcher 1975).

This complete formulation of the Richards function contains the LVB ($n = 0$), LVB allometric ($n = \frac{\beta-1}{\beta}$), LVB isometric ($n = \frac{2}{3}$), logistic ($n = 2$), and Gompertz ($n = 1$) models as special cases. Parameter estimation is summarized in above sections for each special case.

The parameter n is solely determined by the ratio $p/r = n^{1/(1-n)}$. Fletcher (1975) noted the difficulty in estimating the parameter n because the ratio p/r is very flat as a function of n . Thus, the parameter n should be determined from auxiliary information, which is the same recommendation in section 4.2.3 regarding β . Ebert (1980) presented two methods for estimating parameters with mark-recapture data (see also section 4.4).

4.3.5. Schnute Growth Model

Schnute (1981) developed a general four-parameter growth model that contains most of the preceding growth models as special cases. Rather than modeling the instantaneous rate of change, Schnute concentrates on logarithmic or relative rate of change

$$Z = \frac{d}{dt} \ln Y \equiv \left(\frac{1}{Y} \right) \frac{dY}{dt}.$$

The simplest assumption that can be made about Z is that its relative rate of change is linear, i.e.

$$\left(\frac{1}{Z}\right) \frac{dZ}{dt} \equiv \frac{d}{dt} \ln Z = -(\kappa + \gamma Z).$$

When an S-shaped growth curve results, the parameter γ is related to the ratio of the weight at the inflection point to the asymptotic weight, and κ^{-1} is related to the distance along the t axis to the inflection point. Rewriting this pair of equations as

$$\begin{aligned} \frac{dY}{dt} &= YZ \\ \frac{dZ}{dt} &= -Z(\kappa + \gamma Z), \end{aligned} \quad (4.30)$$

this system can be solved if two initial conditions are given; namely, $Y(\tau_1) = y_1$ and $Y(\tau_2) = y_2$ for two time points τ_1 and τ_2 . It can be shown that this pair of equations is equivalent to the quadratic nonhomogeneous differential equation

$$\frac{d^2Y}{dt^2} = \frac{dY}{dt}[-\kappa + (1 - \gamma)Z].$$

The two time points τ_1 and τ_2 are to be specified by the user, such as the youngest and oldest ages observed. The model then consists of four parameters, κ , γ , y_1 , and y_2 . Alternatively, parameters y_1 and y_2 can be specified by the user, with parameters τ_1 and τ_2 estimated.

There are four solutions to this system of differential equations (4.30), corresponding to whether κ and/or γ are equal to 0:

Case 1. $\kappa \neq 0, \gamma \neq 0$:

$$Y(t) = \left\{ y_1^\gamma + (y_2^\gamma - y_1^\gamma) \frac{1 - \exp[-\kappa(t - \tau_1)]}{1 - \exp[-\kappa(\tau_2 - \tau_1)]} \right\}^{1/\gamma}, \quad (4.31)$$

Case 2. $\kappa \neq 0, \gamma = 0$:

$$Y(t) = y_1 \exp \left\{ \ln \left(\frac{y_2}{y_1} \right) \frac{1 - \exp[-\kappa(t - \tau_1)]}{1 - \exp[-\kappa(\tau_2 - \tau_1)]} \right\}, \quad (4.32)$$

Case 3. $\kappa = 0, \gamma \neq 0$:

$$Y(t) = \left[y_1^\gamma + (y_2^\gamma - y_1^\gamma) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]^{1/\gamma}, \quad (4.33)$$

Case 4. $\kappa = 0, \gamma = 0$:

$$Y(t) = y_1 \exp \left[\ln \left(\frac{y_2}{y_1} \right) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]. \quad (4.34)$$

The four solutions of the differential equation admit eight different curve patterns depending on values of κ and γ : curves may or may not have an upper, lower, left-side,

or right-side asymptote, inflection point, or a zero value for a t -intercept (see Schnute 1981, figure 2). The general LVB allometric weight model is equivalent to case 1 with positive parameters, where $1/\gamma = \beta$. Thus, the LVB length model is a special case with $\gamma = 1$; the LVB isometric weight model is a special case with $\gamma = \frac{1}{3}$. The Gompertz curve is equivalent to case 2 with a positive κ parameter. Schnute's treatment of the Richards curve is parameterized with an exponent $p = -n$, which corresponds to case 1 with $\kappa > 0$ and $\gamma < 0$. The more general treatment in section 4.3.4 allows coefficients to have any sign. The logistic growth model is a special case of case 1 with $\gamma = -1$ and $\kappa > 0$. Case 3 contains power series laws for growth such as linear and quadratic. Case 4, the most restrictive case, assumes growth is a power function with t as the exponent. If $\kappa < 0$, then the growth model exhibits positive acceleration as age progresses; this situation results in nonasymptotic behavior. Figure 4.8 illustrates the different shapes of the Schnute growth model for selected values of κ and γ .

Schnute (1981) gave expressions for calculating asymptotes and inflection points from the four parameters. For case 1, the asymptote is

$$Y_\infty = \left[\frac{y_2^\gamma - e^{-\kappa(\tau_2-\tau_1)} y_1^\gamma}{1 - e^{-\kappa(\tau_2-\tau_1)}} \right]^{1/\gamma},$$

and the weight at the inflection point is

$$Y_I = Y_\infty(1 - \gamma)^{1/\gamma}.$$

For case 2, the asymptote is

$$Y_\infty = \exp \left[\frac{\ln y_2 - e^{-\kappa(\tau_2-\tau_1)} \ln y_1}{1 - e^{-\kappa(\tau_2-\tau_1)}} \right],$$

and the weight at the inflection point is

$$Y_I = Y_\infty/e,$$

in agreement with the result of section 4.3.3. For cases 3 and 4, neither an asymptote nor an inflection point are present.

Estimation

Any of the four cases can be fitted with nonlinear least squares. The choice of the most appropriate case for a set of data is made by considering the statistical significance of the κ and γ coefficients. One algorithm is to examine case 1, then cases 2 and 3, and then case 4. Case 1 is initially selected as the best model. If κ or γ is not significantly different from 0 in case 1, then case 3 or case 2, respectively, is tentatively selected. Only if the other parameter is not significantly different from 0 in these cases would case 4 be selected.

Alternatively, Schnute (1981) gave an F test procedure analogous to the general linear model to compare the cases, which is also discussed in section 4.5.2. Let RSS_x be the residual sum of squares of case x with f_x degrees of freedom. The estimate $\hat{\sigma}_x^2$ is equal to RSS_x/f_x , the residual mean square. The residual sum of squares will

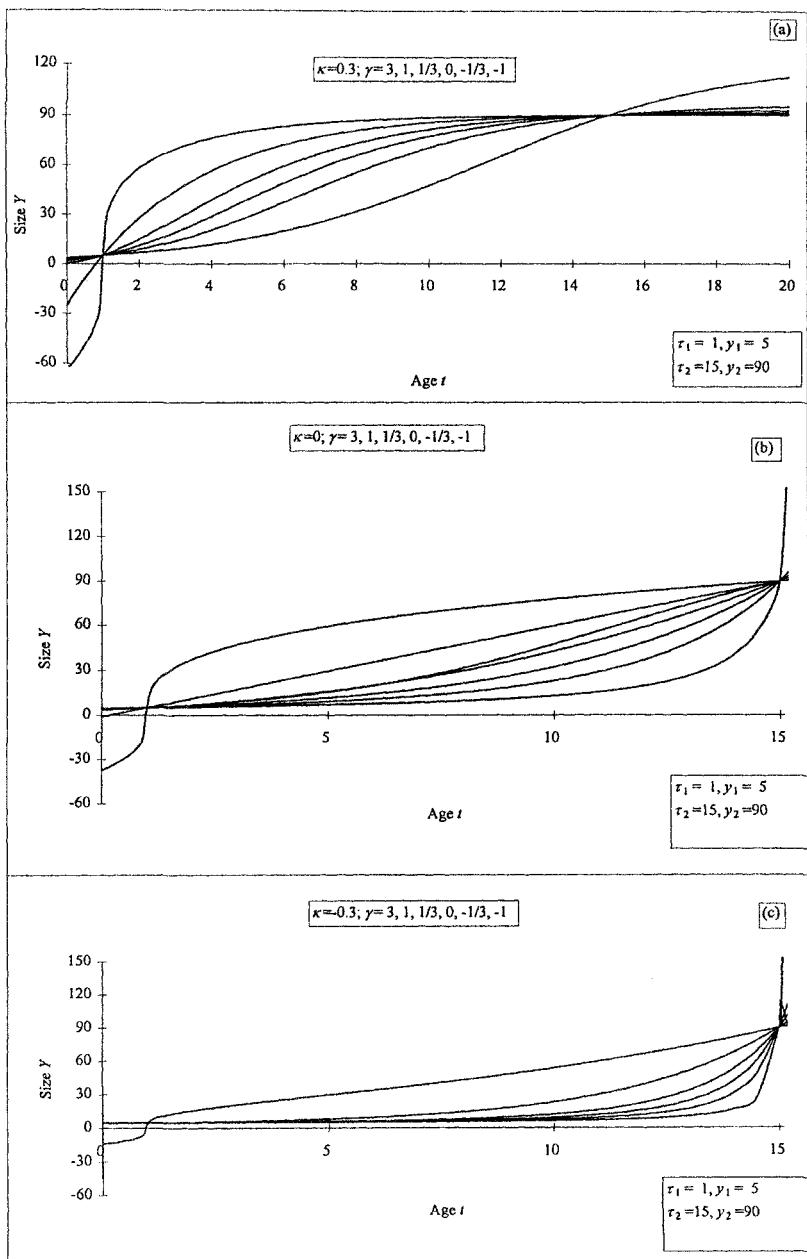


Figure 4.8. The relationship between size, Y , and age, t , for selected values of κ and γ in the Schnute growth model.

always be lower for a model with additional parameters. Suppose that case x has more parameters than case y . To test the null hypothesis that case x and case y are the same versus the hypothesis that case x is better than case y , compute the statistic

$$F = \frac{\text{RSS}_y - \text{RSS}_x}{f_y - f_x} / \hat{\sigma}_x^2 \quad (4.35)$$

and compare to the critical value of the F distribution for a one-sided test of level α with numerator and denominator degrees of freedom $f_y - f_x$ and f_x , respectively. For the Schnute models, a typical battery of tests would compare cases 1 and 2, cases 1 and 3, cases 2 and 4, cases 3 and 4, and cases 1 and 4. The choice between cases 2 and 3 is based on the one having the lowest RSS because they have the same number of parameters. The best model is the model with the fewest parameters that is tested to be the same as case 1 and that meets the underlying assumptions of the least squares and regression procedure (homoscedasticity, goodness of fit, etc.).

Given the ubiquity of the LVB length model (section 4.2), an additional case 5 can be added to the roster of cases, corresponding to $\gamma = 1$. If the confidence interval for γ contains the value 1, then the LVB model is selected. The residual sum of squares from a fit of the LVB model can also be used in the F test comparison.

Schnute suggested by example that his parameterization was statistically stable, in the sense that convergence of nonlinear least squares was obtained, when other parameterizations failed to converge. As two of the four parameters in Schnute's model are expected value parameters (see section 4.2.1), one would expect a greater stability than for either the LVB allometric or Richards parameterizations. The selection of the most parsimonious model (case) is handled by the statistical procedure rather than forcing the user to make arbitrary decisions. Schnute's approach was slow to find its way into general literature, perhaps because easy-to-use least squares computer software was not available.

Should the application of case 1 of Schnute's growth model lead to a statistically better fit to a set of growth data than the LVB model, one might interpret this result as evidence that anabolic and catabolic processes changed as a function of age. Lipinski and Roeleveld (1990) showed this interpretation is incorrect by application to growth of plastic squid. They also showed that although the LVB model appeared to fit the data as well as the Schnute model, a statistical test showed the Schnute model was superior.

Measures of nonlinearity are available for assessing the violation of the assumptions of nonlinear regression (Bates and Watts 1988). In application to Pacific hake, Welch and McFarlane (1990) used these measures and found that Schnute's model was much more nonlinear than the LVB model. The inherent nonlinearity of Schnute's model may lead to bias in parameter estimation and inaccuracy of confidence interval coverage (Welch and McFarlane 1990). They suggested that the four-parameter Schnute model be used with caution and be used primarily to determine the overall shape of a growth model. Their results indicated that the additional flexibility provided by a four-parameter model was not necessary. The statistical hypothesis tests outlined above provide a means for reducing the four-parameter model to a reduced-parameter model. An additional consideration that follows from their results is that tests based on residual sums of squares or likelihood may be better than examining confidence intervals to select the most parsimonious model.

Example 4.5. Pacific halibut

With the data set from examples 4.3 and 4.4 (table 4.5), Schnute growth models are fitted with an additive error structure. (Similar models can be obtained for a multiplicative error structure.) The values of τ_1 and τ_2 are 4 and 28, corresponding to the youngest and oldest ages in the data. Parameter estimates and summary statistics from the nonlinear least squares procedure are shown in tables 4.8 and 4.9 for cases 1, 2, 5, and 4. The procedure does not converge for case 3 because the estimate of y_1 becomes negative, no matter what initial parameter values or τ_1 are selected. A negative y_1 is a mathematical inconsistency for case 3 because a negative number raised to a power is indefinite. Convergence of case 1, a four-parameter model, in light of nonconvergence of the four-parameter LVB model of section 4.2.3, is evidence that the Schnute parameterization is more statistically stable.

Cases 1 and 2 provide similar parameter estimates and overlapping confidence intervals. The confidence interval for γ contains 0, and the F statistic of 1.5 is small, indicating that cases 1 and 2 are adjudged to be equally appropriate for this data set ($P > .25$). Cases 1 and 2 produce an almost identical fit to the weight–age data, forming an S-shaped curve that satisfactorily fits the data (figure 4.9).

The residual sum of squares is smaller for cases 1 and 2 (table 4.9) than for the comparable LVB allometric model A in table 4.6, which assumes an exponent of 3.24. Thus, the Schnute models are better for this data set. Case 2 with a positive value for κ is equivalent to the Gompertz model, which confirms the satisfactory fit observed in section 4.3.3. Parameter estimates differ in the two sections because previously a multiplicative error structure was assumed, which is more appropriate for this data set due to increasing variability with age. The multiplicative error structure favors a higher asymptote and higher inflection point for this data set for the LVB, Gompertz, and Schnute case 1 models.

Table 4.8. Parameter estimates from the Schnute growth model for the Pacific halibut example.

	Schnute model			
	Case 1	Case 2	Case 5	Case 4
$\hat{w}_1 \pm 1 \text{ SE}$	2.1 ± 1.1	0.9 ± 0.5	-3.5 ± 2.4	10.2 ± 1.7
95% CI for w_1	(−0.3, 4.4)	(−0.2, 1.9)	(−8.4, 1.5)	(6.6, 13.7)
$\hat{w}_2 \pm 1 \text{ SE}$	58.5 ± 2.5	59.7 ± 2.2	64.0 ± 3.1	73.3 ± 6.0
95% CI for w_2	(53.3, 63.8)	(55.2, 64.3)	(57.5, 70.6)	(60.9, 85.8)
$\hat{\kappa} \pm 1 \text{ SE}$	0.221 ± 0.086	0.147 ± 0.018	0.006 ± 0.014	0
95% CI for κ	(0.040, 0.402)	(0.109, 0.186)	(−0.024, 0.036)	
$\hat{\gamma} \pm 1 \text{ SE}$	-0.63 ± 0.66	0	1	0
95% CI for γ	(−2.02, 0.76)			
\hat{W}_∞	62.0	67.8	491	None
W_I	28.5	24.9	None	None
Correlations				
(\hat{w}_1, \hat{w}_2)	−0.262	0.467	0.304	−0.541
$(\hat{w}_1, \hat{\kappa})$	0.696	−0.919	−0.692	
$(\hat{w}_1, \hat{\gamma})$	−0.852			
$(\hat{w}_2, \hat{\kappa})$	−0.665	−0.699	−0.782	
$(\hat{w}_2, \hat{\gamma})$	0.541			
$(\hat{\kappa}, \hat{\gamma})$	−0.966			

Table 4.9. Summary statistics and hypothesis tests from the Schnute growth model for the Pacific halibut example.

	Schnute model			
	Case 1	Case 2	Case 5	Case 4
Residual sum of squares	152.2	162.9	326.5	1226.5
Residual mean square ($\hat{\sigma}^2$)	8.462	8.575	17.185	61.326
$\hat{\sigma}$	2.909	2.928	4.146	7.831
F versus Case 1		1.2 ($P > .25$)	20.6 ($P < .001$)	63.5 ($P < .001$)
F versus Case 2				62.0 ($P < .001$)
F versus Case 5				52.4 ($P < .001$)

Case 5, the LVB model with exponent 1, does not have an inflection point and consequently does not fit the sigmoidal data well. Case 4 also does not provide an acceptable fit to the data (figure 4.9). The F tests versus cases 1 and 2 indicate that both cases 1 and 2 are superior to cases 5 and 4. The confidence interval about κ does not include 0, another indication that case 4 is unacceptable. Finally, the form of case 4 is a power function of age, which is not suitable for data with an inflection point or an asymptote. The failure of the 95% confidence interval to include the value $\gamma = 1$ suggests that case 5 (the LVB length model) is not appropriate for these data. ■

4.3.6. Schnute-Richards Growth Model

Schnute and Richards (1990) proposed a five-parameter model to provide an omnibus approach to modeling fish growth, maturity, and survivorship data. For the latter two variables, a limiting value of 1 for the proportion of mature fish or number of fish dying makes possible the consideration of only a four-parameter model. The general model includes most growth laws mentioned previously, as well as the logit-type models found in analysis of survival. The basic form of this model is

$$Y(t) = Y_\infty \left(1 + \delta e^{-\kappa t^\nu} \right)^{1/\gamma}. \quad (4.36)$$

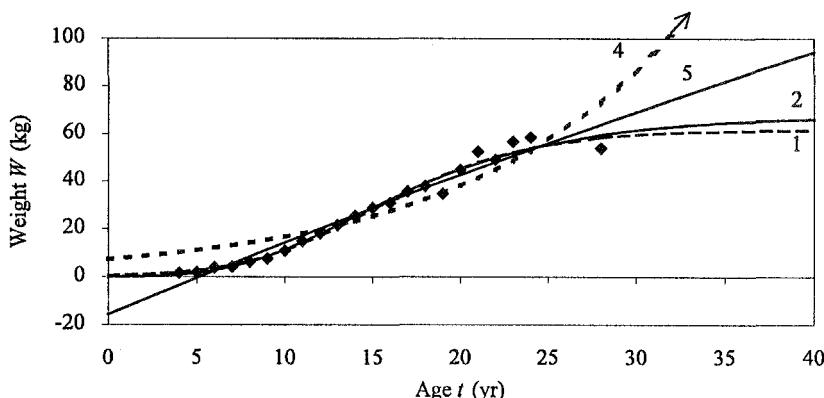


Figure 4.9. Observed and predicted weight from the Schnute growth model versus age for the Pacific halibut example.

Essentially, this model is a generalization of the Schnute growth model with age t replaced with t^ν . Hence, equivalent representations of Schnute's cases can be obtained from (4.31)–(4.34) with each age parameter τ or variable t replaced with τ^ν or t^ν . For example, case 1 from (4.31) becomes

$$Y(t) = \left\{ y_1^\gamma + (y_2^\gamma - y_1^\gamma) \frac{1 - \exp[-\kappa(t^\nu - \tau_1^\nu)]}{1 - \exp[-\kappa(\tau_2^\nu - \tau_1^\nu)]} \right\}^{1/\gamma}, \quad (4.37)$$

Conceptually, this model would apply if age is an imperfect measure of the independent variable actually related to growth. The Schnute-Richards model results if the relationship between the independent variable and age is allometric.

Analytical and graphical descriptions of model properties, an overview of special cases, and details of likelihood and parameter estimation are given by Schnute and Richards (1990). Schnute's four-parameter model is clearly a special case of (4.37) with $\nu = 1$. The LVB length model (in its Schnute case 5 parameterization) is a special case of (4.36) with $\gamma = 1$ and $\nu = 1$. The Gompertz model is a special case of (4.36) with $\gamma = 0$. This model would be useful in situations where even a four-parameter model does not provide an adequate fit to a set of data. The F test procedure in section 4.3.5 can be used to compare various submodels and/or to choose the most parsimonious model.

4.4. MARK-RECAPTURE DATA

Mark-recapture (or tagging) studies are frequently conducted to obtain growth information as well as information concerning migration and abundance. Especially when determining age is difficult for a fish species, growth information can be deduced from the relationship between the change in size of a marked (or tagged) fish and the amount of elapsed time between marking and recapture. Two analytical approaches apply to mark-recapture data; the first applicable when growth is related to elapsed time, the second when ages are also determined. This section covers constant parameter models; individual variation models are found in section 4.7. As in section 4.3, we denote the size of an individual as Y , which can represent length L , weight W , or any other size measurement.

4.4.1. Elapsed Time Models

Suppose that a mark-recapture experiment is conducted in which n fish are recaptured. The fish need not be released nor recaptured at the same time, as long as times of release and recapture are recorded for each fish. It is presumed that the age of the fish is not determined either at the time of marking or at recapture. Suppose that fish i was of length $Y_{1i} = Y(t_{1i})$ at age t_{1i} when tagged and of length $Y_{2i} = Y(t_{2i})$ at age t_{2i} when recaptured. The elapsed time between marking and recapture is the only temporal information available, denoted as $\Delta t_i = t_{2i} - t_{1i}$. Growth is the change of length, $\Delta Y_i = Y_{2i} - Y_{1i}$. The essential data set for estimation of growth is then $\{\Delta Y_i, Y_{1i}, \Delta t_i\}$, $i = 1, \dots, n$, or alternatively, $\{Y_{2i}, Y_{1i}, \Delta t_i\}$.

Suppose that the LVB model adequately describes growth. Further assume that an additive error structure applies to growth. From (4.10),

$$\Delta Y_i = (Y_\infty - Y_{1i})(1 - e^{-\kappa \Delta t_i}) + \epsilon_i, \quad (4.38)$$

where ϵ_i is a random error term with mean 0 and variance σ^2 . Estimates of parameters Y_∞ and κ can be obtained by nonlinear least squares. Chapman (1961) derived a linearized version of (4.38) for the situation of constant elapsed time for all fish.

Alternatively, (4.38) can be recast with dependent variable Y_{2i} as a function of Y_{1i} and Δt_i , as

$$Y_{2i} = Y_\infty(1 - e^{-\kappa\Delta t_i}) + Y_{1i}e^{-\kappa\Delta t_i} + \epsilon_i. \quad (4.39)$$

The choice between (4.38) and (4.39) depends on whether the error in growth increment or recapture size is constant.

From mark-recapture data alone, only these two parameters can be estimated. To fully specify the growth model, parameter t_0 would have to be obtained from auxiliary information. If a value for length Y_i at a particular age t_i is known, then the LVB model (4.9) can be solved for t_0 , as shown in the example below.

A similar type of analysis is applicable to any growth model that can be written as a function of only elapsed time, Δt_i , and size measurements such as length or weight. Each growth model presented in previous sections can be converted from a size-age model to an age-size model, from which elapsed time can be derived; Ebert (1980) did so for the Richards growth model.

This conversion is demonstrated for the Schnute growth models (4.31)–(4.34); similar derivations may be constructed for other models. The mark-recapture versions for the four cases of Schnute's growth model were derived by Baker et al. (1991). For case 1, equation (4.31) is solved for age t as a function of size Y , or

$$t = \tau_1 - \frac{1}{\kappa} \ln \left[1 - \frac{Y^\gamma - y_1^\gamma}{y_2^\gamma - y_1^\gamma} (1 - e^{-\kappa(\tau_2 - \tau_1)}) \right] \quad (4.40)$$

Two equations are obtained by replacing t and Y in (4.40) by t_{1i} and Y_{1i} in the first equation and t_{2i} and Y_{2i} in the second. Subtracting these two equations yields an expression for Δt_i , which is then rearranged as

$$Y_{2i} = \left[Y_{1i}^\gamma e^{-\kappa\Delta t_i} + \frac{y_2^\gamma - y_1^\gamma e^{-\kappa(\tau_2 - \tau_1)}}{1 - e^{-\kappa(\tau_2 - \tau_1)}} (1 - e^{-\kappa\Delta t_i}) \right]^{1/\gamma} \quad (4.41a)$$

$$= [Y_{1i}^\gamma e^{-\kappa\Delta t_i} + \xi^\gamma (1 - e^{-\kappa\Delta t_i})]^{1/\gamma}. \quad (4.41b)$$

Equation (4.41b) is a function of only three parameters, κ , γ , and ξ , in contrast to the original model with four parameters. Thus, the process of subtracting two equations results in one less parameter that can be estimated from elapsed-time mark-recapture data. From section 4.3.5, parameter ξ is equal to Y_∞ . Because absolute age is not used in the model, it is intuitive that a fully determined growth curve cannot be obtained from elapsed-time mark-recapture data. For the other cases, the equivalent equations to (4.40) for age as a function of size from (4.31) through (4.34) are:

Case 2:

$$t = \tau_1 - \frac{1}{\kappa} \ln \left[1 - \frac{\ln Y - \ln y_1}{\ln y_2 - \ln y_1} (1 - e^{-\kappa(\tau_2 - \tau_1)}) \right] \quad (4.42)$$

Case 3:

$$t = \tau_1 + \frac{Y^\gamma - y_1^\gamma}{y_2^\gamma - y_1^\gamma} (\tau_2 - \tau_1) \quad (4.43)$$

Case 4:

$$t = \tau_1 + \frac{\ln Y - \ln y_1}{\ln y_2 - \ln y_1} (\tau_2 - \tau_1). \quad (4.44)$$

These functional forms can be used to fit age-size relationships.

The equivalent equations to (4.41) for mark-recapture data from (4.42) through (4.44) are:

Case 2:

$$\begin{aligned} Y_{2i} &= \exp \left[(\ln Y_{1i}) e^{-\kappa \Delta t_i} \right. \\ &\quad \left. + \frac{\ln y_2 - (\ln y_1) e^{-\kappa(\tau_2 - \tau_1)}}{1 - e^{-\kappa(\tau_2 - \tau_1)}} (1 - e^{-\kappa \Delta t_i}) \right] \end{aligned} \quad (4.45a)$$

$$= \exp \left[(\ln Y_{1i}) e^{-\kappa \Delta t_i} + (\ln \xi) (1 - e^{-\kappa \Delta t_i}) \right] \quad (4.45b)$$

Case 3:

$$Y_{2i} = \left(Y_{1i}^\gamma + \frac{y_2^\gamma - y_1^\gamma}{\tau_2 - \tau_1} \Delta t_i \right)^{1/\gamma} \quad (4.46a)$$

$$= (Y_{1i}^\gamma + \xi^\gamma \Delta t_i)^{1/\gamma} \quad (4.46b)$$

Case 4:

$$Y_{2i} = Y_{1i} \exp \left(\frac{\ln y_2 - \ln y_1}{\tau_2 - \tau_1} \Delta t_i \right) \quad (4.47a)$$

$$= Y_{1i} \exp [(\ln \xi) \Delta t_i] = Y_{1i} \xi^{\Delta t_i}. \quad (4.47b)$$

For all these cases, the parameterization in terms of ξ illustrates the general principle that one less parameter can be estimated from mark-recapture data than is contained in the growth model itself. This is a consequence of the lack of information on absolute age.

The two parameterizations for each case are among many that could be chosen. The equations numbered with an "a" are partial expected value parameterizations that should have relatively low parameter effects curvature. For these parameterizations, values for τ_1 and τ_2 must be specified, and one of the parameters of the model must be specified as well (this will usually be y_1). Baker et al. (1991) suggested that y_1 can often be obtained from auxiliary size-age information.

The equations numbered with a "b" are parameterized in terms of ξ , which avoids the necessity of specifying y_1 , τ_1 , and τ_2 . For cases 1 and 2, ξ corresponds to the asymptote Y_∞ . For the nonasymptotic cases 3 and 4, ξ is chosen to be similar to cases 1 and 2, respectively. In addition, case 5, the LVB model, can be obtained in both parameterizations from (4.41a) and (4.41b) by setting $\gamma = 1$.

An additive or multiplicative error term may be added to the parameterizations to complete the specification of the model. Nonlinear least squares is then used to obtain

parameter estimates. The best model can be selected in the same way as for size-age data in section 4.3.5 which used the general linear model theory. In application to two data sets, Baker et al. (1991) found that different models were appropriate for different data sets, suggesting that reliance on the LVB model is ill-advised.

Outliers and negative growth ($Y_{2i} < Y_{1i}$) frequently occur in mark-recapture data sets. Advice regarding these issues is the domain of standard statistical textbooks. For example, there are tests for outliers and methods of fitting parameters for specific outliers. One cautionary note is that there should be suitable justification for removing outliers or data points with negative growth. Such observations may actually describe growth variation in individuals or measurement errors that are important in the understanding of growth. The removal of outliers can bias parameter estimates if the outliers are indeed valid observations of growth (Francis 1988b). A better approach is to model the presence of outliers with a Bernoulli probability distribution, as shown in Francis (1988b). This topic is considered further in section 4.7, where measurement error models are described.

Two further caveats are pertinent to the use of mark-recapture data for determining growth parameters. First, it must be assumed that the marking or tagging of fish does not affect growth. In practice, there are situations where this assumption does not appear to be valid (McFarlane and Beamish 1990). In some cases, the experimental design may lead to the perception of growth effects, when in fact there may be none (Trites 1991).

Second, growth parameters determined from age-size data have different interpretations from those determined from mark-recapture data when individual variation in growth is present (Francis 1988a). When fitting age-size data, variation is assumed in size as a function of age as the independent variable. When fitting mark-recapture data, variation is assumed in size at recapture or growth as a function of size at marking and elapsed time. For an elapsed time of one year, for example, a mark-recapture model predicts the mean size (or growth) one year later for an individual of a given size. In contrast, a size-age model predicts the mean size (or growth) at the next age for an individual of a given age. Francis showed that differences in growth rate occur by using the two approaches in actual and simulated populations and suggested that researchers should be cautious in comparing growth parameters from the two approaches as a means of validation. Further support for this suggestion was found by Baker et al. (1991), who isolated different growth curve shapes from the two approaches in two case studies. Francis (1988b) also suggested reparameterizations of the LVB model with parameters for three sizes-at-age and two growth increments-at-size to clarify the differences between models. Francis (1995) reparameterized the models in Baker et al. (1991) analogously.

Example 4.6. Rainbow trout in the Kenai River

The mark-recapture data set in table 4.10 is a one in three subset of the data set used by Baker et al. (1991). There is no negative growth in the data set, but observation 93 appears to be an outlier, showing growth of 166 mm over only 0.389 year. This observation is included in subsequent analysis, so that the true underlying variation in the data set can be determined.

The five cases of Schnute's growth model are fitted to the data set in both the "a" and "b" parameterizations with nonlinear least squares. As the data represent length, the models are rewritten with L for the length variables and l for the length parameters.

Table 4.10. Mark–recapture data for Kenai River rainbow trout (Baker et al. 1991).

Obs.	L_2	L_1	Δt	Obs.	L_2	L_1	Δt
1	249	239	0.175	52	409	332	0.841
2	272	259	0.060	53	411	384	1.098
3	279	244	0.211	54	412	357	0.912
4	295	281	0.093	55	413	336	0.914
5	305	300	0.060	56	415	385	0.846
6	312	241	0.999	57	420	353	0.320
7	320	218	0.986	58	423	355	0.235
8	324	234	0.914	59	425	361	0.945
9	330	321	0.137	60	427	334	0.920
10	334	245	1.205	61	428	340	1.095
11	337	323	0.654	62	428	427	0.159
12	343	336	0.063	63	430	359	0.956
13	345	269	0.824	64	431	380	0.315
14	349	257	0.871	65	432	349	0.841
15	349	349	0.090	66	435	351	1.043
16	351	263	0.953	67	437	323	1.246
17	356	322	0.975	68	440	354	1.016
18	358	336	0.115	69	441	357	1.347
19	362	257	0.252	70	442	430	0.140
20	363	358	0.068	71	448	351	1.098
21	364	281	0.914	72	448	448	0.090
22	365	238	1.087	73	450	258	1.290
23	365	332	0.945	74	451	268	1.339
24	366	315	0.887	75	455	381	0.928
25	368	259	0.980	76	460	430	0.353
26	369	353	0.104	77	463	426	1.038
27	370	300	0.912	78	467	437	0.296
28	371	338	1.070	79	473	410	0.906
29	373	361	0.156	80	482	476	0.901
30	374	330	0.983	81	486	465	0.802
31	377	300	0.925	82	490	377	1.246
32	379	284	0.898	83	496	311	1.205
33	382	307	0.211	84	500	418	0.936
34	384	297	0.887	85	505	418	0.966
35	384	384	0.071	86	510	478	0.296
36	388	335	0.994	87	511	485	1.062
37	390	364	0.843	88	512	485	1.090
38	390	380	0.115	89	519	459	0.999
39	391	387	0.063	90	521	459	0.994
40	394	394	0.099	91	535	523	0.175
41	395	297	1.040	92	544	431	1.103
42	397	268	1.109	93	555	389	0.389
43	398	306	0.851	94	572	569	0.216
44	399	364	0.799	95	587	576	0.290
45	400	397	0.208	96	590	580	0.876
46	402	249	0.876	97	591	563	0.353
47	403	363	1.027	98	597	592	0.879
48	405	324	1.062	99	616	614	0.057
49	406	339	0.994	100	637	628	0.887
50	407	334	0.860	101	650	628	0.895
51	408	310	1.060	102	731	720	1.207

Table 4.11. Parameter estimates using five cases and two parameterizations of Schnute's growth model as applied to Kenai River rainbow trout mark-recapture data.

Case	θ	$\hat{\theta} \pm 1 \text{ SE}$	$\hat{\kappa} \pm 1 \text{ SE}$	$\hat{\gamma} \pm 1 \text{ SE}$	$r(\hat{\theta}, \hat{\kappa})$	$r(\hat{\theta}, \hat{\gamma})$	$r(\hat{\kappa}, \hat{\gamma})$	RSS
1a	l_2	657 ± 43	0.146 ± 0.118	2.09 ± 0.78	-0.74	0.39	-0.89	84033
1b	L_∞	736 ± 136	0.146 ± 0.118	2.10 ± 0.78	-0.95	0.72	-0.89	84033
2a	l_2	624 ± 27	0.440 ± 0.046	0	-0.84			90646
2b	L_∞	632 ± 30	0.440 ± 0.046	0	-0.88			90646
3a	l_2	701 ± 35	0	2.98 ± 0.39	-0.94			85192
3b	ξ	319 ± 20	0	2.98 ± 0.40	0.96			85192
4a	l_2	1216 ± 159	0	0				228450
4b	ξ	1.18 ± 0.02	0	0				228450
5a	l_2	637 ± 32	0.295 ± 0.047	1	-0.91			85767
5b	L_∞	659 ± 43	0.295 ± 0.047	1	-0.95			85767

The correlation between parameter estimates is denoted r .

From Baker et al. (1991), the values needed to implement parameterization "a," obtained from auxiliary information about size and absolute age, are selected to be $\tau_1 = 2$ (the youngest age in the data), $l_1 = 234$ mm (average length at age 2), and $\tau_2 = 12$ (the oldest age in the data). (As mentioned in section 4.2.1, an intermediate age for τ_2 may improve parameter estimation.)

Parameter estimates, along with their standard errors and correlations, and RSSs for these fits are given in table 4.11. Both parameterizations have identical RSS's for each case, indicating identical fits to the data. The "a" parameterization has smaller correlations and smaller coefficients of variation for the length parameter than the "b" parameterization, suggesting that the expected value parameterization "a" is better. Common parameters have nearly the same estimates, standard errors, and correlations.

By using the F statistic in (4.35), tests of the various cases are made (table 4.12). Neither case 3 nor case 5 is significantly different from case 1, and case 3 has the lower sum of squares, indicating that case 3 is the most parsimonious model. On the other hand, use of the LVB model (case 5) would not be inappropriate. [With the larger sample size in Baker et al. (1991), the LVB model was rejected, however.]

Residuals plots versus predicted recapture length, \hat{L}_{2i} , elapsed time, Δt_i , and observed length at marking, L_{1i} , for case 3 show no lack of fit or heteroscedasticity, although the outlier is clearly notable (figure 4.10). Thus, case 3 is selected as the best model. Baker et al. (1991) gave residuals plots for all cases and additive and

Table 4.12. F tests for the Kenai River rainbow trout mark-recapture data set.

Case y versus case x	$f_y - f_x$	f_x	$\hat{\sigma}_x$	F	P
2 versus 1	1	99	848.8	7.8	<.01
3 versus 1	1	99	848.8	1.4	>.10
5 versus 1	1	99	848.8	2.0	>.10
4 versus 1	2	99	848.8	170.1	<.01
4 versus 2	1	100	906.5	152.0	<.01
4 versus 3	1	100	851.9	168.2	<.01
4 versus 5	1	100	857.7	166.4	<.01

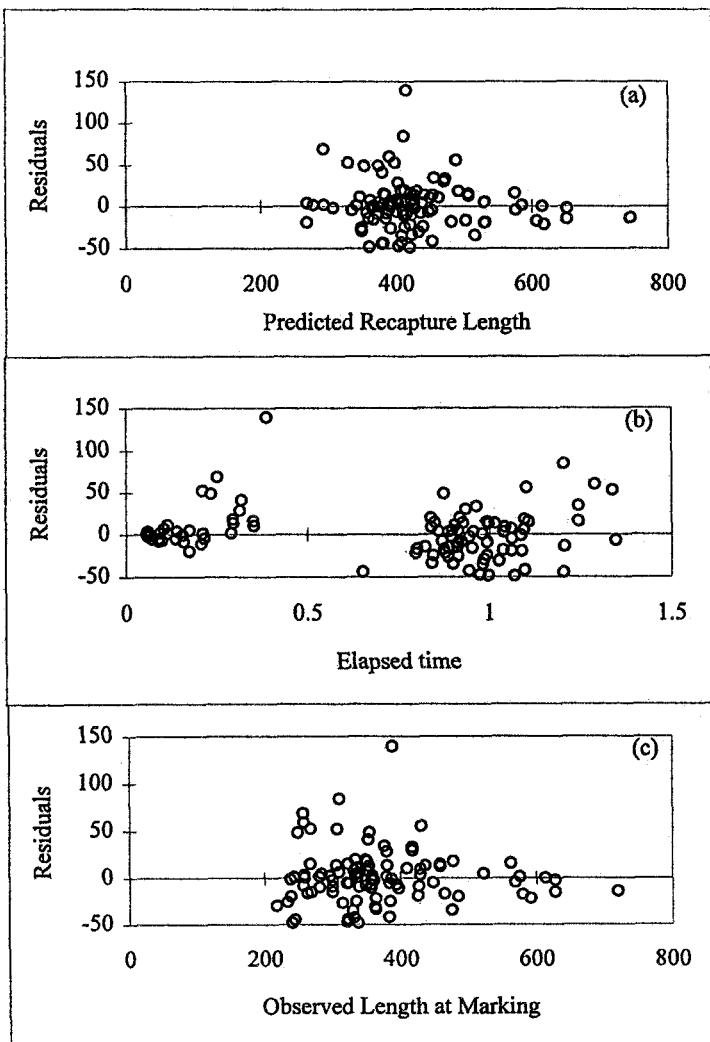


Figure 4.10. Residuals $L_{2i} - \hat{L}_{2i}$ versus (a) predicted recapture length \hat{L}_{2i} , (b) elapsed time Δt_i , and (c) observed length at marking L_{1i} for Case 3 of Schnute's growth model for the Kenai River rainbow trout mark-recapture example.

multiplicative error structures. Except in the poorest fitting models, it is difficult to reject a model on the basis of residuals plots.

The predicted growth model is shown in figure 4.11 for different values of the length at marking. These curves can be viewed as conditional growth curves given fish of different sizes. The growth curve with marking length 0 is a depiction of the length-age growth curve, scaled so that $l_0 = t_0 = 0$. To rescale the axis to the correct value of t_0 , the auxiliary information from parameterization "a" is needed. From (4.43), the value of t_0 corresponding to $L = 0$ is

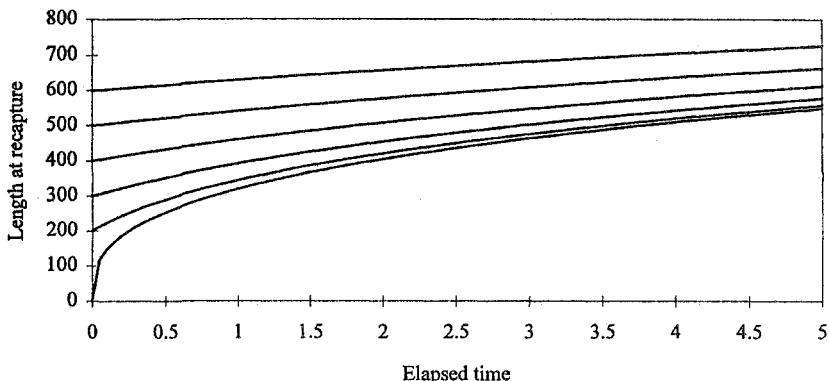


Figure 4.11. Predicted length at recapture \hat{L}_2 as a function of elapsed time Δt for different values of initial length at recapture L_1 (corresponding to where the curves cross the y-axis) for Case 3 of Schnute's growth model for the Kenai River rainbow trout mark-recapture example.

$$t_0 = \tau_1 - \frac{l_1^\gamma}{l_2^\gamma - l_1^\gamma} (\tau_2 - \tau_1),$$

which for this example becomes $t_0 = 1.60$. This can be visually confirmed in figure 4.11 by noting that $l_1 = 234$ on the growth curve corresponds to about 0.4 on the elapsed time scale. As the actual age is 2, this results in a t_0 of about 1.6. ■

4.4.2. Models with Aging Data

In this mark–recapture experiment, additional information is available about the ages t_{1i} and t_{2i} at marking and recapture, respectively. The essential data for estimating growth are $\{Y_{1i}, Y_{2i}, t_{1i}, t_{2i}\}, i = 1, \dots, n$.

The first approach would be to simply fit a size–age model from the pooled information from both time periods. A disadvantage of this approach is that the population at marking may be different from the population at recapture, resulting in a growth model applicable to neither. Growth curves at marking and recapture could be developed separately to overcome this problem. A second disadvantage is that information concerning individual growth is not fully exploited by pooling the data. If one or more individual parameters could be estimated for each individual fish, then the distribution of growth parameter estimates could be examined to determine the best overall parameter for the population.

McCaughran (1981, 1987) developed such an approach for the allometric size–age relationship in (4.23). On a logarithmic scale, fish sizes at marking and recapture, respectively, are given by

$$\ln Y_{1i} = \ln \alpha_i + \beta_i \ln t_{1i} \quad (4.48a)$$

$$\ln Y_{2i} = \ln \alpha_i + \beta_i \ln t_{2i}, \quad (4.48b)$$

where α_i and β_i are growth parameters for fish i . Solving this system of two equations and two unknowns, one obtains

$$\hat{\beta}_i = \frac{\ln Y_{2i} - \ln Y_{1i}}{\ln t_{2i} - \ln t_{1i}}$$

$$\text{and } \widehat{\ln \alpha_i} = \ln Y_{1i} - \hat{\beta}_i \ln t_{1i} \quad (4.49a)$$

$$= \frac{\ln Y_{1i} \ln t_{2i} - \ln Y_{2i} \ln t_{1i}}{\ln t_{2i} - \ln t_{1i}}. \quad (4.49b)$$

An overall estimate of each parameter can be obtained from some function of the individual estimates. McCaughran (1981) recommended the median of each set of parameter estimates (calculated as a weighted estimator based on the difference of the logarithms of ages) because it can be shown to be median-unbiased. Here, it suffices to write

$$\hat{\alpha} = \text{med} \{ \hat{\alpha}_i \} \quad (4.50a)$$

$$\hat{\beta} = \text{med} \{ \hat{\beta}_i \}, \quad (4.50b)$$

where $\hat{\alpha}_i = \exp(\widehat{\ln \alpha_i})$.

In some situations, two independent sets of information, one from mark-recapture and the other from size-age data, are available. Kirkwood (1983) developed a maximum likelihood model for this experimental design, which assumes common constant parameters for all individuals in the population. Kirkwood's aim was to develop predictions of age from size data, which led him to model the errors in age and elapsed time as a function of size and change in size. The mark-recapture component of the model is a transformation of (4.10), written as

$$\Delta t_i = -\frac{1}{\kappa} \ln \left(1 - \frac{\Delta Y_i}{Y_\infty - Y_{1i}} \right) + \epsilon_{1i}, \quad (4.51a)$$

where the $\{\epsilon_{1i}, i = 1, \dots, n_1\}$ are assumed to be independent, normally distributed errors with mean zero and variance σ_1^2 . The size-age component of the model is a transformation of (4.9), written as

$$t_i = t_0 - \frac{1}{\kappa} \ln \left(1 - \frac{Y_i}{Y_\infty} \right) + \epsilon_{2i}, \quad (4.51b)$$

where the $\{\epsilon_{2i}, i = 1, \dots, n_2\}$ are assumed to be independent, normally distributed errors with mean zero and variance σ_2^2 . By assuming that all errors are independent of each other, a likelihood equation for the combined data is easily constructed. Maximizing the likelihood produces estimates of Y_∞ , κ , t_0 , σ_1^2 , and σ_2^2 . The model can be extended to estimate separate parameters of Y_∞ and κ from each data set and to test for equality of parameters with likelihood ratio tests. Problems with fitting (4.51b) can occur when variability in size is high for older ages because the term in parentheses becomes negative for measurements $Y_i > Y_\infty$, and the logarithm of a negative number is not real. Kirkwood's approach may also be used with size and change of size as the dependent variables, as in (4.11) and (4.38). Kirkwood's approach has less utility in situations where individual variation in parameters is high because then the growth parameters are not strictly comparable (Francis 1988a; see section 4.7).

4.5. COMPARISON OF GROWTH MODELS

Two types of comparisons are needed when growth models are applied to data. First, a method is needed for choosing the best model for a particular data set among competing models and error structures, which may have different parameters. Second, one of the greatest needs in population research is the study of differences in growth among sexes, areas, population components, or other such groupings. Differences among areas may indicate different stock components requiring separate management regimes. Differences between sexes may result in more complicated investigations of dynamics (e.g., Quinn 1981). Differences in growth may be related to environmental factors and variation in latitude, lending greater understanding of growth processes (Appeldoorn 1982).

4.5.1. Choosing the Best Model

The first decision in choosing the best growth model for a data set is to select candidate models based on the shape of the desired curve (asymptote, inflection point, etc.) and biological assumptions upon which the models are derived. Schnute's growth model (section 4.3.5) is a logical choice because it is based on a reasonable assumption of linear relative growth acceleration, which results in a wide class of models. Schnute's procedure also contains a method for choosing the best submodel based on the RSS. The LVB class of models in section 4.2 is also frequently selected because it is used in other analyses. Analysis of residuals after fitting a growth model (Draper and Smith 1981) is useful to determine whether the model lacks fit in any part of the range of the independent variable of the model.

The second decision is to determine the appropriate error structure for the data. The selection of an error structure can have profound effects on the resulting parameter estimates (Schnute 1991). Generally, an additive error structure is selected if variability about a fitted growth curve appears constant, and a multiplicative error structure is selected when the variability increases. Other error structures have been developed that specify variation as a function of size or age (Francis 1988b). Some functional variance forms are later derived in section 4.7. Analysis of residuals after fitting a growth model is the most important tool in checking for acceptable error structure and model fit. An inappropriate error structure is indicated by decreasing or increasing variation as a function of the independent variable or predicted dependent variable of the growth model. Lack of model fit is indicated by patterns in the residuals away from the origin.

If the probability distribution for the error structure is modeled, the likelihood of the parameters can be determined given the data. An error structure that produces a higher likelihood than another is preferred when the number of parameters is the same. An example of this approach using the normal probability distribution showed that a model with a constant coefficient of variation was preferred to one with a constant variance (Kingsley 1979).

The final decision is to choose the most parsimonious model (i.e., the model that fits the data acceptably with the fewest number of parameters). When one of two competing models is a submodel of the other (i.e., nested), a statistical comparison can be made with an F test as in Schnute's approach, with likelihood ratio tests when a probability distribution of the error structure is specified (section 4.5.2), or with Kappenman's procedure (section 4.5.2). Other comparative situations should rarely occur. However,

should one want to compare a three-parameter Gompertz model with a four-parameter LVB model, then the above procedures should be at least approximately valid.

The Akaike information criterion (AIC) is also a means of selecting the best model, even when the models are not hierarchical (Akaike 1973, Buckland et al. 1993). The AIC is defined as

$$AIC = -2 \ln \mathcal{L} + 2p,$$

where $\ln \mathcal{L}$ is the log likelihood evaluated at the maximum likelihood estimates, and p is the number of model parameters. The AIC is calculated for candidate models, and the most parsimonious one has the lowest AIC. If one compares two nested models with a difference of one parameter with the AIC, this is equivalent to a likelihood ratio test (see section 4.5.2) at significance level 0.157 (Buckland et al. 1993).

An alternative criterion is the Bayesian information criterion (BIC; Akaike 1973, Adkison et al. 1996), defined as

$$BIC = -2 \ln \mathcal{L} + p \ln(n),$$

where n is the number of observations. The BIC forms an approximation to Bayes factors, an important consideration when the model is to be used for forecasting. The AIC tends to be a conservative criterion in that a model with more parameters results than when using the BIC or likelihood ratio tests, but the BIC is more likely to result in a parsimonious model.

4.5.2. Comparing Different Data Sets

This section presents various methods for comparing growth models from different data sets. Classical methods of comparison (Rao 1958, Allen 1976, Misra 1980) involve linearization of growth curves, using techniques of the general linear model (Draper and Smith 1981). We emphasize techniques appropriate to the nonlinear nature of most growth curves. Cerrato (1990) provided a convenient summary of many of the methods listed below as applied to the LVB model. Using bivariate confidence interval and Monte Carlo methods, he concluded that the likelihood ratio procedure (see “Likelihood ratio tests,” below) is the preferred procedure.

Before discussing various approaches, it should first be mentioned that there are essentially four different estimation approaches to be used in conjunction with hypothesis testing, depending on the equality of model variances and the equality of growth parameters among the different data sets. Let Θ_i be the parameter set and σ_i^2 be the model variance for the i th data set. The variances $\{\sigma_i^2\}$ are referred to as “nuisance” parameters in the statistical literature, as they are usually not explicitly estimated but rather fall out of the estimation process. The four estimation approaches, explained in greater detail in the section “Likelihood ratio tests” below, are:

Approach 1. Different variances σ_i^2 , different parameter sets Θ_i : a separate regression is done for each data set.

Approach 2. Different variances σ_i^2 , common parameter set Θ : the likelihood is directly maximized, or a common regression is performed with the technique of iteratively reweighted least squares.

Approach 3. Common variance σ^2 , different parameter sets Θ_i : a common regression is done with each data set having its own parameter set. Alternatively,

results from separate regressions can be used. The growth parameter estimates are identical to approach 1, and the variance estimate can be calculated by pooling the RSS from the data sets.

Approach 4. Common variance σ^2 , common parameter set Θ : in this situation, a common regression is done by pooling the data sets.

Generally, it is most appropriate to compare approaches 1 and 2 or approaches 3 and 4, as these pairs treat model variance among the data sets in the same way. For these comparisons, the null hypothesis is that growth parameters are constant across data sets. Whether to compare approaches 1 and 2 or approaches 3 and 4 depends on the equality of variances, which can be tested with standard multisample variance tests (Seber 1984). Unfortunately, these variance tests are not robust to departures from the underlying normality assumption. It is also tempting to compare approaches 1 and 4 because they both use the same regression technique, only with different data sets. In this comparison, the null hypothesis is that both growth parameters and variances are constant across data sets.

One-parameter tests

One may wish to compare individual parameters of a growth model between two different data sets; for example, the growth parameter κ between two data sets. Suppose that a parameter θ is of interest. Let θ_i be from the i th data set, with estimate $\hat{\theta}_i$ and estimated standard error s_i . Sample size of each data set is n_i , resulting in $f_i = n_i - p$ degrees of freedom, where p is the number of parameters in the growth model. The goal is to test the null hypothesis $H_0 : \theta_1 = \theta_2 = \theta$ versus $H_a : \theta_1 \neq \theta_2$ at significance level α . There is no simple analog of the common t statistic (based on a pooled variance) for this problem because the parameter estimates are not averages of data. The Fisher-Behrens statistic

$$z = \frac{|\hat{\theta}_1 - \hat{\theta}_2|}{\sqrt{s_1^2 + s_2^2}} \quad (4.52)$$

is used for comparisons for which it need not be assumed that variance is constant. This statistic is compared to the critical value of a normal distribution, $z_{1-\alpha/2}$ (Kingsley 1979), or a t distribution, $t_{1-\alpha/2, f}$ (Cerrato 1990), where f , the overall degrees of freedom, is calculated from

$$f = \left[\frac{1}{f_1} \left(\frac{s_1^2}{s_1^2 + s_2^2} \right)^2 + \frac{1}{f_2} \left(\frac{s_2^2}{s_1^2 + s_2^2} \right)^2 \right]^{-1}.$$

One-sided hypotheses can be constructed in an analogous manner. The test is asymptotically correct.

A large-sample chi-square test (Rao 1973) can be used when the sample size is large, as often happens in growth studies. Furthermore, the chi-square test is appropriate for comparing multiple data sets. It can be shown that this test is equivalent to the preceding test when two data sets are compared.

Let the previous notation be generalized for R data sets. The goal is to test at significance level α the null hypothesis $H_0 : \theta_1 = \theta_2 = \dots = \theta_R = \theta$ versus

$H_a : \theta_i \neq \theta_j$ for at least one pair (i, j) . A pooled estimate from the R data sets is computed as

$$\widehat{\theta}_p = \left(\sum_{i=1}^R \frac{\widehat{\theta}_i}{s_i^2} \right) / \left(\sum_{i=1}^R \frac{1}{s_i^2} \right),$$

the minimum-variance estimator of θ when the null hypothesis of equality is true. The test statistic

$$\chi^2 = \sum_{i=1}^R \frac{(\widehat{\theta}_i - \widehat{\theta}_p)^2}{s_i^2} \quad (4.53)$$

is asymptotically distributed as a χ^2 random variable with $R - 1$ degrees of freedom. The null hypothesis of equality is rejected if χ^2 is greater than the appropriate χ^2 critical value.

For the LVB model, Gallucci and Quinn (1979) suggested using the parameter $\omega = \kappa L_\infty$ for a more robust test than using either κ or L_∞ , because their estimates are strongly negatively correlated. Because ω is the projected growth rate at the origin t_0 , the omega test is especially appropriate when data sets do not reach the estimated asymptotic length \widehat{L}_∞ . Kingsley (1979) suggested that multivariate tests were more appropriate, in part because he observed a negative correlation between $\widehat{\omega}$ and $\widehat{\kappa}$. Gallucci and Quinn (1979) responded that multivariate tests are not robust when normality is not present. Appeldoorn (1982) found ω a useful parameter for comparing growth of a species on a latitudinal axis.

To use ω with the Rao chi-square test, the standard error of $\widehat{\omega}$ is calculated from the delta method approximation of the variance of a product (Seber 1982)

$$\text{CV}^2(\widehat{\omega}) = \text{CV}^2(\widehat{\kappa}) + \text{CV}^2(\widehat{L}_\infty) + 2\widehat{\rho} \text{CV}(\widehat{\kappa}) \text{CV}(\widehat{L}_\infty),$$

where CV, the coefficient of variation, is the standard error divided by the estimate, and $\widehat{\rho}$ is the estimated correlation between $\widehat{\kappa}$ and \widehat{L}_∞ . Alternatively, the standard error of $\widehat{\omega}$ can be estimated by reparameterizing the growth curve in terms of ω and κ and estimating ω directly by nonlinear least squares.

If all parameters of a growth model are to be compared one at a time for an overall test of equality of growth, the analyst may wish to adjust the significance level α of each individual test. This adjustment is made because the chances of making an error are increased with repeated testing. The simplest adjustment makes use of the Bonferroni inequality to set the individual significance level at $\alpha_p = \alpha/p$ for each of the p tests (Miller 1966). The overall significance level for the set of p tests will be lower than α . Various range and multiple comparisons tests in the case of several data sets have better performance (Miller 1966). For example, the Duncan procedure uses an error rate α_p that satisfies $\alpha = 1 - (1 - \alpha_p)^p$, which is exact when comparisons are independent.

F test

The F test is analogous to Schnute's comparison of models in section 4.3.5 and is analogous to the general linear model approach of comparing models (Neter et al. 1989). This approach assumes that the variance parameter σ^2 is constant across data sets. A "full" model consists of separate parameters for each data set. A "reduced" model consists of sets of common parameters among some data sets. If a reduced

model is not significantly different from the full model, the reduced model is selected as the best model. Data sets with common parameters are said to be statistically similar.

The most common situation is when the full model consists of different parameters for all data sets and the reduced model consists of common parameters among data sets. Suppose that the growth model has p parameters, denoted $\Theta = (\theta_1, \dots, \theta_p)'$, where the prime denotes the transpose of a vector. The goal is to test at significance level α the null hypothesis $H_0 : \Theta_1 = \Theta_2 = \dots = \Theta_R = \Theta$ versus $H_a : \Theta_i \neq \Theta_j$ for at least one pair (i, j) .

Let RSS_i be the residual sum of squares from fitting a growth model to the i th data set with n_i observations (from approach 3 above). The residual degrees of freedom, f_i , is then $n_i - p$. The sum of squares for the full model is

$$\text{RSS}_x = \sum_{i=1}^R \text{RSS}_i$$

with residual degrees of freedom

$$f_x = \sum_{i=1}^R f_i = n - Rp,$$

where n is the combined number of observations. The residual mean square is

$$\hat{\sigma}_x^2 = \text{RSS}_x/f_x.$$

In contrast, the reduced model, which corresponds to the null hypothesis of equality, is fitted by pooling all data sets and estimating a single set of parameters (from approach 4 above). Its residual sum of squares is denoted RSS_y with residual degrees of freedom $f_y = n - p$.

The F statistic from (4.35)

$$F = \frac{\text{RSS}_y - \text{RSS}_x}{f_y - f_x} / \hat{\sigma}_x^2$$

is used to test the null hypothesis. The numerator degrees of freedom is $f_y - f_x = (R - 1)p$, and the denominator degrees of freedom is $f_x = n - Rp$. The test is asymptotically correct when variance is constant among data sets (Cerrato 1990). To find which data sets differ, comparisons among subsets of the data can be made.

Sample reuse method

The sample reuse method provides a unique method for comparing different data sets, as presented by Kappenman (1981). This method is a departure from classical hypothesis testing in that no level of significance is used for the test. The method chooses as the best model the one that best predicts data when data points are omitted from the data set one at a time.

Suppose that there are two data sets and that the null hypothesis is that the data come from one population (reduced model) versus the alternative that they come from two populations (full model). For data set i , the j th observation, Y_{ij} , is removed, and

the growth model is fitted to the remaining data. Let \widehat{Y}_{ij} be the predicted value of the deleted observation. Compute the squared deviation of prediction error for each data set as

$$D_{2i} = \sum_{j=1}^{n_i} (Y_{ij} - \widehat{Y}_{ij})^2,$$

and combine the two for the total prediction error for the full model,

$$D_2 = D_{21} + D_{22}. \quad (4.54)$$

For the reduced model, pool the data and carry out the same procedure, omitting one observation at a time. Let D_1 be the prediction error for the pooled data. The test of hypothesis is simply to choose H_0 that there is one population if $D_1 < D_2$ and to choose H_a that there are two populations if $D_2 < D_1$.

The simplicity of this approach is appealing, in that the best model is the one that best predicts the data when omitted one at a time. The procedure is computationally time-consuming for nonlinear models because nonlinear least squares would have to be performed for each deleted data set. This amounts to performing $2n$ nonlinear regressions compared to just one to three with other approaches. Kappenman's method is easily generalized to R data sets. Finally, the procedure can be used also to compare two models for a single data set. The best model is the one that best predicts the data when each data point is omitted one at a time.

In the same spirit of the sample reuse approach, randomization tests (Edgington 1980, Hagen and Quinn 1991) can be used to determine whether the full model is better than the reduced model. The difference of the RSSs or the F statistic given above could be the statistic of interest, and the pooled data set would be randomly sampled into two data sets with sample sizes equal to the original sets. The random sampling process would be replicated many times, and the null hypothesis would be rejected if the original statistic was at the extreme end of the empirical distribution of the statistic from the replications.

Likelihood ratio tests

Tests of equality of parameters between data sets based on the theory of likelihood ratio tests have been constructed by Kimura (1980), Cohen and Fishman (1980), Kirkwood (1983), and Cerrato (1990). The likelihood of parameter estimates given the data is constructed from an assumed probability distribution for the data. Parameter estimates that maximize the likelihood are termed maximum likelihood estimates (MLE). Likelihood ratio tests are constructed from the ratio of the likelihoods of MLEs for full and reduced models. A significant ratio indicates that a reduced model is not statistically similar to the full model, so that the full model remains the best model. Likelihood ratio tests can be used to compare a full model with a reduced model for a single data set (analogous to the F test in section 4.3.5) or to compare a single growth model among two or more data sets, as now shown. Let \widehat{Y}_{ij} be the predicted size from a model with parameter vector Θ_i for observation j of the i th data set, as before. Likelihoods are derived for each of the four approaches described in this section, and then likelihood ratio tests are constructed. Only the normal distribution is used, but other distributions can be used analogously.

Full models In approach 1, there are different variances, σ_i^2 , and different parameter sets, Θ_i . By assuming a normal distribution with additive error for the growth data and different variances σ_i^2 among data sets, the likelihood of the parameters given data set i is

$$\mathcal{L}_i(\Theta_i, \sigma_i | \{Y_i\}) = (2\pi\sigma_i^2)^{-n_i/2} \exp\left[-\frac{1}{2\sigma_i^2} \sum_{j=1}^{n_i} (Y_{ij} - \hat{Y}_{ij})^2\right]. \quad (4.55)$$

The likelihood, \mathcal{L}_i , for this problem is maximized by minimizing the sum of squares, as demonstrated in earlier sections. As the likelihood can be a very small number for a large sample size, it is generally best to do calculations on a log scale. The MLE's, $\hat{\Theta}_i$, are then substituted into (4.55) to calculate the maximum log likelihood, resulting in

$$\max \ln \mathcal{L}_i(\hat{\Theta}_i, \hat{\sigma}_i | \{Y_i\}) = -\frac{n_i}{2} \left[\ln(2\pi\hat{\sigma}_i^2) + 1 \right], \quad (4.56)$$

where the MLE of σ_i^2 is

$$\hat{\sigma}_i^2 = \sum (Y_{ij} - \hat{Y}_{ij})^2 / n_i = \text{RSS}_i / n_i.$$

The joint maximum log likelihood $\ln \mathcal{L}_F$ for the full model is then

$$\ln \mathcal{L}_F = \sum \max \ln \mathcal{L}_i.$$

In approach 3, there is common variance, σ^2 , and different parameter sets, Θ_i . In this case, a pooled estimate of variance $\hat{\sigma}^2 = \sum_i \text{RSS}_i / n$ from separate regressions with different parameter sets is used in place of $\hat{\sigma}_i^2$ in (4.55). The parameter estimates are identical with those from approach 1. The maximum log likelihood $\ln \mathcal{L}_F$ for this full model is obtained from (4.56) with n_i and $\hat{\sigma}_i^2$ replaced by n and $\hat{\sigma}^2$.

Reduced models In approach 2, there are different variances, σ_i^2 , and a common parameter set, Θ . For this reduced model, it is necessary to maximize the log likelihood (4.55) directly, which is equivalent to minimizing an adjusted sum of squares

$$S' = \sum_{i=1}^R \frac{1}{\sigma_i^2} \sum_{j=1}^{n_i} (Y_{ij} - \hat{Y}_{ij})^2 = \sum_{i=1}^R \frac{1}{\sigma_i^2} \text{RSS}_i.$$

The optimization can be done directly with respect to Θ and the σ_i^2 with appropriate software.

Alternatively, the method of iteratively reweighted least squares utilizes nonlinear least squares software, by performing the nonlinear regression given the variance estimates, calculating the variance estimates from the regression, and iterating until the process converges. With two data sets, this can be accomplished as follows: let $\lambda^2 = \sigma_1^2 / \sigma_2^2$ and estimate this from the ratio of residual mean squares or variances by doing separate regressions. Adjust the second data set and model by multiplying by λ . Perform a standard nonlinear regression with the adjusted data set to get parameter estimates, new residual mean squares or variances, and an updated estimate of λ . Repeat until convergence is obtained. The maximum log likelihood $\ln \mathcal{L}_R$ for the reduced

model is calculated analogously to the full model by substituting variance estimates $\hat{\sigma}_i^2 = \text{RSS}_i/n_i$ into (4.56) and then summing across data sets.

In approach 4, there is common variance, σ^2 , and a common parameter set, Θ . When variance is constant among data sets, the likelihood for the reduced model is constructed from (4.55), only without subscripts on common parameters. Parameter estimates are obtained from pooled data and nonlinear least squares. The maximum likelihood $\ln \mathcal{L}_R$ is obtained from (4.56) with n_i and $\hat{\sigma}_i^2$ replaced by n and $\hat{\sigma}^2$.

Tests The likelihood ratio test statistic is

$$\chi^2 = -2(\ln \mathcal{L}_R - \ln \mathcal{L}_F) = -2 \ln(\mathcal{L}_R/\mathcal{L}_F), \quad (4.57a)$$

which is thus proportional to the logarithm of the ratio of the likelihoods. The asymptotic distribution is a chi-square distribution with degrees of freedom equal to the difference in the degrees of freedom between the full and reduced models. If the test statistic is greater than the χ^2 critical value, the hypothesis of equality is rejected.

Suppose that approaches 1 and 2 or approaches 3 and 4 are to be compared among R data sets. The hypothesis test is $H_0 : \Theta_i = \Theta_j$ for all pairs (i, j) versus $H_a : \Theta_i \neq \Theta_j$ for at least one pair (i, j) . There are $f = Rp - p = (R - 1)p$ degrees of freedom.

Suppose that approaches 1 and 4 are to be compared. The hypothesis test is $H_0 : \Theta_i = \Theta_j; \sigma_i^2 = \sigma_j^2$ for all pairs (i, j) versus $H_a : \Theta_i \neq \Theta_j; \sigma_i^2 \neq \sigma_j^2$ for at least one pair (i, j) . The null hypothesis is that both variances and growth parameters are the same among data sets; the alternative hypothesis is that either the variance or one growth parameter differs among data sets. There are $f = R(p+1) - (p+1) = (R-1)(p+1)$ degrees of freedom for this test.

Alternatively, Cerrato (1990) noted that the modified test statistic

$$F = \frac{n - f - p}{f} (e^{\chi^2/n} - 1), \quad (4.57b)$$

using χ^2 calculated in (4.57a), is asymptotically distributed as an F distribution with f and $n - f - p$ degrees of freedom. This modified statistic is applicable to comparisons of approaches 1 and 2 or approaches 3 and 4. In the situation of constant variance (approaches 3 and 4), this test simplifies to the F test given above (Cerrato 1990).

This approach is applicable for any probability distribution by developing the appropriate likelihood. Kingsley (1979) constructed likelihoods for a model with a constant CV rather than a constant variance. Cohen and Fishman (1980) showed how to develop a factorial analysis for comparison of growth parameters among multiple factors, such as sex and subspecies.

Hotelling's T^2 tests

Multiparameter analogues to the one-parameter, two-sample test in equation (4.52) have been developed by Kingsley (1979), Bernard (1981), and Cerrato (1990). All approaches assume that a set of parameter estimates are distributed as multivariate normal distributions and use Hotelling's T^2 statistic from multivariate methods (Mardia et al. 1979, Seber 1984) as the basis of the test.

Bernard's (1981) approach is an attempt to develop an analogue to the one-parameter t test to compare LVB model parameters, assuming that the variance-covariance matrices of the estimates are identical. He presents a formula for pooled

variance–covariance of the estimates and for the variance of the difference of parameter estimates for two data sets. However, the variance of estimates from a nonlinear least squares procedure is not analogous to the variance of a set of individual multivariate observations, which leads to a test statistic that is likely too large. The following approach is derived from his approach, correcting this problem and generalizing it to any growth model.

Let Θ_1 and Θ_2 be column vectors of p parameters from a growth model. Fitting the growth model to two data sets with n_1 and n_2 observations produces the estimates $\widehat{\Theta}_1$ and $\widehat{\Theta}_2$, with estimated variance–covariance matrices $\widehat{\mathbf{S}}_1$ and $\widehat{\mathbf{S}}_2$. The residual degrees of freedom for each data set is $f_i = n_i - p$. Let $n = n_1 + n_2$ and $f = f_1 + f_2$. The theory of nonlinear least squares indicates that the asymptotic distribution of $\widehat{\Theta}_i$ is multivariate normal with mean Θ_i and variance–covariance matrix Σ_i/n_i (Seber and Wild 1989). Thus an estimate of Σ_i is $\widehat{\Sigma}_i = n_i \widehat{\mathbf{S}}_i$.

The structure of comparing two populations is now similar to the standard multivariate comparison of two populations (Seber 1984), where $\widehat{\Theta}_i$ is used in place of each mean and $\widehat{\Sigma}_i$ is used in place of the variance–covariance matrix for an individual vector. Assuming that the underlying asymptotic matrices Σ_i are identical ($\Sigma_i = \Sigma$), a pooled estimate $\widehat{\Sigma}$ weights by the residual degrees of freedom of each data set, or

$$\widehat{\Sigma} = \frac{f_1}{f} \widehat{\Sigma}_1 + \frac{f_2}{f} \widehat{\Sigma}_2 = \frac{f_1}{f} n_1 \widehat{\mathbf{S}}_1 + \frac{f_2}{f} n_2 \widehat{\mathbf{S}}_2. \quad (4.58)$$

Let $\widehat{\Delta\Theta} = \widehat{\Theta}_1 - \widehat{\Theta}_2$. The estimated variance–covariance matrix of $\widehat{\Delta\Theta}$ is

$$\widehat{\mathbf{V}} = \widehat{\text{Var}}(\widehat{\Delta\Theta}) = \left(\frac{1}{n_1} + \frac{1}{n_2} \right) \widehat{\Sigma},$$

assuming that each data set is independent. This equation simplifies to

$$\widehat{\mathbf{V}} = 2\widehat{\mathbf{S}} + \frac{n_1 - n_2}{n_1 n_2} \left(\frac{f_1}{f} n_1 \widehat{\mathbf{S}}_1 - \frac{f_2}{f} n_2 \widehat{\mathbf{S}}_2 \right), \quad (4.59)$$

where $\widehat{\mathbf{S}}$ is an average of the two estimated variance–covariance matrices weighted by degrees of freedom, or

$$\widehat{\mathbf{S}} = \frac{f_1}{f} \widehat{\mathbf{S}}_1 + \frac{f_2}{f} \widehat{\mathbf{S}}_2. \quad (4.60)$$

The matrix $\widehat{\mathbf{V}}$ reduces to $2\widehat{\mathbf{S}}$ when sample sizes are the same ($n_1 = n_2$). The Hotelling T^2 statistic from Seber (1984) is then

$$T_1^2 = (\widehat{\Delta\Theta})' (\widehat{\mathbf{V}})^{-1} (\widehat{\Delta\Theta}). \quad (4.61)$$

The null hypothesis $H_0 : \Theta_1 = \Theta_2$ versus $H_a : \Theta_1 \neq \Theta_2$ is rejected if $T_1^2 > T_{1-\alpha}^{*2}$, where

$$T_{1-\alpha}^{*2} = \frac{fp}{f-p+1} F(p, f-p+1)_{1-\alpha}, \quad (4.62)$$

where $f = n - 2p$ and $F(p, f-p+1)_{1-\alpha}$ is the appropriate tabled F critical value. Simultaneous Roy-Bose confidence intervals are suggested by Bernard (1981) to determine which parameter differences are most important, given by

$$\widehat{\Delta\theta_j} \pm T_{1-\alpha}^* \sqrt{v_j},$$

where $\sqrt{v_j}$ is pooled standard error of the j th difference of parameter estimates, obtained by taking the square root of the j th diagonal element of $\widehat{\mathbf{V}}$. Bernard discussed the assumptions underlying the Hotelling T^2 test, pointing out that the test is robust to non-normality when large data sets are collected. Seber (1984) discussed the robustness of the general multivariate comparison procedure. The robustness to non-normality is good for a variety of alternative distributions, and robustness to the common Σ assumption is good when sample sizes are close.

Bernard also suggested calculating

$$F_{0i} = \frac{(\hat{\theta}_{i1} - \hat{\theta}_{i2})^2}{v_i} \frac{f - p + 1}{fp}$$

as a relative index of the importance of each parameter i . The most important parameters contributing to growth differences have the largest F_{0i} values.

The assumption of common Σ matrices needs not be made, as shown by Kingsley (1979). This assumption is probably invalid when a large discrepancy in sample sizes occurs between data sets. Kingsley's approach is a multivariate generalization of the Fisher-Behrens statistic (4.52). To carry out this test, a vector, ν , must be found to maximize the Hotelling T_2^2 statistic given by

$$T_2^2 = \frac{\nu'(\widehat{\Delta\Theta})(\widehat{\Delta\Theta})'\nu}{\nu'\widehat{\mathbf{S}}_1\nu + \nu'\widehat{\mathbf{S}}_2\nu}, \quad (4.63)$$

which is given by the leading eigenvector of $(\widehat{\mathbf{S}}_1 + \widehat{\mathbf{S}}_2)^{-1}(\widehat{\Delta\Theta})(\widehat{\Delta\Theta})'$. The statistic T_2^2/p is compared with the critical value of the F table with numerator degrees of freedom, p , and the smaller of $n_1 - p$ and $n_2 - p$ as the denominator degrees of freedom. The test is conservative for these degrees of freedom. Kingsley (1979) presented an example of this approach applied to polar bear data.

An alternative approach when variance-covariance matrices are unequal was given by Cerrato (1990). The approach is also a generalization of the one-parameter Fisher-Behrens statistic (4.52). The variance-covariance matrix of $\widehat{\Delta\Theta}$ is $\widehat{\mathbf{V}}_3 = \widehat{\mathbf{S}}_1 + \widehat{\mathbf{S}}_2$ and the test statistic is

$$T_3^2 = (\widehat{\Delta\Theta})'\widehat{\mathbf{V}}_3^{-1}(\widehat{\Delta\Theta}). \quad (4.64)$$

For a growth model with p parameters, the residual degrees of freedom for each data set is $f_i = n_i - p$. The effective overall degrees of freedom, f , to use as suggested by Cerrato can be found from

$$f^{-1} = \frac{1}{f_1} \left(\frac{(\widehat{\Delta\Theta})'\widehat{\mathbf{V}}_3^{-1}\widehat{\mathbf{S}}_1\widehat{\mathbf{V}}_3^{-1}(\widehat{\Delta\Theta})}{T_3^2} \right)^2 + \frac{1}{f_2} \left(\frac{(\widehat{\Delta\Theta})'\widehat{\mathbf{V}}_3^{-1}\widehat{\mathbf{S}}_2\widehat{\mathbf{V}}_3^{-1}(\widehat{\Delta\Theta})}{T_3^2} \right)^2 \quad (4.65)$$

and f lies between the smaller of f_1 and f_2 and their sum $f_1 + f_2$. The null hypothesis $H_0 : \Theta_1 = \Theta_2$ versus $H_a : \Theta_1 \neq \Theta_2$ is rejected if $T_3^2 > T_{1-\alpha}^{*2}$, where $T_{1-\alpha}^{*2}$ is given in (4.62). This approach does not require the calculation of an eigenvector, which makes it easier to apply than Kingsley's approach.

Presumably, these tests with unequal variance–covariance matrices would be poorer than the common matrix approach when the common matrix assumption is valid (Seber 1984). However, if the Σ_i matrices are quite dissimilar, these tests should be far better.

Several tests of common matrices exist, but many are nonrobust to the presence of nonnormal distributions (Seber 1984). Also, the asymptotic distribution of $\widehat{\Sigma}_i$ for a nonlinear model is unknown (G.A.F. Seber, 1993, personal communication). Given these caveats, a likelihood ratio test of $H_0 : \Sigma_1 = \Sigma_2$ has the test statistic

$$\chi^2 = n \ln(\det \widehat{\Sigma}) - [n_1 \ln(\det \widehat{\Sigma}_1) + n_2 \ln(\det \widehat{\Sigma}_2)],$$

where \det stands for determinant. Under the null hypothesis, the test statistic for linear models has a χ^2 distribution with $p(p+1)/2$ degrees of freedom, and p is the number of parameters of the growth model.

Example 4.7. Rougheye rockfish females and males

The length–age data set used in section 4.2 for rougheye rockfish (table 4.3) comprises both females and males; the null hypothesis is that the growth of both sexes is the same. Figure 4.4 suggests that females may grow faster and become larger than males, but a statistical test is needed to confirm this observation. The LVB model used in section 4.2 for the pooled data is again used; two parameterizations are examined: $\{L_\infty, \kappa, t_0\}$ and $\{l_1, l_2, \kappa\}$ (Schnute case 5). To provide the necessary parameter estimates and summary statistics, each of the four estimation approaches at the start of section 4.5.2 is applied to the data. Approaches 1 and 2 (with different variances σ_i^2) are summarized in table 4.13; approaches 3 and 4 (with common variance σ^2) are summarized in table 4.14. Approaches 1 and 3 have different parameters by sex; approaches 2 and 4 have common parameters. Fits for the two parameterizations and estimates of common parameter κ are essentially identical for each estimation approach.

The results illustrate some features of the estimation approaches. Approach 1, which uses different regressions for each sex, provides an estimate of the ratio of variances λ of 0.9015. Approach 2, which uses this initial estimate in iteratively reweighted least squares, converges to a similar estimate of 0.9046. Approach 3, with a common variance and different parameters between sexes, has identical parameter estimates and residual statistics as approach 1, but the standard errors of the estimates differ because of the differences between the individual and common variance estimates. Some minor differences in parameter estimates occur between approaches 2 and 4; the differences are more apparent in the $\{L_\infty, \kappa, t_0\}$ parameterization. Standard errors are quite similar, and the residual sums of squares are close. Bartlett's test of equality of variance ($F = 18.31/14.88 = 1.23$ with 250 and 289 degrees of freedom) is not significant ($P = .092$), suggesting that approaches 3 and 4 are appropriate.

For purposes of illustration, both the different variances and common variance approaches are used in the tests below. The necessary intermediate calculations and test statistics of the single parameter, F , and likelihood ratio tests are given in tables 4.13 (different variances) and 4.14 (common variance). The Hotelling T^2 test calculations are in tables 4.15 and 4.16. The sample reuse method is not used, because of the large number of nonlinear regressions required.

Single-parameter tests: Using the methods of that section, z and χ^2 statistics are calculated for $L_\infty, \kappa, t_0, \omega, l_1$, and l_2 . P values are identical for the two test statistics,

Table 4.13. Parameter estimates and summary statistics of nonlinear least squares fits to rougheye rockfish data classified by sex.

Parameter	Approach 1			Approach 2		
	Female	SE	Male	SE	Pooled	SE
n	253		292		545	
L_∞	57.81	1.38	53.40	0.93	55.12	0.77
κ	0.0430	0.0035	0.0527	0.0038	0.0488	0.0026
t_0	-5.474	0.788	-4.086	0.700	-4.602	0.518
$r(L_\infty, \kappa)$	-0.935		-0.882		-0.908	
ω	2.49	0.15	2.81	0.16	2.69	0.11
l_1	15.90	0.76	14.66	0.84	15.17	0.57
l_2	57.05	1.14	53.12	0.84	54.69	0.68
<i>F</i> test						
Separate parameters; approach 1 (full model)						
RSS	3764.6		5346.6			
f	250		289			
RMS	15.1		18.5			
σ^2	14.88		18.31		0.9015 = λ	
Common parameters; approach 2 (reduced model)						
σ^2	15.23		18.61		0.9046 = λ	
RSS	3852.6		5433.7		9286.3	
f	250		289		542	
RMS	15.4		18.8		17.1	
<u>Full model</u>			<u>Reduced model</u>			
RSS	9111.2				9286.3	
f	539				542	
RMS	16.9					
F	3.45					
$F_{\text{crit}}(3,539)$	2.62					
P -value	0.016					
Univariate tests						
	z	P	$\hat{\theta}_p$	χ^2	P	
L_∞	2.65	.008	54.78	7.02	.008	
κ	1.88	.060	0.0475	3.53	.060	
t_0	1.32	.188	-4.698	1.73	.188	
ω	1.50	.134	2.64	2.24	.134	
l_1	1.09	.274	15.34	1.20	.274	
l_2	2.78	.006	54.50	7.70	.006	
z_{crit}	1.96					
f	449					
χ^2_{crit}	3.84					
Likelihood ratio test						
	Female		Male			
Max ln \mathcal{L}	-702.051		-840.327			
Full		-1542.38				
Max ln \mathcal{L}	-704.973		-842.687			
Reduced		-1547.66				
χ^2	10.56		F^*		3.52	
χ^2_{crit}	7.81		$F_{\text{crit}}(3,539)$		2.62	
P	.014				.015	

In approach 1, separate regressions for females and males were made; in approach 2, iteratively reweighted least squares was used.

Table 4.14. Parameter estimates and summary statistics of nonlinear least squares fits to rough-eye rockfish data classified by sex.

Parameter	Approach 3				Approach 4	
	Female	SE	Male	SE	Pooled	SE
n	253		292		545	
L_{∞}	57.81	1.46	53.40	0.89	54.91	0.76
κ	0.0430	0.0037	0.0527	0.0037	0.0492	0.0026
t_0	-5.474	0.835	-4.086	0.669	-4.538	0.517
$r(L_{\infty}, \kappa)$	-0.935		-0.882		-0.905	
ω	2.49	0.16	2.81	0.16	2.70	0.11
l_1	15.89	0.81	14.65	0.80	15.12	0.58
l_2	57.04	1.21	53.12	0.80	54.51	0.67
<i>F</i> test						
RSS	3764.6		5346.6		9284.3	
f	250		289		542	
	Full model			Reduced model		
RSS	9111.2				9284.3	
f	539				542	
RMS	16.9					
F	3.41					
$F_{\text{crit}}(3,539)$	2.62					
P	.017					
Univariate Tests						
	z	P	$\hat{\theta}_p$	χ^2	P	
L_{∞}	2.57	.010	54.60	6.63	.010	
κ	1.86	.063	0.0479	3.46	.063	
t_0	1.30	.195	-4.628	1.68	.195	
ω	1.48	.138	2.65	2.20	.138	
l_1	1.09	.276	15.27	1.19	.276	
l_2	2.70	.007	54.32	7.30	.007	
z_{crit}	1.96					
f	420					
χ^2_{crit}	3.84					
Likelihood ratio test						
	Female		Male			
max ln \mathcal{L}	-715.176		-825.651			
Full		-1540.83				
Reduced		-1545.94				
χ^2	10.2			F^*	3.41	
χ^2_{crit}	3.84			$F_{\text{crit}}(3,539)$	2.62	
P	.017				.017	

The variance of males and females was assumed constant. Approach 3 has separate parameters by sex, and approach 4 has common parameters.

a consequence of comparing exactly two data sets. Only L_∞ and l_2 are significant at $\alpha = 0.05$. For an experimentwise level of $\alpha = 0.05$ for all six tests, the appropriate α_p level is $0.05/6 = 0.008$ (Bonferroni) or $1 - 0.95^{1/6} = 0.009$ (Duncan). As l_2 is still significant, we conclude that there is evidence that growth differs between sexes.

F test: This test uses full and reduced model sum of squares in that section. The full model RSS is the same for approaches 1 and 3 because the parameter estimates are the same. The reduced model RSSs from approaches 2 and 4 differ slightly due to different parameter estimates. The RSS for approach 4 is slightly higher because a weighted sum of squares is used as the objective function. The *F* statistics are nearly the same for the two sets of approaches and indicate that a significant difference in growth occurs between the sexes ($P = .016\text{--}.017$).

Likelihood ratio test: This test uses MLEs of variance ($\hat{\sigma}_i^2$ or $\hat{\sigma}^2$) instead of residual mean squares, as shown in that section. Both the χ^2 and *F* statistics give similar *P* values. For the common variance approaches 3 and 4 in table 4.14, the *F* statistic is identical to the RSS *F* statistic, as expected by theory. For the different variances approaches 1 and 2 in table 4.13, the two *F* statistics differ, but only slightly. For any of the likelihood ratio statistics, a significant difference in growth occurs between the sexes ($P = .014\text{--}.017$).

Hotelling T^2 test: Calculations for formulae in that section are given in table 4.15 using parameter estimates from approach 1. Under the assumption of common Σ matrices, the Hotelling statistic produces a *P* value similar to previous approaches. Under the assumption of different Σ matrices, the effective degrees of freedom is somewhat lower ($f = 427$ versus 539) and the test statistic is slightly lower as well, leading to a larger *P* value. In either case, the null hypothesis of equality is rejected. Examination of the Roy-Bose confidence intervals and values of F_{0i} suggests that the parameter l_2 is different.

Table 4.16 summarizes the Hotelling statistics and *P* values for different estimation approaches and parameterizations. Also given is the result of the test for equal Σ matrices. The statistic T_3^2 based on different Σ matrices is logically not calculated for approach 3, which assumes common variance. *P* values are higher using the $\{L_\infty, \kappa, t_0\}$ parameterization, suggesting that parameterizations with high correlations perform poorer. In one case, the test statistic is no longer significant, showing that different conclusions can be reached depending on the parameterization. This result does not happen with the *F* test or likelihood ratio test, which are based on residual sums of squares or residual variances. This conclusion is supported by the work of Cerrato (1990) as well. Thus, a statistically stable parameterization should be used with the Hotelling T^2 approach.

Statistic T_3^2 has higher *P* values than statistic T_1^2 , suggesting that the assumption of a common Σ matrix has greater power. The *P* values using estimates from approach 3, which assumes common variance, are different (slightly higher) than those from approach 1, which shows that the common variance assumption and the common Σ matrix assumption are not equivalent.

The likelihood ratio test of equal Σ matrices is soundly rejected. This result favors the use of statistic T_3^2 over T_1^2 . However, the actual magnitudes of the matrices are not that dissimilar in table 4.15, and the theory of the test under nonlinear models is unknown. Fortunately, no discrepancy occurs in the test results using different approaches; hence, the hypothesis of common growth parameters is rejected.

Table 4.15. Hotelling T^2 calculations for the test of equality between sexes with parameters l_1 , l_2 , and κ for rougheye rockfish data in SE Alaska (Nelson and Quinn 1987).

Parameters	Female			Male		
l_1	15.900			14.660		
l_2	57.050			53.120		
κ	0.043			0.053		
Correlation matrix	1.000			1.000		
	0.468	1.000		0.427	1.000	
	-0.694	-0.909	1.000	-0.707	-0.857	1.000
S_i	5.78E-1	4.05E-1	-1.85E-3	7.06E-1	3.01E-1	-2.26E-3
	4.05E-1	1.30E+0	-3.63E-3	3.01E-1	7.06E-1	-2.74E-3
	-1.85E-3	-3.63E-3	1.23E-5	-2.26E-3	-2.74E-3	1.44E-5
Σ_i	1.46E+2	1.03E+2	-4.67E-1	2.06E+2	8.80E+1	-6.59E-1
	1.03E+2	3.29E+2	-9.18E-1		2.06E+2	-7.99E-1
	-4.67E-1	-9.18E-1	3.10E-3	-6.59E-1	-7.99E-1	4.22E-3
Σ	1.78E+2	9.48E+1	-5.70E-1			
	9.48E+1	2.63E+2	-8.54E-1			
	-5.70E-1	-8.54E-1	3.70E-3			
$\Delta\Theta$	1.240	$\Delta\Theta'$	1.240	3.930	-0.010	
	3.930					
	-0.010					

	Common variance assumption			Different variances assumption		
\mathbf{V}	1.31E+0	6.99E-1	-4.20E-3		1.28E+0	7.07E-1
	6.99E-1	1.94E+0	-6.30E-3		7.07E-1	2.01E+0
	-4.20E-3	-6.30E-3	2.73E-5		-4.10E-3	-6.36E-3
\mathbf{V}^{-1}	1.94E+0	1.09E+0	5.50E+2		1.99E+0	1.11E+0
	1.09E+0	2.67E+0	7.84E+2		1.11E+0	2.66E+0
	5.50E+2	7.84E+2	3.02E+5		5.70E+2	8.05E+2
T_1^2	10.261			T_3^2	9.717	
P -value	.017			P -value	.023	
Numerator f	3 = p			num. f	3	
Denominator f	537 = $f-p+1$			den. f	425	
F_{crit}	2.622			F_{crit}	2.626	
T^{*2}	7.894			T^{*2}	7.915	
Conclusion: reject H_0				Conclusion: reject H_0		
Roy-Bose intervals						
T^*	2.810					
	Lower	Upper		F_0		
Δl_1	-1.982	4.462		0.388		
Δl_2	0.017	7.843		2.644		
$\Delta \kappa$	-0.024	0.005		1.145		

Estimates are from approach 1.

Table 4.16. Hotelling T^2 test statistics and P values using approaches 1 and 3 for two parameterizations: $\{L_\infty, \kappa, t_0\}$ and $\{l_1, l_2, \kappa\}$, and test of equal Σ matrices.

	$\{L_\infty, \kappa, t_0\}$	$\{l_1, l_2, \kappa\}$
Approach 1: Different variances		
T_1^2	8.801	10.261
P	.033	.017
T_3^2	7.599	9.717
P	.058	.023
Approach 3: Common variance		
T_1^2	8.285	9.656
P	.042	.023
Test of common Σ matrices		
	Females	Males
$\det \Sigma_i$	9.461	18.044
χ^2	130.510	
χ^2_{crit}	12.592	
f	6	
P	.000	

Summary: All test results are remarkably similar in rejecting the null hypothesis of common growth parameters with a P value in the range .01–.03. If one accepts the hypothesis of common variance, then a comparison of approaches 3 and 4 with the F test (or equivalent likelihood ratio test) in table 4.14 is the most appropriate, which has a P value of .017. The significantly different growth parameter is length at the oldest age l_2 (or asymptotic length L_∞), suggesting that females grow to a larger size than males. The predicted growth curves by sex are shown in figure 4.4. ■

4.6. SCALE AND OTOLITH MEASUREMENTS

The use of scales for age and growth studies dates back to at least 1898 (Carlander 1987). A contemporary approach to collecting measurement data is to use measurements of scales or otoliths to predict age, length, or weight of fish. For example, the International Pacific Halibut Commission has collected only otoliths from its sampling program for several years and uses predictive regression to obtain Pacific halibut length and weight (Quinn et al. 1983a). In particular, otolith weight is a good predictor of both fish length and weight. Boehlert (1985) and Nelson and Quinn (1987) have successfully used otolith measurements to predict age for rockfish species. This is especially necessary for rockfish because they live to be very old, and direct aging is variable and costly in time and money. Several contemporary uses and models for otoliths and scales are given in the excellent volume by Summerfelt and Hall (1987). Models using scales or otoliths are drawn from previous models presented. Allometric or polynomial models are mostly used to establish relationships.

Back-calculation of sizes of a fish from annulus measurements is frequently undertaken to understand fish growth and processes affecting the fish's current size. Any hard part (e.g., scale, otolith, vertebra, fin ray) that exhibits annuli can be used for

back-calculation; we use the word "scale" as a generic term for such a hard part. If L_c is the size of fish at capture, S_c the corresponding scale size, and $\{S_t\}$ the scale annulus measurements, then the goal of back-calculation is to determine $\{L_t\}$, the corresponding lengths at each annulus. Care must be taken in simple extrapolation of earlier sizes because the relationship between annulus growth and fish growth may not be linear. Several papers propose and compare linear and nonlinear approaches (Ricker 1975a, Carlander 1981, Guteuter 1987, Weisberg and Frie 1987, Campana 1990, Casselman 1990, Francis 1990). Regardless of the problems with back-calculation, annulus measurements are useful as a proxy for fish growth. Annulus measurements can be analyzed for year-class and annual effects and related to environmental variables (Hagen and Quinn 1991).

Francis (1990) provided a critical review of back-calculation methods, showing that several commonly-used methods (one a regression approach) are flawed. In performing the method of back-calculation, the relationship between fish size and scale size must be specified: $f(L)$ is the possibly nonlinear relationship between mean scale size at a given fish size; $g(S)$ is the possibly nonlinear relationship between mean fish size at a given scale size. The function f is determined from a regression of S versus L ; the function g is determined from a regression of L versus S .

Francis (1990) provided two approaches based on simple, explicit hypotheses and derived equations from each approach that are statistically correct when the underlying hypothesis is true. The only way to choose between the two hypotheses is with a validation experiment because the empirical data described above do not make one hypothesis more likely than the other.

The first hypothesis, called the scale-proportional, is that if a scale from a fish captured is relatively larger than the average scale for a fish of that size, then the scale would be relatively larger than average throughout its life. Under this hypothesis, the ratio of the average scale size to the scale size of a particular fish is constant throughout its life; therefore

$$\frac{f(L_t)}{S_t} = \frac{f(L_c)}{S_c} \quad (4.66)$$

for any annulus t . This leads to the back-calculation relationships

$$f(L_t) = \frac{S_t}{S_c} f(L_c) \quad (4.67a)$$

$$\text{or} \quad L_t = f^{-1} \left[\frac{S_t}{S_c} f(L_c) \right], \quad (4.67b)$$

where f^{-1} is the inverse function of f .

The second hypothesis, called the body proportional, is that if a fish captured is relatively larger than the average fish with a given scale size, then the fish would be relatively larger than average throughout its life. Under this hypothesis, the ratio of the average fish size to the size of a particular fish at a given scale size is constant throughout its life; therefore

$$\frac{g(S_t)}{L_t} = \frac{g(S_c)}{L_c} \quad (4.68)$$

for any annulus t . This leads to the back-calculation relationship

$$L_t = \frac{g(S_t)}{g(S_c)} L_c. \quad (4.69)$$

Francis (1990) gave equations for the special case when the relationships are linear and showed how many historical approaches are special cases of the approaches above. He also gave examples, discussed validation and heteroscedasticity, and discussed the need for hypothesis testing and extensions of back-calculation models.

Lee's phenomenon occurs when back-calculated lengths at a given age are observed to decrease with increasing age of the fish used in the back-calculation (Lee 1912, Ricker 1975a), which leads to the somewhat counter-intuitive impression that older, bigger fish are slower growing. This phenomenon is observed either because it really happens [Ricker (1975a) gave an argument based on natural selection], because of size-selective mortality [see Ricker (1975a) and below], or because of error caused by back-calculation (see below).

Some other notable essays related to back-calculation can be culled from a sizable literature. Carlander (1981) showed intuitively why the regression method of back-calculation is flawed. Gutreuter (1987) showed that the proportional method is better than the regression method based on statistical efficiency. He also suggested that back-calculation be restricted to most recent annuli to avoid bias due to size-biased sampling, which may produce Lee's phenomenon. Weisberg and Frie (1987) used general linear models to account for environmental effects on scales. Smale and Taylor (1987) suggested an approach to distinguish Lee's phenomenon from back-calculation error.

4.7. VARIATION IN GROWTH

Most of the models in this chapter have come from differential equations or other similar formulations that have constant parameters. Such models are conceptually limited in at least three ways. First, growth in many populations changes during the season due to changes in environmental conditions. Fishes found in the ocean environment are buffered against seasonal effects more than fishes found in smaller bodies of water or, at a greater extreme, more than terrestrial species due to the high capacity of water to retain heat. However, terrestrial species in particular and even tropical species have differences in growth rates over the season, probably due to changes in food availability and greater metabolic requirements. For some intertidal species, there is evidence that growth follows a fortnightly cycle due to the effect of tides (Gonzalez 1987). Monthly or quarterly cycles may occur in other species.

Second, the representation of growth variability by a single parameter (e.g., σ for additive or multiplicative error represented by ϵ) may be too simplistic because individuals quite often show extreme differences in growth. A possible improvement would be to have separate growth parameters for each fish and connect growth for the population by considering the distribution across individuals.

Third, the lack of consideration of error in the differential equation suggests that stochasticity is being treated as an add-on, rather than an integral part of the modeling. The use of stochastic differential or difference equations may lead to a better understanding of stochastic growth processes.

Each of these approaches to variation in growth is considered in the following subsections. In addition, several other factors could produce growth differences, such as depth, sex, habitat, locality, weather (Day 1992); latitude (Appeldoorn 1982), and interannual, genetic, and year-class factors (Hagen and Quinn 1991). Some authors

classify factors related to an individual as “endogenous” and those related to external events as “exogenous.” Our purpose is not to explore which factors are most important in fish populations but rather to provide the tools for such explorations. Finally, there may be density-dependent factors that affect growth. For example, average growth of fish may be smaller for stronger year-classes. A simple model for density-dependent growth is described in section 3.1.5; more complicated models relating density-dependent processes to growth are needed but are beyond the scope of this book.

4.7.1. Seasonal Growth

The generalization of growth to include seasonal differences has been investigated by many authors (Pitcher and MacDonald 1973, Cloern and Nichols 1978, Pauly and Gaschutz 1979, Hoenig and Hanumara 1982, Appeldoorn 1987, Moreau 1987, Francis 1988b, Akamine 1993); Pawlak and Hanumara (1991) provided a summary and comparison of models. Most models use the LVB model as the base equation and have the same intrinsic form of adding sinusoidal variation, although several different parameterizations have been used.

To apply seasonal models, age must be recorded on a fine enough scale to define the seasonal variation. For example, if seasonal growth is on an annual cycle, then it might be necessary to determine age on a daily or weekly basis. Quite often this requires the assignment of a fixed birthdate within the year for all fish in a year-class (Appeldoorn 1987).

One possible differential equation for seasonal growth is

$$\frac{dY}{dt} = \kappa(Y_\infty - Y) \{1 - \delta \cos[(2\pi/\Omega)(t - t_1)]\}, \quad (4.70)$$

with initial condition $Y(t_0) = 0$, which was first proposed by Hoenig and Hanumara (1982) using a period Ω of 1 year. The rightmost term in (4.70) modifies the original LVB equation (4.9) by a factor varying sinusoidally over period Ω from $1 - \delta$ at times $t_1 \pm k\Omega$ to $1 + \delta$ at times $t_1 \pm k\Omega/2$, where k is any integer.

For age data recorded in units of a year, an annual cycle would use a period $\Omega = 1$, a fortnightly cycle would use a period $\Omega = 1/26$, and so on. For age data recorded in units of a day, an annual cycle would use a period $\Omega = 365.25$, and so on. Phase shift parameter t_1 adjusts the curve for where the low and high points occur, as explained further below.

To prevent shrinkage (negative growth), the right-hand side of (4.70) must be non-negative. Because the cosine function is bounded in absolute value by 1, this condition requires that $\delta \leq 1$.

The solution to the differential equation with initial condition $Y(t_0) = 0$ results in the generalized equation

$$Y(t) = Y_\infty \left\{ 1 - e^{-\kappa[t-t_0-(\phi[t]-\phi[t_0])]} \right\}, \quad (4.71)$$

where

$$\phi(t) = \left(\frac{\delta\Omega}{2\pi} \right) \sin[(2\pi/\Omega)(t - t_1)]. \quad (4.72)$$

The amplitude of the sine curve, $\delta\Omega/2\pi$ in (4.72), is proportional to the amplitude parameter δ . For an annual cycle, a phase shift $t_1 = 0$ would have the respective high

and low parts of the sine curve at 1/4 and 3/4 of the way through the year, a phase shift $t_1 = 1/4$ at the start and 1/2 of the way through the year, and so on. A graphical comparison of the LVB model (figure 4.12) with seasonal LVB models with phase shifts of 0 and 1/4 shows the sinusoidal variation induced by (4.71).

In figure 4.12, the value $\delta = 1$ is used for the seasonal curves, and as a result, each curve has flat places centered about a point where the derivative (4.70) is 0. These points occur at the value of the phase shift parameter t_1 and at all successive cycle points $t_1 \pm k\Omega$, where k is any integer.

Adding seasonal variation to other size-age models can be accomplished analogously by replacing t with $t - \phi(t)$ and any time parameter t_x with $t_x - \phi(t_x)$. Similarly, mark-recapture models in section 4.4.1 can be modified by replacing elapsed time Δt by $\Delta t + \phi(t_2) - \phi(t_1)$ (Francis 1988b). Appeldoorn (1987) derived a similar likelihood approach. Pitcher and MacDonald (1973) developed a switching model, which shuts off growth during part of the year. Akamine (1993) presented a generic formulation for any time-specific function $f(t)$ and gives examples of its application for cumulative water temperature, a sine function, and two periodic functions that switch off for a period of time.

4.7.2. Individual Variation in Growth

Sainsbury (1980) first incorporated individual variation in growth. Much of this section is derived from that essay and an extension of that approach by Hampton (1991a). The basic concept of this approach is that each individual, i , in a population has its own growth parameters, denoted by the vector Θ_i . If many observations on the same individual were taken, then it would be possible to estimate Θ_i . Indeed, this was the basis of the method of McCaughran in section 4.4.2 for a two-parameter growth model. From the individual parameter estimates, population statistics such as the mean, median, and variance could be estimated from standard sampling theory.

However, such data are rarely collected from fish populations. An alternative approach keeps the concept of individual variation but connects individuals through an underlying statistical distribution. This approach has only been applied to the LVB model, but in principle it could be adapted to other growth models.

Suppose that each individual has its own growth parameters ($Y_{\infty i}$, κ_i); all indi-

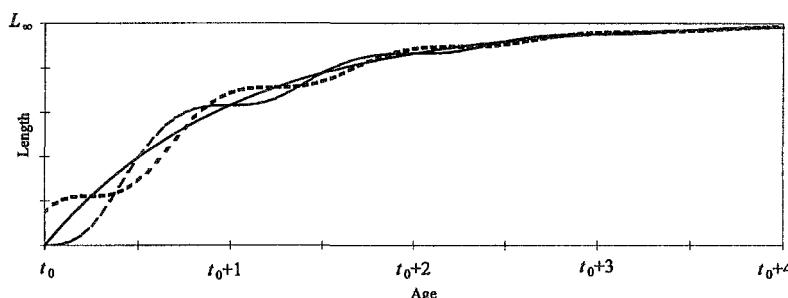


Figure 4.12. Seasonal LVB growth curves with an annual cycle ($\Omega = 1$) and an amplitude parameter $\delta = 1$. (Dashed line) phase-shift parameter $t_1 = 0$; (Dotted line) phase-shift parameter $t_1 = 1/4$; (Solid line) nonseasonal curve (equivalent to $\delta = 0$).

viduals are assumed to have the same initial time parameter t_0 in order to get closed-form solutions. Each individual's growth parameters are assumed to come from independent statistical distributions, with a mean and variance; thus

$$\begin{aligned} Y_\infty &\sim (\mu_\infty, \sigma_\infty^2), \kappa \sim (\mu_\kappa, \sigma_\kappa^2), \\ \text{and } E[f(Y_\infty)g(\kappa)] &= E[f(Y_\infty)]E[g(\kappa)], \end{aligned} \quad (4.73a)$$

where the subscripts are dropped for readability, and f and g are arbitrary functions. By writing the LVB model from (4.9) as

$$Y_T = Y_\infty(1 - e^{-\kappa T}), \quad (4.73b)$$

where $T = t - t_0$, the expected value or mean of Y given adjusted time T from (4.73a,b) is

$$E[Y|T] = \mu_T = \mu_\infty \left[1 - E(e^{-\kappa T}) \right]. \quad (4.74)$$

As $e^{-\kappa T}$ is a convex function of T [i.e., its second derivative is ≥ 0], it follows from Jensen's inequality that $e^{-\mu_\kappa T} \leq E(e^{-\kappa T})$, showing that

$$\mu_T = \mu_\infty \left[1 - E(e^{-\kappa T}) \right] \leq \mu_\infty \left(1 - e^{-\mu_\kappa T} \right). \quad (4.75)$$

The biological interpretation of (4.75) is that mean size at age is less than that obtained by substituting mean parameters into the LVB equation. The implication of this result is that parameter estimates obtained by fitting a constant parameter LVB model to data from a population with individual variation do not estimate the mean values of those parameters.

From the formula for the variance of a product of two independent random variables, x and y (Seber 1982),

$$V(xy) = E^2(x)V(y) + E^2(y)V(x) + V(x)V(y), \quad (4.76)$$

the variance of size at age by using $x = Y_\infty$ and $y = 1 - e^{-\kappa T}$ is

$$V[Y|T] = \sigma_T^2 = \sigma_\infty^2 \left[1 - 2E(e^{-\kappa T}) + E(e^{-2\kappa T}) \right] + \mu_\infty^2 V(e^{-\kappa T}). \quad (4.77)$$

Better understanding of the nature of growth variation requires further structure in the model because of the confounding effects of the moments of $e^{-\kappa T}$ in (4.77). Sainsbury makes the further assumption that κ has a gamma distribution, $\Gamma(\alpha, \beta)$, with probability density function

$$f(\kappa) = \frac{\beta}{\Gamma(\alpha)} (\beta\kappa)^{\alpha-1} e^{-\beta\kappa}, \quad \kappa \geq 0. \quad (4.78)$$

The mean and variance of κ are

$$\mu_\kappa = \alpha/\beta \quad \text{and} \quad \sigma_\kappa^2 = \alpha/\beta^2,$$

from which the squared coefficient of variation ξ_κ is derived as

$$\xi_\kappa = \frac{\sigma_\kappa^2}{\mu_\kappa^2} = \frac{1}{\alpha}.$$

From the moment-generating function

$$\psi(t) = E(e^{t\kappa}) = (1 - t/\beta)^{-\alpha},$$

the expected value of $e^{-x\kappa T}$ is

$$E(e^{-x\kappa T}) = (1 + xT/\beta)^{-\alpha} = [1 + (x\mu_\kappa T)\xi_\kappa]^{-1/\xi_\kappa}. \quad (4.79)$$

Using the variance definition $V(x) = E(x^2) - E^2(x)$ and substituting appropriate moments from (4.79) into (4.74) and (4.77), the mean and variance of size at adjusted time T are

$$\mu_T = \mu_\infty [1 - (1 + T/\beta)^{-\alpha}] = \mu_\infty \left[1 - (1 + \mu_\kappa T \xi_\kappa)^{-1/\xi_\kappa} \right] \quad (4.80)$$

$$\begin{aligned} \sigma_T^2 &= \sigma_\infty^2 [1 - 2(1 + T/\beta)^{-\alpha} + (1 + 2T/\beta)^{-\alpha}] \\ &\quad + \mu_\infty^2 \left[(1 + 2T/\beta)^{-\alpha} - (1 + T/\beta)^{-2\alpha} \right], \\ &= \sigma_\infty^2 \left\{ 1 - 2[1 + (\mu_\kappa T) \xi_\kappa]^{-1/\xi_\kappa} + [1 + (2\mu_\kappa T) \xi_\kappa]^{-1/\xi_\kappa} \right\} \\ &\quad + \mu_\infty^2 \left\{ [1 + (2\mu_\kappa T) \xi_\kappa]^{-1/\xi_\kappa} - [1 + (2\mu_\kappa T)(\xi_\kappa/2)]^{-1/(\xi_\kappa/2)} \right\} \\ &= k_1(T) \sigma_\infty^2 + k_2(T) \mu_\infty^2. \end{aligned} \quad (4.81)$$

A special case of Sainsbury's model with variation in Y_∞ and no variation in κ was derived by Kirkwood and Somers (1984). Using L'Hôpital's rule, it can be shown that

$$(1 + \theta x)^{-1/x} \rightarrow e^{-\theta}, \quad \text{as } x \rightarrow 0,$$

so that the mean in (4.80) and variance in (4.81) converge to

$$\mu_T = \mu_\infty \left(1 - e^{-\mu_\kappa T} \right) \quad (4.82)$$

$$\sigma_T^2 = \sigma_\infty^2 \left(1 - 2e^{-\mu_\kappa T} + e^{-2\mu_\kappa T} \right) = \sigma_\infty^2 (1 - e^{-\mu_\kappa T})^2, \quad (4.83)$$

as $\xi_\kappa \rightarrow 0$. These equations also follow directly from (4.73b). So, as the relative variation in κ goes to zero, the expected size at age converges to the constant parameter growth curve, and its variance at age converges to a function that increases monotonically with age. The implication of this result is that if there is no variation in κ , then standard fitting of the LVB model will describe the average size at age in the population. The increasing function of variance suggests that either a multiplicative error structure or weighted least squares be used.

When relative variation, ξ_κ , is not small, the magnitude of the difference in mean size at age between an individual variation model and a constant parameter model and the pattern of variation in size at age are not straightforward by examining (4.80) and (4.81). It is clear that both depend on the mean growth parameter, μ_κ , and its relative variance parameter, ξ_κ . In figure 4.13, μ_T and σ_T^2 are plotted for two values of μ_κ and

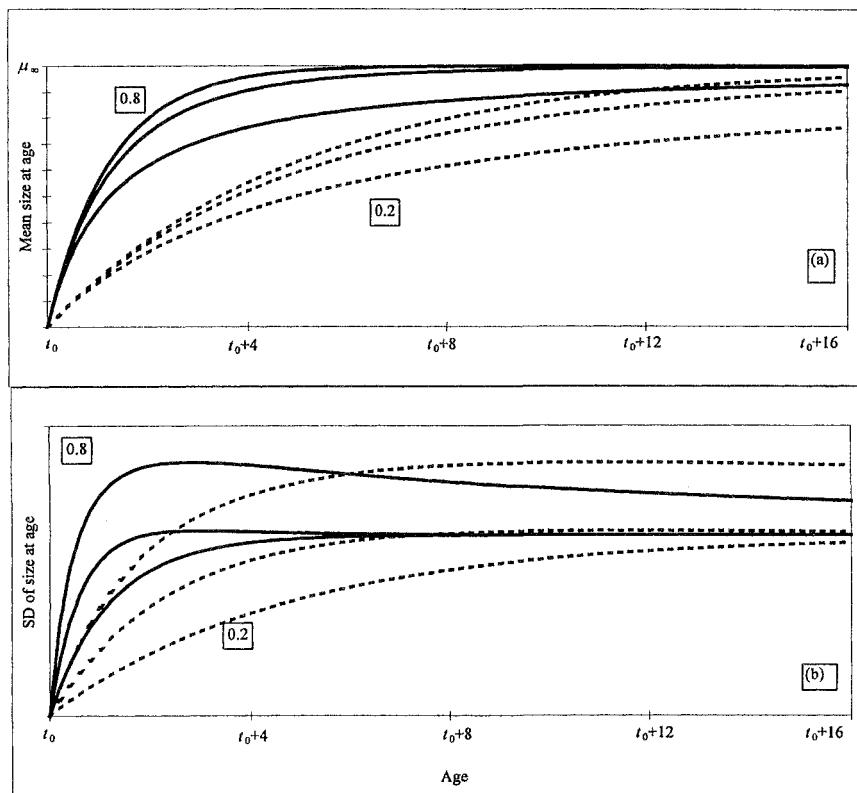


Figure 4.13. (a) Mean size at age μ_T and (b) standard deviation (SD) of size at age σ_T for Sainsbury's individual variation model as a function of age for two values of the expected value μ_κ (0.2, 0.8) and three values of the coefficient of variation $\sqrt{\xi_\kappa}$ (0.1, 0.5, 1.0) of growth parameter κ . Other parameters used to generate the graph are $\mu_\infty = 100$, $t_0 = 0$, and $\sqrt{\xi_\infty} = 0.25$ (coefficient of variation of Y_∞).

three values of $\sqrt{\xi_\kappa}$, showing that the magnitude of difference and pattern of variation are highly dependent on the parameters. When μ_κ is relatively small, the difference between mean size at age is largest at higher ages, and vice versa (figure 4.13a). Unless relative variation, ξ_κ , is low, the magnitude of difference can be quite large. However, if $\sqrt{\xi_\kappa}$ is <0.25 , the difference between the two curves is small. When μ_κ is small, the pattern of variation is an increasing one as a function of age, reaching an asymptote (figure 4.13b). When μ_κ is large, the pattern is the same except at a high level of ξ_κ , where it reaches a peak and then declines. However, given the typical range of variation in individuals of most fish populations, Sainsbury concluded that serious errors are not likely to result from analysis of size-age data with constant parameter models.

The mark-recapture equations for Sainsbury's model are similar to those previously developed, so the above implications carry over. The general equations (4.74) and (4.77) for mean size and variance at age can be translated into equations for mean size at recapture and variance of size at recapture. By using (4.9) and noting (4.38) and (4.39),

$$E(Y_2|Y_1, T) = Y_1 + (\mu_\infty - Y_1)[1 - E(e^{-\kappa T})] \quad (4.84)$$

$$\begin{aligned} V(Y_2|Y_1, T) &= \sigma_\infty^2 \left[1 - 2E(e^{-\kappa T}) + E(e^{-2\kappa T}) \right] \\ &\quad + (\mu_\infty - Y_1)^2 V(e^{-\kappa T}), \end{aligned} \quad (4.85)$$

which are the same as before except with μ_∞ replaced with $\mu_\infty - Y_1$ and Y replaced with $\Delta Y = Y_2 - Y_1$. Variable T in this situation is the elapsed time Δt . With the assumption of the gamma distribution for κ , (4.80) and (4.81) become

$$E(Y_2|Y_1, T) = Y_1 + (\mu_\infty - Y_1) \left[1 - (1 + \mu_\kappa T \xi_\kappa)^{-1/\xi_\kappa} \right] \quad (4.86)$$

$$V(Y_2|Y_1, T) = k_1(T) \sigma_\infty^2 + k_2(T) (\mu_\infty - Y_1)^2. \quad (4.87)$$

Sainsbury showed how the individual variation results in a decrease in the average growth increment and, consequently, an underestimate of μ_κ and an incorrect pattern of variation σ_κ^2 (or ξ_κ) if a constant parameter model is used. Furthermore, serious overestimates of mean size at age can result from analysis of mark-recapture data with constant parameter models. When substantial individual variation is present, a thorough analysis of growth cannot be obtained from mark-recapture data alone, due to the effects of mortality, age composition, and truncation of the Y_∞ distribution as larger individuals are considered.

The basic individual variation model of Sainsbury was extended by Hampton (1991a) to include recapture and release-size measurement errors. Recapture measurement error [which can also be interpreted as model error (Hampton 1991a)] is easily handled by adding an error, ϵ , to (4.86), which is assumed to have mean 0 and variance σ_ϵ^2 (i.e., additive error). Release size error is included because tagged fish often struggle a great deal, creating errors in measurement. If Y_1 is the true release size and Y'_1 is the measurement of release size, then one model of error is

$$Y'_1 = Y_1 + \mu_\delta + \delta, \quad (4.88)$$

where μ_δ is the bias in measurement and δ is the additive error with mean 0 and variance σ_δ^2 . Considering both types of error, (4.39) is modified to be

$$\begin{aligned} Y_2 &= Y_1 + (Y_\infty - Y_1)(1 - e^{-\kappa T}) + \epsilon \\ &= (Y'_1 - \mu_\delta - \delta) + [Y_\infty - (Y'_1 - \mu_\delta - \delta)](1 - e^{-\kappa T}) + \epsilon, \end{aligned} \quad (4.89)$$

where T is the elapsed time. From (4.89), the mean and variance of recapture size given Y'_1 and T are

$$\begin{aligned} E(Y_2|Y'_1, T) &= (Y'_1 - \mu_\delta) \\ &\quad + [\mu_\infty - (Y'_1 - \mu_\delta)] \left[1 - (1 + \mu_\kappa T \xi_\kappa)^{-1/\xi_\kappa} \right] \end{aligned} \quad (4.90)$$

$$\begin{aligned} V(Y_2|Y'_1, T) &= k_1(T) \sigma_\infty^2 + k_2(T) [\mu_\infty - (Y'_1 - \mu_\delta)]^2 \\ &\quad + \sigma_\epsilon^2 + \sigma_\delta^2 E(e^{-2\kappa T}), \end{aligned} \quad (4.91)$$

where the expected value term in (4.91) can be calculated using (4.79). The parameters μ_δ and σ_δ^2 are obtained from auxiliary repeated measurements of size. In practice, these

repeated measurements may be from recaptured fish caught shortly after tagging. Equations (4.90) and (4.91) are slight generalizations for positive μ_s of those in Hampton (1991a).

Estimation

For size-age data, the set of measurements as before is denoted $\{Y_i, t_i\}$ for $i = 1, \dots, n$. Let μ_i be the mean size at age corresponding to age t_i from any of the models above [i.e., from (4.9), (4.74), (4.80), or (4.82)], where $t_i - t_0$ is substituted for T . Let σ_i^2 be the corresponding variance at age [i.e., σ^2 , (4.77), (4.81), (4.83), respectively]. The exact distribution of Y_i is unknown in the individual variation models, being the product of a complex function of random variables Y_∞ and κ as in (4.73b). Sainsbury (1980) assumed that Y_i can be approximated by a normal distribution with mean μ_i and variance σ_i^2 . For any of these models, the log likelihood can then be written

$$\ln \mathcal{L} = - \sum_{i=1}^n \frac{1}{2} \ln(2\pi\sigma_i^2) - \sum_{i=1}^n \frac{1}{2\sigma_i^2} (Y_i - \mu_i)^2. \quad (4.92)$$

Equation (4.92) can be maximized as a function of the parameters of the model, or conversely, its negative can be minimized. For some models, (4.92) can be simplified. One important example is the additive error model (4.11), for which the constant variance parameter can be treated as a nuisance parameter and estimated after the fact by the residual mean square, as explained in section 4.2. For other models, the variance parameter(s) must be estimated directly.

If a multiplicative error structure like (4.12) is postulated, then the log likelihood equation is written in terms of $\ln Y_i$ rather than Y_i . Parameter estimation results in estimates of the mean of log size as a function of age; transformation back to the size scale yields estimates of the median of size as a function of age. Corrections to obtain mean size at age follow from the lognormal distribution. A simple correction from the theory of the lognormal distribution is $\exp(\mu + \frac{1}{2}\sigma^2)$, where μ and σ^2 are the mean and the variance on the transformed scale (Parzen 1960). A more complicated but more accurate correction is given by Gavaris (1980). It should be noted that with skewed distributions that the mean may not be the best measure of central tendency and that the median may be a more reliable statistic (cf. section 1.3.4).

For mark-recapture data, the set of measurements is denoted $\{Y_{2i}, Y_{1i}, \Delta t_i\}$ for $i = 1, \dots, n$, as before. Let μ_i be the mean recapture size at age corresponding to release size, Y_{1i} (or Y'_{1i} in the case of release error), and elapsed time, Δt_i , from any of the models above [i.e., from (4.39), (4.86), or (4.90), where Δt_i is substituted for T]. Let σ_i^2 be the corresponding variance at age [i.e., σ^2 , (4.87), or (4.91), respectively]. The conditional distribution of Y_{2i} given Y_{1i} (or Y'_{1i}) and Δt_i is also unknown and must also be approximated by a normal distribution. The log likelihood equation is the same as (4.92) with the revised definitions of mean and variance.

Hampton (1991a) developed a suite of models with various sources of error, gave likelihood equations for the models to estimate parameters, and used likelihood ratio tests to find the best model. The models include the standard LVB model with additive measurement error, the Kirkwood and Somers model, the Sainsbury model, the latter two models with additive measurement error, and the latter two models with both release error and additive measurement error. Several examples of the form of the negative log likelihood are also given.

In application to southern bluefin tuna mark–recapture data, Hampton (1991a) first used a small set of length–age data to arrive at an estimate of the constant t_0 parameter. After fitting seven models to the mark–recapture data, he found that variation in κ was small. The best model was the Kirkwood and Somers model with the addition of additive measurement error. Simulation studies indicated that biased parameter estimates occurred when this measurement error was not included. He also showed that the normality assumption was not a bad assumption using simulation.

Francis (1988a) extended Sainsbury's model to allow Y_∞ and κ to be correlated and to use a lognormal distribution for the distribution of κ . Although no formulae are given, he also included constant mortality $Z = \kappa$ to occur. His purpose was to show that comparing growth parameters obtained from size–age data and mark–recapture data are not comparable when individual variation and mortality are present. An intuitive reason for this is that the average annual growth increment for an individual of a given size is different from the average annual growth for an individual of a given age. In the first case, growth is measured from the size distribution of the population; in the second case, growth is measured from the age distribution.

Example 4.8. Rainbow trout in the Kenai River

Individual variation models are applied to the data in example 4.6 (table 4.10) to determine whether significant bias occurs by using the constant variation model. Lafferty and Quinn (1987) determined that measurement errors for rainbow trout were minor, so no attempt is made to include release measurement error. Seven models are applied to the data: three models with one source of variation (σ_e^2 , σ_∞^2 , or σ_κ^2), three models with two of these sources of variation, and one model with all three sources of variation. The likelihood (4.92) for each model was maximized by using a nonlinear function optimizer contained within a spreadsheet on a personal computer.

Parameter estimates, the intermediate parameter ξ_k , and the log likelihoods are shown in table 4.17. Model 1 is the same as case 5b in table 4.11. Model 2 with variation in Y_∞ has a much lower likelihood than model 1, while model 3 with variation in κ has a slightly higher likelihood. Of the models with two sources of variation, model 6 with variation in both κ and Y_∞ has the highest likelihood. Model 7 with all three sources of variation converges to model 6. Except for model 2, the parameter estimates of μ_∞ and μ_κ are not much different. Estimates of variance parameters vary enormously depending on the model.

Likelihood ratio tests can be constructed as in section 4.5.2, involving a test statistic which is the negative of twice the difference in log likelihoods. These tests can be made for models with common parameters, and the test statistics can be compared to a χ^2 critical value with degrees of freedom equal to the difference in the number of parameters, p . These test results, shown in table 4.17, indicate that only model 2 is significantly poorer than any other model in explaining the data. This model with variation only in Y_∞ is inadequate in explaining growth of rainbow trout, requiring a model that would also have other variation. The other models, despite treating variation in growth so differently, have similar likelihoods. With the small sample of 102 fish, it is not surprising that the components of growth variation cannot be distinguished. Given the small difference in likelihoods and the small difference in parameter estimates among other models, there does not appear to be large bias in the constant variation model. Hampton (1991a), using an example with a larger sample size of more than

Table 4.17. Parameter estimates and likelihood calculations for various individual variation models applied to the rainbow trout data in table 4.10.

Model	1: σ_ϵ^2	2: σ_∞^2	3: σ_κ^2	4: $\sigma_\epsilon^2, \sigma_\infty^2$	5: $\sigma_\epsilon^2, \sigma_\kappa^2$	6: $\sigma_\infty^2, \sigma_\kappa^2$	7: $\sigma_\epsilon^2, \sigma_\infty^2, \sigma_\kappa^2$
$\hat{\mu}_\infty$	659.1	581.2	669.5	658.7	664.1	665.3	665.3
$\hat{\mu}_\kappa$	0.295	0.481	0.312	0.296	0.289	0.322	0.322
$\hat{\sigma}_\infty^2$	0	23300	0	2073	0	1236	1236
$\hat{\sigma}_\kappa^2$	0	0	0.282	0	0.013	0.247	0.247
$\hat{\sigma}_\epsilon^2$	841	0	0	749	694	0	0
$\hat{\xi}_\kappa$	0	0	0.904	0	0.046	0.766	0.766
p	3	3	3	4	4	4	5
$\ln \mathcal{L}$	-488.187	-499.828	-487.946	-487.982	-487.508	-486.533	-486.533
Likelihood ratio statistics							
Versus model 7	3.309	26.590	2.826	2.897	1.951	0.000	
P	.191	.000	.243	.089	.163	1.000	
Versus model 6		26.590	2.826				
P		.000	.093				
Versus model 5	1.358		0.875				
P	.244		.350				
Versus model 4	0.411	24.639					
P	.521	.000					

1700, was able to make more definitive conclusions regarding growth variation in tuna. ■

4.7.3. Stochastic Growth

The concept of stochastic growth refers to a process that incorporates an underlying growth model for the population with random variation affecting an individual at all stages of life. Such variation induces dependence in the growth data; the size of a fish depends on all previous random effects. Two types of stochastic growth models are considered: one based on a difference equation form and one based on a differential equation form.

Difference equation setting

Each individual is subjected to annual random innovations added to a common growth process (Cohen and Fishman 1980). Size, Y_t , is modeled as

$$Y_t = \alpha + \rho Y_{t-1} + U_t, \quad (4.93)$$

where U_t is an independent, normally distributed random variable with mean zero and variance σ^2 . The Ford coefficient, ρ , is $\exp(-\kappa)$ as in section 4.3.1, and α is $Y_\infty(1 - \rho)$. Given a fish of size Y_1 , it can be shown from (4.93) that the conditional probability distribution of size Y_2 after elapsed time, Δt , is a normal distribution with mean

$$\mu(Y_2|Y_1, \Delta t) = Y_\infty - (Y_\infty - Y_1)\rho^{\Delta t} \quad (4.94)$$

and variance

$$\text{Var}(Y_2|Y_1, \Delta t) = \sigma^2 \frac{1 - \rho^{2\Delta t}}{1 - \rho^2}. \quad (4.95)$$

If modeling of growth increment, $\Delta Y = Y_2 - Y_1$, is necessary, then (4.94) is modified by subtracting Y_1 , and (4.95) remains the same.

If it is further assumed that the size Y_1 is a normal random variable with mean M and variance σ_M^2 , then the unconditional distribution of size Y_2 can be shown to be a normal distribution with mean

$$\mu(Y_2|\Delta t) = Y_\infty - (Y_\infty - M)\rho^{\Delta t} \quad (4.96)$$

and variance

$$\text{Var}(Y_2|\Delta t) = \text{Var}(Y_2|Y_1, \Delta t) + \rho^{2\Delta t}\sigma_M^2. \quad (4.97)$$

This approach has applications for both size-age and mark-recapture data. For size-age data, the stochastic growth version of the LVB model follows from the above equations with $Y_1 = 0$ at starting age t_0 . The distribution of size Y_2 at any other age t is then normal with mean and variance from (4.94) and (4.95), respectively, where $\Delta t = t - t_0$. Alternatively, if the distribution of size at age 0 is assumed normal with mean M and variance σ_M^2 , then the distribution at any other age is normal with mean and variance from (4.96) and (4.97), respectively.

For mark-recapture data, the same equations apply, only with Y_1 interpreted as the size at release, Y_2 as the size at recapture, and Δt as the elapsed time. Equations (4.94) and (4.95) apply if the conditional distribution is to be used. This is the usual case, as the distribution of release sizes is generally complex. However, if the distribution of release sizes can be modeled by a simple normal distribution, then (4.96) and (4.97) can be applied.

As pointed out by Francis (1988b), an interesting feature of this model is that the variance in (4.95) or (4.97) appears to be unrelated to the mean or to release size. However, if one views the process as a function of release size, Y_1 , and mean recapture size, now notated as $\mu(Y_2)$, a different picture emerges. By rearranging (4.94) as

$$\rho^{\Delta t} = [Y_\infty - \mu(Y_2)]/(Y_\infty - Y_1)$$

and substituting into (4.95), one obtains

$$\text{Var}(Y_2|Y_1, \mu(Y_2)) = \frac{\sigma^2}{1 - \rho^2} \left\{ 1 - \left[\frac{Y_\infty - \mu(Y_2)}{Y_\infty - Y_1} \right]^2 \right\},$$

showing the dependence on both mean size and on release size. The variance increases monotonically from 0 to $\sigma^2/(1 - \rho^2)$ as mean size goes from Y_1 to Y_∞ . The variance is also a decreasing function of Y_1 , which is intuitive considering that greater growth can occur when Y_1 is smaller.

An easy modification of this approach can be made by using the Gompertz growth model in place of the LVB model. If $\ln Y_t$ is substituted for Y_t in the above methodology, then the growth model being used is actually the Gompertz (cf. section 4.3.3). Deriso and Parma (1988) used the Gompertz model in constructing a length-based model (see chapter 9).

Estimation of parameters follows directly from the maximum likelihood method using either the conditional distribution of Y_2 given Y_1 and Δt or the unconditional

distribution if appropriate. Cohen and Fishman (1980) presented likelihood functions for two sexes and several subspecies and demonstrate the likelihood ratio tests for equality of parameters.

Differential equation setting

Stochastic differential equations have been applied to growth of individuals by Sandland and Gilchrist (1979), White and Brisbin (1980), Garcia (1983), and Seber and Wild (1989), among others. The same formalisms also apply to population growth curves; appropriate references are found in Sandland and Gilchrist (1979). Our treatment follows that of Seber and Wild (1989), which goes into greater depth and has several examples, including application of the Richards growth model (cf. section 4.3.4). For comparison with the difference equation setting, we present the stochastic differential equation application to the LVB model, a special case of the Richards.

We denote Y as the size variable (e.g., L or W) and t as the time or age variable and presume that our data consist of measurements of an individual at equally spaced intervals of time. A general model that includes stochastic variation may be written

$$\frac{dY}{dt} = h_{\Theta}(Y, t) + \sigma_{\Psi}(Y, t)\epsilon(t), \quad (4.98a)$$

where h is the derivative of the underlying deterministic growth curve with parameter set Θ , σ is a variance function with parameter set Ψ , and ϵ is a stochastic Gaussian process with an expected value of 0 and variance of 1. This process is assumed to be stationary: either (1) a white-noise (or delta-correlated) process where $\text{corr}[e(t), e(u)] = 0$ for $t \neq u$, or (2) a stationary correlation process where $\text{corr}[e(t), e(u)] = \rho(|t - u|)$ and ρ is some function. The differential equation (4.98a) does not generally have a closed-form solution.

Time models If it is also assumed that h and σ are functions only of time, then the stochastic differential equation (4.98a) can be written

$$\frac{dY}{dt} = h_{\Theta}(t) + \sigma_{\Psi}(t)\epsilon(t). \quad (4.98b)$$

The solution to (4.98b) is a Gaussian process

$$Y(t) = Y_0 + \int_{t_0}^t h_{\Theta}(u)du + \int_{t_0}^t \sigma_{\Psi}(u)\epsilon(u)du, \quad (4.99)$$

where $Y(t_0) = Y_0$. Given Y_0 , the expected value of (4.99) is

$$E(Y) = Y_0 + \int_{t_0}^t h_{\Theta}(u)du. \quad (4.100)$$

The variance in Y for a white-noise process is

$$V(Y) = \int_{t_0}^t \sigma_{\Psi}^2(u)du, \quad (4.101a)$$

and for a stationary correlation process, it is

$$V(Y) = \int_{t_0}^t \int_{t_0}^t \sigma_\Psi(u)\sigma_\Psi(v) \rho(|u - v|) dudv. \quad (4.101b)$$

The covariance between any two sizes, Y_i and Y_j , where $t_i \leq t_j$ for a white-noise process is

$$\text{cov}(Y_i, Y_j) = V(Y_i), \quad (4.102a)$$

and for a stationary correlation process, it is

$$\text{cov}(Y_i, Y_j) = \int_{t_0}^{t_j} \int_{t_0}^{t_i} \sigma_\Psi(u)\sigma_\Psi(v) \rho(|u - v|) dudv. \quad (4.102b)$$

The expected value of an increment of size $Y_j - Y_i$ for $t_i < t_j$ is given by (4.100) with Y_0 removed and the limits of the integral(s) replaced with t_i and t_j . The variance in an increment and covariance between increments are given by (4.101a) or (4.101b), and (4.102a) or (4.102b) with the limits so modified. We denote $X_i = Y_{i+1} - Y_i = \Delta Y_i$ as the increment of one unit at t_i , which obeys the increment equations with $j = i + 1$.

Special case. To apply these results to data, specification of the functions h , σ , and for the stationary correlation process, ρ is needed. Seber and Wild (1989) gave the example of a constant variance process where $\sigma_\Psi(t) = \sigma$ and the continuous analogue of a positive autoregression process of order 1 for the stationary correlation process, which is given by

$$\text{corr}[e(t), e(u)] = e^{-\lambda|t-u|}. \quad (4.103)$$

For either of these two processes with constant variance, the model (4.103) can be written

$$Y_i = Y_0 + \int_{t_0}^t h_\Theta(u)du + E_i, \quad (4.104)$$

where $E_i = \sigma \int_{t_0}^t \epsilon(u)du$. The expected value of (4.104) is identical to (4.100). The model for a growth increment X_i is

$$X_i = \int_{t_i}^{t_{i+1}} h_\Theta(u)du + e_i, \quad (4.105)$$

where $e_i = \sigma \int_{t_i}^{t_{i+1}} \epsilon(u)du$. Hence the accumulated error, E_i , in (4.104) is just the sum of the increment errors e_i in (4.105). The expected value of an increment is

$$E(X_i) = \int_{t_i}^{t_{i+1}} h_\Theta(u)du. \quad (4.106)$$

For the uncorrelated error process, variances in size Y_i and growth increment X_i from (4.101a) are

$$\sigma_{Y_i}^2 = V(Y_i) = (t_i - t_0)\sigma^2 \quad (4.107a)$$

$$\sigma_{X_i}^2 = V(X_i) = (t_{i+1} - t_i)\sigma^2. \quad (4.108a)$$

Covariance between sizes is still given by (4.102a) and covariance between growth increments is 0, since growth increments are independent.

For the stationary correlation process, variances from (4.101b) are

$$\sigma_{Y_i}^2 = V(Y_i) = \frac{2\sigma^2}{\lambda^2} [\lambda(t_i - t_0) + e^{-\lambda(t_i - t_0)} - 1] \quad (4.107b)$$

$$\sigma_{X_i}^2 = V(X_i) = \frac{2\sigma^2}{\lambda^2} [\lambda(t_{i+1} - t_i) + e^{-\lambda(t_{i+1} - t_i)} - 1]. \quad (4.108b)$$

By breaking the integral in (4.102b) into two pieces for v between t_0 and t_i and between t_i and t_j , the covariance $\text{cov}(Y_i, Y_j)$ between sizes becomes

$$\begin{aligned} \sigma_{Y_{ij}} &= \int_{t_0}^{t_i} \left(\int_{t_0}^{t_i} \sigma^2 e^{-\lambda|u-v|} du \right) dv + \int_{t_i}^{t_j} \left(\int_{t_0}^{t_i} \sigma^2 e^{-\lambda|u-v|} du \right) dv \\ &= \sigma_{Y_i}^2 + \frac{\sigma^2}{\lambda^2} e^{-\lambda(t_j - t_0)} \{ [e^{\lambda(t_j - t_i)} - 1][e^{\lambda(t_i - t_0)} - 1] \}. \end{aligned} \quad (4.109)$$

From Seber and Wild (1989), the covariance $\text{cov}(X_i, X_j)$ between increments X_i and X_j is

$$\sigma_{X_{ij}} = \frac{\sigma^2}{\lambda^2} e^{-\lambda(t_{j+1} - t_i)} \{ [e^{\lambda(t_{j+1} - t_j)} - 1][e^{\lambda(t_{i+1} - t_i)} - 1] \}. \quad (4.110)$$

With the size data, the variance–covariance matrix Σ_Y can be formed from $\{\sigma_{Y_i}^2, \sigma_{Y_{ij}}\}$, and the above theory indicates that the data set is distributed as multivariate normal, for which vector $\{\mathbf{Y}_i\}$ has probability density function

$$f(\{\mathbf{Y}_i\}) = (2\pi)^{-n/2} |\det[\Sigma_Y]|^{-1/2} \exp(-\frac{1}{2} \mathbf{E}' \Sigma^{-1} \mathbf{E}), \quad (4.111)$$

where \mathbf{E} is the vector of errors, $E_i = Y_i - E[Y_i]$ and \det is shorthand for determinant. The analogous treatment for increments replaces Y with X and \mathbf{E} with \mathbf{e} . Treating this distribution as a likelihood, parameter estimates can be obtained from maximum likelihood methods. For increment data in the white noise case, weighted least squares is the equivalent procedure. If the data consist of several individuals with repeated measurements, then the composite likelihood is the product of the individual likelihoods.

Several authors (e.g., Sandland and Gilchrist 1979, Schnute 1981) prefer to model relative growth rate $Z = d \ln Y/dt = (1/Y)dY/dt$ instead of growth rate itself. Conceptually, this would seem to pose no difficulties except to replace Y by a new variable $V = \ln Y$ in the formulae above and interpret the results in terms of relative quantities. However, the solution to (4.98b) depends on the type of calculus used. The solutions above are appropriate under Stratonovich calculus or an autocorrelated Gaussian process but not under Ito calculus; see Seber and Wild (1989, appendix C) for details, who justify the use of Stratonovich calculus.

LVB model. The function $h_\Theta(t)$ in (4.98b) for the LVB model needs to be the derivative of the growth curve expressed as a function of t . Hence from (4.8) and (4.9),

$$h_\Theta(t) = \frac{dY}{dt} = \kappa Y_\infty e^{-\kappa(t-t_0)}. \quad (4.112)$$

With the usual initial condition $Y_0 = 0$, the stochastic model (4.104) is then

$$Y_i = Y_\infty \left[1 - e^{-\kappa(t_i - t_0)} \right] + E_i, \quad (4.113)$$

with expected value from (4.105) of

$$E[Y_i] = Y_\infty \left[1 - e^{-\kappa(t_i - t_0)} \right]. \quad (4.114)$$

Thus the mean size at age lies on the deterministic growth curve.

The model for a growth increment, X_i , from (4.105) is

$$\begin{aligned} X_i &= Y_\infty \left[e^{-\kappa(t_i - t_0)} - e^{-\kappa(t_{i+1} - t_0)} \right] + e_i \\ &= [Y_\infty - E(Y_i)] \left[1 - e^{-\kappa(t_{i+1} - t_i)} \right] + e_i, \end{aligned} \quad (4.115)$$

which corresponds to the additive error model (4.38), except that the errors may not be independent and identically distributed. The expected value of an increment from (4.106) is

$$E(X_i) = Y_\infty \left[e^{-\kappa(t_i - t_0)} - e^{-\kappa(t_{i+1} - t_0)} \right] = [Y_\infty - E(Y_i)] \left[1 - e^{-\kappa(t_{i+1} - t_i)} \right] \quad (4.116)$$

The variance and covariance terms (4.107)–(4.110) depend on variance parameter set $\Psi = \{\sigma^2, \lambda\}$; the growth parameter set $\Theta = \{Y_\infty, \kappa, t_0\}$ only affects the mean. As before, t_0 cannot be estimated from increment data.

Size models Seber and Wild (1989) also considered stochastic models with the deterministic growth portion as a function of size rather than time, written generally as

$$\frac{dY}{dt} = h_\Theta(Y) + \sigma_\Psi(t)\epsilon(t). \quad (4.117)$$

Only in certain models is this differential equation tractable; one example is the linear model with time-varying coefficients

$$h_\Theta(Y) = \beta(t)Y + \xi(t).$$

The LVB and Richards (with known exponent) are two special cases of this model. We consider the simpler LVB solution; Seber and Wild give the more general Richards solution.

LVB model. The function $h_\Theta(Y)$ for the LVB model from (4.8) is

$$h_\Theta(Y) = -\kappa Y + \kappa Y_\infty. \quad (4.118)$$

For a white-noise process scaled by function $\sigma_\Psi(u)$, (4.118) has the solution

$$Y_i = Y_\infty \left[1 - e^{-\kappa(t_i - t_0)} \right] + E_i, \quad (4.119)$$

where the error term E_i is given by

$$E_i = \int_{t_0}^t e^{\kappa(t-u)} \sigma_\Psi(u) dw, \quad (4.120)$$

where dw is the derivative of a Wiener process appropriate to the discontinuous variance function. The expected value from (4.119) is

$$E(Y_i) = Y_\infty \left[1 - e^{-\kappa(t_i - t_0)} \right], \quad (4.121)$$

showing that the mean size at age lies on the deterministic growth curve. The covariance between Y 's (and hence the variance with $i = j$) for this white-noise process is

$$\text{cov}(Y_i, Y_j) = \int_{t_0}^{\min(t_i, t_j)} e^{-\kappa(t_i + t_j - 2u)} \sigma_\Psi^2(u) du. \quad (4.122)$$

For the constant variance case, this yields

$$\text{cov}(Y_i, Y_j) = \frac{\sigma^2}{2\kappa} e^{-\kappa(t_i + t_j)} \left[e^{2\kappa \min(t_i, t_j)} - e^{2\kappa t_0} \right], \quad (4.123)$$

which provides an alternative variance–covariance formulation to the time models. For $t_i \leq t_j$, the variance using (4.123) is

$$V(Y_i) = \frac{\sigma^2}{2\kappa} \left[1 - e^{-2\kappa(t_i - t_0)} \right], \quad (4.124)$$

showing that the variance is an asymptotic function of t_i . The construction of the variance–covariance matrices and the likelihood is the same as for the time models. Seber and Wild did not derive formulae for increments with size models or for the case of a stationary correlation process. Several different fitting procedures for time and size models based on approximations and a discrete formulation of the error process are found in Seber and Wild (1989).

4.7.4. Comparison

In this section, a comparison of several of the previous LVB-type models for growth are compared in regard to the consequences of using them to model growth of a population. First, the different impacts on mean size and variance at age are examined for (1) the additive error model (4.11), (2) the multiplicative error model (4.12), (3) the Sainsbury model of section 4.7.2 with variation in both Y_∞ and κ , (4) the Kirkwood-Somers model, the special case of the Sainsbury model with $\sigma_\kappa^2 = 0$, (5) the Sainsbury model with $\sigma_\infty^2 = 0$, and (6) the Cohen-Fishman stochastic model of section 4.7.3.

Mean size at age is shown in figure 4.14a for the six models with the same values for parameters κ (or equivalently, μ_κ) and Y_∞ (or equivalently, μ_∞). Models 1, 4, and 6 have mean sizes that fall on the LVB curve generated with the parameters. These models have constant parameters, except that model 4 has variation in Y_∞ . However, the variation does not affect mean sizes. Models 3 and 5 have mean sizes lower than the curve as a consequence of the variation in κ . These curves approach Y_∞ but with lower curvature. Hence, one would expect a lower value of κ than the mean μ_κ from a random sample of the population. These curves may be similar to one using the median value of κ , although no studies have addressed this issue. Model 2 produces a curve with mean sizes above the LVB curve with mean parameters as a consequence of the

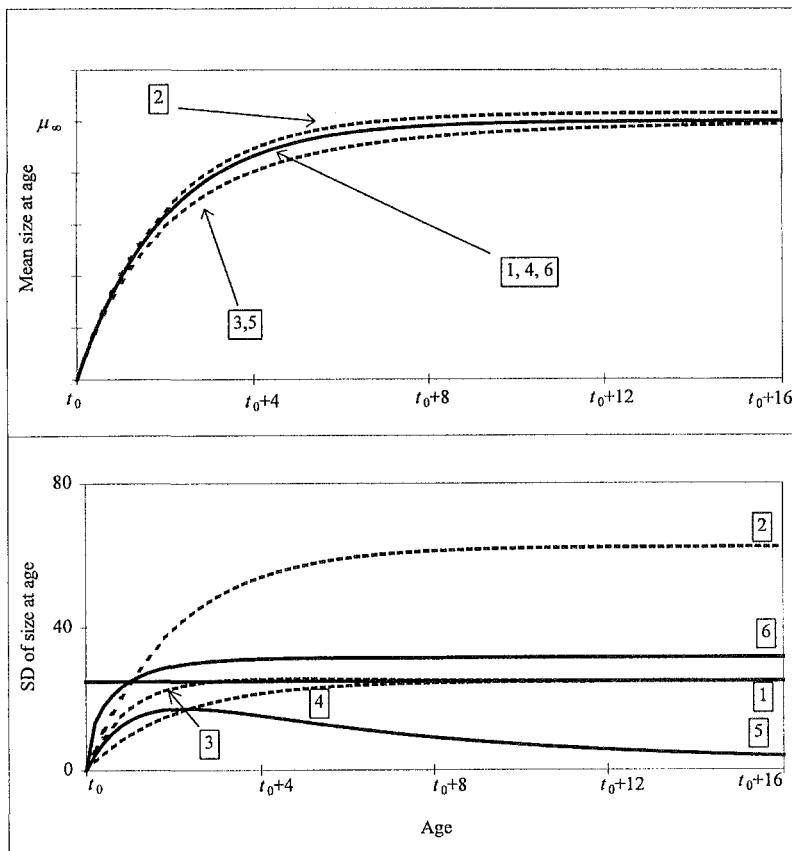


Figure 4.14. (a) Mean size at age μ_T and (b) standard deviation (SD) of size at age σ_T for LVB-type models: 1, additive error ($\sigma = 25$); 2, multiplicative error ($\sigma = 0.5$); 3, Sainsbury ($\sqrt{\xi_\infty} = 0.25$, $\sqrt{\xi_k} = 0.5$); 4, Kirkwood-Somers ($\sqrt{\xi_k} = 0$); 5, Sainsbury with $\sqrt{\xi_\infty} = 0$; and 6, Cohen-Fishman ($\sigma = 25$). Other parameters used to generate the graph are $\mu_\infty = 100$, $\mu_\kappa = 0.5$, and $t_0 = 0$.

lognormal distribution. The median sizes, however, do fall on the LVB curve. Thus, the issue of whether biased estimates of size at age occur depends on which measure of central tendency is selected.

The standard deviation (SD) in size at age is shown in figure 4.14b for the six models. The scale of the curves is not important because a variance parameter can be changed to adjust the height of the curves; the variance parameters were chosen to give graphic contrast. Model 1 has constant variance at age, which is fairly unrealistic for the youngest ages where size is small. However, constant variance may not be an unrealistic assumption for the range of ages sampled. For example, some of the other models have fairly constant variance after about age 4. Except for model 5, the other models produce similar variance patterns, which rise without inflection to an apparent asymptote over the range plotted. Model 3 with variation in both Y_∞ and κ has the capability of producing a peaked curve (cf. figure 4.13b), but in this case

has an asymptotic variance curve. Model 4 with variation in only Y_∞ produces a curve proportional to mean size at age. Model 2 with multiplicative error also produces a curve proportional to mean size at age, where the constant of proportionality is $\exp(\sigma^2) - 1$ from the lognormal formula for variance. Model 6 with stochastic growth produces an asymptotic curve; however, the rate of increase is higher at smaller ages. Finally, model 5 with variation only in κ produces a peaked curve that decreases as size approaches Y_∞ , which is intuitive.

A different comparison examines the different kinds of stochastic growth models. As the means of all stochastic models lie on the growth curve, it suffices to compare variance and covariance in size at age. The different models and variables are (1) variance in the time model with a white-noise process from (4.107a), (2) the corresponding covariance from (4.102a), which is identical, (3) variance in the time model with a stationary correlation process from (4.107b), (4) the corresponding covariance from (4.109), (5) variance in the size model with a white-noise process from (4.124), (6) the corresponding covariance from (4.123), and (7) variance in the Cohen-Fishman model from (4.95).

The same parameters used in the previous comparison are used here, except that σ is kept constant. The comparison is on a square-root scale so that units of size are maintained. The value of λ in the correlation process is chosen for graphical contrast. The covariance is between all ages and the last age of 16.

The SD curves all have the same pattern of an increasing function which seems to rise to an asymptote (figure 4.15). The asymptotic levels and the rates at which the asymptote is approached differ among the models for a constant value of σ^2 because the different methods integrate σ^2 into the variance differently. The variance is proportional to $t_i - t_0$ for the white-noise time model; hence the SD is a function of the square root in curve 1 and is not asymptotic. SD for the stationary correlation model (curve 3) is a complicated function of λ in (4.107b). If λ becomes large (which results in decreased autocorrelation), the variance also becomes proportional to $t_i - t_0$ as in the white-noise model. The variance for the size model [curve 5 on a square root scale] is proportional to $\{1 - \exp[-2\kappa(t_i - t_0)]\}/(2\kappa)$. Comparing this with (4.121), the variance is proportional to expected size $E(Y_i)$, multiplied by a factor $\{1 + \exp[-\kappa(t_i - t_0)]\}$. Similarly, variance for the Cohen-Fishman model (curve 7 on a square-root scale) is proportional to $\{1 - \exp[-2\kappa(t_i - t_0)]\}/[1 - \exp(-2\kappa)]$, which shows its similarity to the size model. By adjusting σ^2 , these curves can all be made to resemble each other with the possible exception of curve 1.

The covariance curves differ substantially between the time (curves 2 and 4) and size (curve 6) models (figure 4.15). For the time models, they resemble the variance curves, showing that the correlation between sizes remains high for adjacent times (ages). The size model, however, is an exponentially decreasing function of the greater time between observations i and j .

Thus, although these approaches all have different conceptual origins, they may in practice resemble each other and produce similar parameter estimates. Indeed, it may be difficult to use the statistical fitting measures to determine which model is most appropriate. This may be comforting in the sense that mean size and variance may be properly estimated, but it is discouraging in getting at the nature of growth in a population and its underlying mechanisms. There may be no empirical substitute for mechanistic studies of growth to describe the actual growth processes in a population.

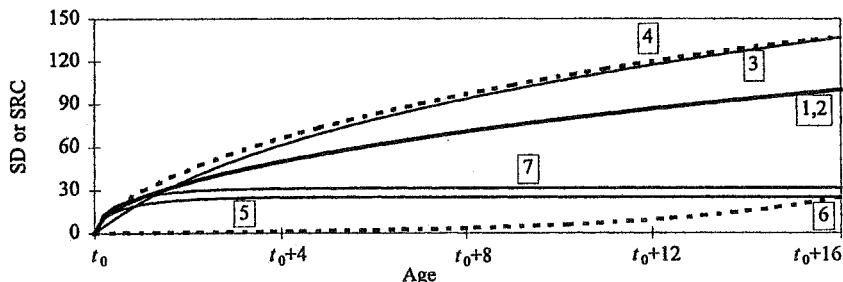


Figure 4.15. Standard deviation (SD) of size at age σ_T and square root of covariance (SRC) between an age and the oldest age t_0+16 for stochastic LVB-type models: 1, SD for a time model with a white-noise process; 2, corresponding SRC; 3, SD for a time model with a stationary correlation process; 4, corresponding SRC; 5, SD for a size model with a white-noise process; 6, corresponding SRC; and 7, SD for the Cohen-Fishman model. For all models, parameters used to generate the graph are $\mu_\infty = 100$, $\mu_k = 0.5$, $t_0 = 0$, and $\sigma = 25$.

However, it is quite often sufficient to proceed with further dynamics of populations with these statistical descriptors.

4.8. FECUNDITY AND MATURITY

The regenerative ability of a population is an important consideration in studies of population dynamics, as introduced in chapter 3. As many of the growth models in previous sections of this chapter have utility in modeling reproductive data, this section discusses the types of reproductive data and their use in constructing meaningful population variables. No attempt is made to present the logistical and sampling difficulties of obtaining reproductive data.

4.8.1. Maturity

The reproductive capacity of a population depends on how many individuals are sexually mature. Generally, sexual maturation is a function of the sex of an individual and its size. We denote the probability that an individual is sexually mature as $m_x(L)$, where x is the sex of an individual (f for females, m for males) and L is its length. We also refer to the probability of being mature as “maturity” itself, for brevity’s sake. The probabilities are generally equal to 0 below some critical size, $L_{1,x}$, increase beyond that size, and are equal to 1 above some critical size, $L_{2,x}$. The size at which 50% of the population is sexually mature, denoted $L_{50,x}$, is a commonly reported statistic. Alternatively, sexual maturity could be expressed in a frequentist sense as the proportion of individuals in a population from various size classes $\{l\}$, where l denotes the midpoint of the interval, resulting in proportions $\{m_{l,x}\}$ for each sex, x .

For later use in age-structured modeling, it is necessary to express sexual maturity as a function of age rather than size. There are at least two ways to do this. First, the process of sexual maturation could be viewed as a process of age instead of size, which would simply involve replacing subscript L or l above with t (or a) for age. The limitation of this approach is that it ignores potential interannual changes in maturity due to interannual changes in growth for the many populations where maturity is better related to size than age.

Second, the relationship between maturity and age could be obtained by transforming size to age via one of the growth curves $L(t)$ or $W(t)$ in sections 4.2 or 4.3. With $m_x(L)$ and $L_x(t)$ viewed as continuous functions, a maturity–age relationship can be easily constructed by forming

$$m_x(t) \equiv m_x [L_x(t)]. \quad (4.125)$$

The simplest model for sexual maturity is a ramp model from Quinn (1981):

$$m_x(L) = \begin{cases} 0, & \text{if } L < L_{1,x} \\ (L - L_{1,x})/(L_{2,x} - L_{1,x}), & \text{if } L_{1,x} \leq L \leq L_{2,x} \\ 1, & \text{if } L > L_{2,x}, \end{cases} \quad (4.126)$$

which has a linear increase between $L_{1,x}$ and $L_{2,x}$ (figure 4.16). Although this model is inflexible in shape, it may be sufficient in some applications. The statistic $L_{50,x}$ for this model is simply $(L_{1,x} + L_{2,x})/2$. This model could also be generalized to include an asymptotic maturity, m_∞ , in place of the value 1.

A common model for maturity is the logistic, where the rate of change is a parabolic function of size. From section 1.1.2 and Seber and Wild (1989), the model representation is

$$m_x(L) = \frac{m_\infty}{1 + e^{-\kappa(L-\gamma)}}, \quad (4.127)$$

where m_∞ , κ , and γ are the parameters of the model. Parameter m_∞ is the asymptotic maturity as $t \rightarrow \infty$, parameter κ represents curvature, and parameter γ is the size at which the inflection point occurs. This point at which the rate of change is maximum occurs at maturity $m_\infty/2$. The statistic $L_{50,x}$ for this model is

$$L_{50,x} = \gamma - \frac{1}{\kappa} \ln(2m_\infty - 1),$$

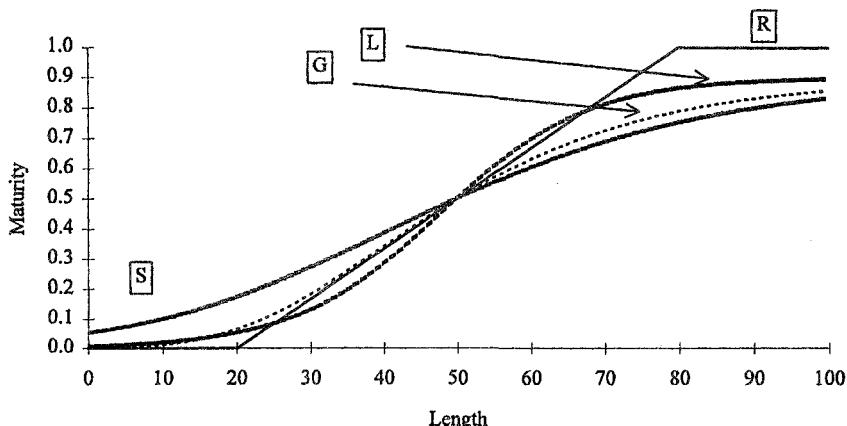


Figure 4.16. The relationship between maturity and length for the ramp (R), logistic (L), Gompertz (G), and Schnute (S) models. The asymptote for the ramp model is 1; for the others, 0.9. Parameter κ is 0.1 for the logistic, 0.05 for the Gompertz, and 0.043 for the Schnute. Parameter γ for the logistic is 47.8, for the Schnute, -0.45. Parameters for the Schnute are chosen so that $m(10) = 0.1$ and $m(90) = 0.8$. Parameter λ for the Gompertz is 0.359.

obtained from (4.127) by setting $m_x(L) = 1/2$ and solving for L . Hence, if $m_\infty = 1$, then γ is equivalent to $L_{50,x}$. A parameterization of the logistic in terms of an initial size and maximum growth rate by Fletcher (1974) was summarized by Seber and Wild (1989).

Any of the growth models of sections 4.1–4.3 can be considered for modeling the relationship of maturity to length or age. The S-shaped logistic curve is forced to have its inflection point half-way along the y -axis. In contrast, the Gompertz curve (section 4.3.3) has its inflection point at $1/e$ along the y -axis. For greater parametric control, the four- or five-parameter growth models of sections 4.3.4–4.3.6 must be used. A graphical comparison of some of these models is given in figure 4.16.

Parameter estimation follows analogously to that for growth models. An important consideration in this situation is the choice of error structure. Frequently, the data are considered as a set of simple random samples without replacement from individuals of a given sex in length (or age) categories, for which n_l is the number in length class $l = 1, \dots, J$, and y_l is the number of those that are mature. The likelihood equation is then a product of binomial distributions, so that the log likelihood can be written as

$$\ln \mathcal{L} = \sum_{l=1}^J \left[\ln \binom{n_l}{y_l} + y_l \ln m_l + (n_l - y_l) \ln(1 - m_l) \right], \quad (4.128)$$

where m_l is the true proportion of mature individuals. By letting m_l be defined from a model $m_x(L)$, it becomes a function of the model parameters, and consequently (4.128) can be maximized as a function of those parameters to get maximum likelihood estimates. Alternatively, it is common to use the normal approximation to the binomial when a large sample of maturity data is taken from each length class, which results in the use of nonlinear least squares with some type of weighting. The weighting could be done by sample size or the inverse of the estimated variance of the proportions.

Many growth models, including the ramp, logistic, LVB, Richards, Schnute, and Schnute-Richards, include a parameter for asymptotic size, which in this case represents asymptotic maturity, m_∞ . It may be desirable in many situations to set $m_\infty = 1$ for those species in which all individuals become mature. On the other hand, it is sometimes better to maintain the extra parametric control by estimating m_∞ . Statistical support for setting $m_\infty = 1$ can be found by fitting models with and without $m_\infty = 1$ and testing whether there is a significant improvement in fit, as described in section 4.3.5. Examination of parameter effects curvature and estimated correlations among parameters can be used to see if parameter estimates are stable (Bates and Watts 1988, Seber and Wild 1989).

4.8.2. Fecundity

One of the most notable characteristics of most fishes as compared to other taxonomic groups is their relatively high fecundity, which can be defined as the number of fertilized eggs produced by a mature female. For each species, a trade-off is made between the size of eggs and number of eggs produced from the amount of energy dedicated to reproduction. The trade-off may vary between individuals within a species and within an individual over time relative to environmental conditions.

The study of fecundity may start with the “gross” fecundity of a mature female—the number of eggs in the ovary. Then the fecundity of a female can be obtained by multiplying by the fertilization success rate, which may depend on the proportion of

mature males within spawning aggregations and other reproductive mechanisms. In any case, it is not unreasonable to assume that the fertilization rate is high. In many situations, collections may be taken just after fertilization, so that "fertilized" fecundity may be determined directly (e.g., Schmitt and Skud 1978).

Although the reproductive situation for many fish species consists of a single spawning event, there are many others, such as marine pelagic and tropical species, that have repeated spawning events during the reproductive season. In this situation, it is generally necessary to consider "batch" fecundity as the number of oocytes released in a single spawning by an individual and "annual fecundity" as the total number released by an individual during the spawning season (Hunter et al. 1985). Thus the frequency of spawning may be as important a consideration as the number of eggs (Hunter and Macewicz 1985).

The entry to modeling fecundity, whichever definition is used, relates fecundity to the volume, V_o , of eggs in the ovaries. If it is assumed that fecundity, \tilde{f} , is allometrically related (cf. section 4.1) to V_o with lognormal error, then the relationship can be written

$$\tilde{f} = \alpha_0 V_o^{\beta_0} e^{\epsilon_0}. \quad (4.129)$$

The lognormal error could represent process error due to different conditions or measurement error in determining fecundity. Note that this assumption includes a proportional relationship (with error) when $\beta_0 = 1$, which is the typical situation. The allometric constant may be necessary when egg size differs among individuals of different sizes. Egg size may be an important consideration in survival to later stages of life, which is often termed "viability."

If it is then assumed that V_o is allometrically related (with error) to body volume, V , with parameters α_1 , β_1 , and ϵ_1 , the relationship can be written similar to (4.129). After some algebra, one can deduce that the relationship between fecundity and volume is

$$\tilde{f} = \alpha_0 \alpha_1^{\beta_0} V^{\beta_0 \beta_1} e^{\epsilon_0 + \beta_0 \epsilon_1} = \alpha_2 V^{\beta_2} e^{\epsilon_2},$$

showing the propagation of the allometric relationship with error. Now, if it is assumed that V is allometrically related to weight, W , with error and that W is allometrically related to length, L (or some other measure of size), then it follows that fecundity is allometrically related to weight and length with error, or

$$\tilde{f} = \alpha_3 W^{\beta_3} e^{\epsilon_3} = \alpha_4 L^{\beta_4} e^{\epsilon_4}. \quad (4.130)$$

For the special case where each relationship is proportional (e.g., $\beta_0 = \beta_1 = \dots = 1$), then the parameter $\beta_3 = 1$. For the special case where, in addition, isometric growth occurs (cf. section 4.1), then the parameter $\beta_4 = 3$. If a different error structure is used in the above relationships (such as additive error), the simple allometric propagation does not occur.

Parameter estimation is the same as for weight-length relationships in section 4.1. For the relationships in (4.130), this would involve making log transformations of the variables and fitting simple linear regressions. If fecundity is measured from subsamples of the ovary, it may be possible to obtain variance estimates of the fecundity data. Then weighted regression could be used, with the weights inversely proportional to the variance estimates (cf. Draper and Smith 1981).

Given the correspondence between fecundity and weight, it follows that any of the weight-age models in section 4.3 would be ideal for determining the relationship between fecundity and age. Parameter estimation requires the choice of an error structure, such as additive or multiplicative. As fecundity is actually an integer quantity, one might suppose that using a discrete rather than a continuous distribution might be important. However, given the variation in fecundity and the large numbers involved, the continuous approximation to the discrete is generally sufficient.

4.8.3. Population Statistics and the Egg Production Method

With the previous models for maturity and fecundity as a function of size or age, it is now possible to calculate population statistics useful for analyses in later chapters. Anticipating later modeling work where subscript t will be used for time, we use subscript a for age in place of t . Subscript x still denotes sex. What follows are calculations as a function of age; the identical quantities as a function of size can be made by substituting l for a . The following development uses discrete ages; the continuous analogue substitutes integrals for summations. We let r be the starting age and A be the oldest age. The starting age may be thought of as the first age of recruitment into the fishery.

Population statistics

In a population sense, a new measure of fecundity, “net fecundity,” is used to represent the average number of fertilized eggs per female, rather than per mature female. This variable is the product of maturity and fecundity, or

$$\tilde{f}_a = m_{a,f} \tilde{f}_a. \quad (4.131)$$

For species with multiple spawning batches, annual fecundity would be used for \tilde{f}_a .

Let age- and sex-specific abundance and average weight be denoted

$N_{a,x}$ = abundance at age a and sex x

$W_{a,x}$ = weight at age a and sex x .

Sex-specific recruitment is then $N_{r,x}$, so total recruitment is $N_r = N_{r,f} + N_{r,m}$.

The population statistics of interest are

$S_{N,x}$ = spawning abundance for sex x

$S_{B,x}$ = spawning biomass for sex x

and $N_0 \equiv \mathcal{E}$ = egg production.

From egg production and recruitment, it is possible to determine survival from the egg stage to the age of recruitment, which we call “early life survival.” Early life survival, denoted S_0 , is the number of recruits divided by the egg production, or

$$S_0 = N_r / \mathcal{E}. \quad (4.132)$$

Formulae for spawning abundance, spawning biomass, and egg production, respectively, are

$$\mathcal{S}_{N,x} = \sum_{a=r}^A m_{a,x} N_{a,x} = \sum_{a=r}^A \mathcal{S}_{N,a,x}, \quad (4.133)$$

$$\mathcal{S}_{B,x} = \sum_{a=r}^A m_{a,x} N_{a,x} W_{a,x} = \sum_{a=r}^A \mathcal{S}_{B,a,x}, \quad (4.134)$$

$$\mathcal{E} = \sum_{a=r}^A f_a N_{a,f} = \sum_{a=r}^A \mathcal{E}_a. \quad (4.135)$$

The eggs equation only uses female abundance, assuming that a sufficient amount of male sex product is available to fertilize eggs. Total spawning abundance and biomass are sums over sex, resulting in $\mathcal{S}_N = \mathcal{S}_{N,f} + \mathcal{S}_{N,m}$ and $\mathcal{S}_B = \mathcal{S}_{B,f} + \mathcal{S}_{B,m}$.

For many populations, sex-specific abundance is not determined, so that only N_a and W_a are available. Quite often, spawning abundance, spawning biomass, and egg production are calculated using female maturity and fecundity data as

$$\mathcal{S}_N = \sum_{a=r}^A m_a N_a = \sum_{a=r}^A \mathcal{S}_{N,a}, \quad (4.136)$$

$$\mathcal{S}_B = \sum_{a=r}^A m_a N_a W_a = \sum_{a=r}^A \mathcal{S}_{B,a}, \quad (4.137)$$

$$\mathcal{E} = \sum_{a=r}^A f_a N_a = \sum_{a=r}^A \mathcal{E}_a. \quad (4.138)$$

The formula for early life survival is the same. Clearly, spawning abundance and biomass are overestimated when male maturation occurs earlier than female maturation. Egg production is always overestimated, which leads to underestimation of early life survival. If the sex ratio does not change too much over time, these statistics may still be useful in the sense that they are proportional to their true counterparts.

Potential improvements might include the use of average maturity over sex or maturity weighted by sex ratio and the redefinition of fecundity to be the average number of fertilized eggs per individual rather than just females. However, fishing can induce changes in sex ratio over age (Deriso and Quinn 1983), so these improvements might be illusory if not followed closely.

One other modification to the definition of fecundity is sometimes made in age-structured models. When male abundance is sufficiently large to provide fertilization of all egg production, then it is only necessary to model the female population. Male abundance can be inferred from the expected sex ratio given a differential mortality model (Quinn 1981). Fecundity is defined in this situation to be the average number of fertilized eggs that will result in females on a per-female basis. This definition of fecundity can be calculated as

$$f_a^* = \chi m_a \tilde{f}_a = \chi f_a, \quad (4.139)$$

where χ is the proportion of fertilized eggs that will result in females. An example of this approach is in Quinn (1981).

With these statistics, several important analyses can be undertaken. Analysis of spawner-recruit relationships (chapter 3) use these three statistics as “spawners.” Spawning abundance, biomass, and egg production per recruit are used in age-structured models to determine acceptable values of fishing mortality and other control parameters (chapters 6 and 11). Renewal theory requires this information to generate subsequent recruitment (chapters 7, 9, and 10). Catch-at-age (chapter 8) and catch-at-length (chapter 9) analyses use spawning information to help stabilize the estimation process.

Egg production method

One important use of egg production statistics is to estimate spawning biomass from egg production surveys (e.g., Hewitt 1985, Smith and Hewitt 1985). A comprehensive overview of the egg production method is found in the report edited by Lasker (1985a), which contains several essays related to modeling, parameter estimation, sampling, aging and staging eggs, and other implementation details. This method compares favorably with a direct survey of larvae, despite the higher aggregation of eggs (Hewitt 1985). The method assumes that a sample of eggs per unit area is unbiased for the true eggs per unit area, that spawning and nonspawning adults are equally available to sampling gear to determine maturity and sex ratio, and that the entire spawning area is sampled representatively in space and time.

The essential basis of the method relies on the relationship between egg production and spawning biomass. If it is assumed that fecundity is proportional to weight (i.e., $\tilde{f}_a = \alpha W_a$) and that the constant of proportionality, α , is known, then (4.138) becomes

$$\mathcal{E} = \alpha \sum m_a W_a N_a = \alpha \mathcal{S}_B. \quad (4.140)$$

Hence an estimate of spawning biomass from egg production is simply

$$\hat{\mathcal{S}}_B = \mathcal{E}/\alpha. \quad (4.141)$$

The egg production method is frequently used with marine pelagic fish, which often are batch spawners (Lasker 1985a). One implementation of the method is applied to the average daily estimate of egg production and ignores complications of age-specific parameters (Stauffer and Picquelle 1980, Parker 1985). In this situation, the estimating equation for spawning biomass is

$$\hat{\mathcal{S}}_B = PA W_f / (\chi_1 \chi_2 \tilde{f}), \quad (4.142)$$

where A is population area, $P = (\mathcal{E}/\tau)/A$ is average egg production per day (τ) per unit area, W_f is average weight of mature females, χ_1 is sex ratio (fraction of spawning population that are mature females, by weight), χ_2 is the fraction of mature females spawning per day, and \tilde{f} is batch fecundity (number of eggs spawned per mature female per batch). Variance estimation and sampling formulae are given by Parker (1985) and Picquelle and Stauffer (1985).

Example 4.9. Northern anchovy off California and Baja California

Northern anchovy surveys of egg production have been conducted since 1980 (Lasker 1985b). In 1984, the following statistics were obtained (Picquelle and Stauffer 1985):

Average daily egg production: $\mathcal{E}/\tau = PA = 12.98 \times 10^{12}$ eggs/day,

Average mature female weight: $W_f = 12.02$ g,

Mature sex ratio: $\chi_1 = 0.582$ mature females per total mature individuals,

Spawning fraction: $\chi_2 = 0.160$ spawning females per mature female,

Batch fecundity: $\tilde{f} = 5485$ eggs per batch per mature female.

Applying (4.142), the estimated 1984 spawning biomass was $\widehat{\mathcal{S}}_B = 305 \times 10^3$ tons, which differs slightly from the reported 309×10^3 tons, perhaps due to rounding. ■

Delay-Difference Models

The class of delay-difference models represents a middle ground between simple, but biologically unrealistic, production models and complicated vector-based age-specific population models. They differ fundamentally from production models in chapter 2 in that delay-difference models explicitly contain the age-structured dynamics of a population, including the lag between spawning and recruitment. The reduction in complexity over formal vector-based models is possible because of simplifying assumptions about the dynamics of the population. A series of delay-difference models of increasing complexity is described in this chapter. We begin with models for which individual size or age does not affect survival or fecundity of adult individuals (i.e., individuals at least r years of age), such as discussed by Allen (1963), Clark (1976b), Deriso (1978, 1980, 1985a), Schnute (1985), and Bergh and Getz (1988).

5.1. ALLEN-CLARK ABUNDANCE MODELS

We will show in chapter 7 that a comprehensive age-based population model known as the Leslie matrix model can be written as

$$\mathbf{N}_{t+1} = \mathbf{M}\mathbf{N}_t,$$

where the elements of the projection matrix \mathbf{M} are coefficients of age-specific annual survival, ℓ_a , or age-specific net fecundity, f_a , and where the vector \mathbf{N}_t represents abundance by age $\{N_{a,t}\}$ for the population at the beginning of year t . A nonlinear model can also be considered in the matrix formulation above by regarding elements of that matrix as functions of other variables.

The Leslie matrix system can be collapsed into a discrete model based on total adult population abundance by making the following assumptions: (1) assume $f_a = 0$ (i.e., no reproduction for ages $a < r$), (2) assume $f_a = f$ (i.e., annual fecundity is independent of age for ages $a \geq r$), and (3) assume $\ell_{a,t} = \ell_t$ (i.e., annual survival is independent of age for ages $a \geq r$).

Let r be the “knife-edge” age of recruitment; ℓ_t be the annual survival fraction for adults; $N_{r,t+1}$ be the number of recruits in year $t + 1$; and $N_{t+1} = \sum_{a=r}^{\infty} N_{a,t}$, the number of adults at the start of year $t + 1$. With assumption 3, the total abundance of adults next year can be written as the sum of adults that survive this year plus recruits:

$$\begin{aligned}
 N_{t+1} &= \sum_{a=r}^{\infty} N_{a,t+1} \\
 &= \sum_{a=r+1}^{\infty} \ell_t N_{a-1,t} + N_{r,t+1} \\
 &= \ell_t N_t + N_{r,t+1},
 \end{aligned}$$

or, in words,

$$\text{Adults}_{t+1} = \text{Surviving Adults}_t + \text{Recruitment}_{t+1}. \quad (5.1)$$

The final step to derive the Allen-Clark delay-difference model is to assume that recruitment is a function of the number of adults present at the time at which they hatch, which is an elaboration of assumptions 1 and 2 above. Then,

$$N_{t+1} = \ell_t N_t + \mathcal{F}(N_{t+1-r}), \quad (5.2)$$

where $N_{r,t+1} = \mathcal{F}(N_{t+1-r})$ is the assumed spawner-recruit function.

At equilibrium, we have the relationship

$$N_* = \frac{1}{(1 - \ell_*)} \mathcal{F}(N_*). \quad (5.3)$$

Figure 5.1 shows the right side of (5.3), which is recruitment scaled by the factor $1/(1 - \ell)$ as a function of N , along with the replacement line. This graph is reminiscent of the discrete generation population models covered in section 3.3 except for the scaling. The scaling occurs because recruitment must be higher to offset losses due to natural mortality. The results on stability and optimal harvesting with the population model (5.2) have many similarities to those of semelparous population models (section 3.3), as shown by Clark (1976b).

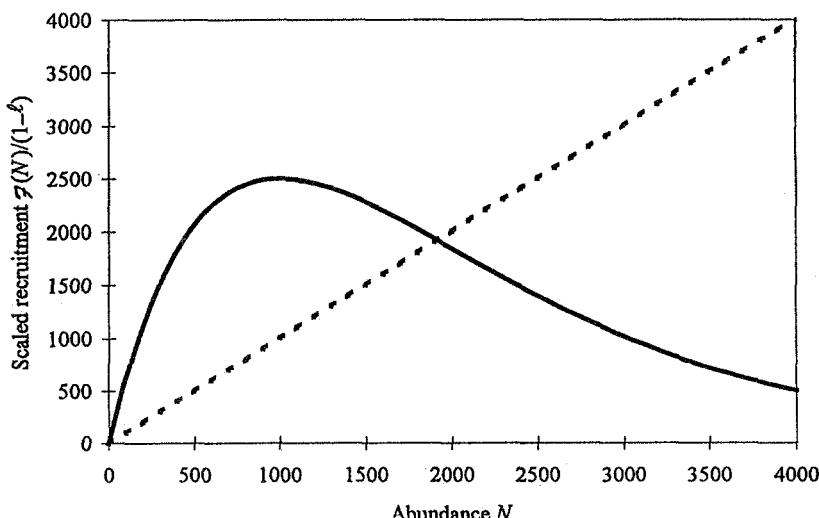


Figure 5.1. Scaled recruitment, $\mathcal{F}(N)/(1 - \ell)$, as a function of abundance, N , for the Allen-Clark model and the corresponding replacement line. The intersection of the two lines shows the equilibrium point.

Linearization of (5.2) about equilibrium (5.3) yields a criterion to determine stability. We show results for the case where adult survival fraction is constant, $\ell_t = \ell$. To see this derivation, let

$$z_t = N_t - N_*,$$

then

$$z_{t+1} = \ell z_t + \mathcal{F}(N_{t+1-r}) - \mathcal{F}(N_*).$$

By taking the first-order Taylor expansion of $\mathcal{F}(N)$ around equilibrium value $F(N_*)$, we get a local approximation

$$z_{t+1} \approx \ell z_t + Dz_{t+1-r},$$

where

$$D = \frac{d}{dN} [\mathcal{F}(N)]|_{N=N_*} = \mathcal{F}'(N_*).$$

Now substitute $y^t = z_t$ into the above linear equation and simplify to derive the characteristic equation, a r th-order polynomial,

$$y^r - \ell y^{r-1} - D = 0.$$

The solution z_t is locally stable if and only if all roots of the characteristic equation have modulus $|y| < 1$. A sufficient condition for stability is given by Clark (1976b) as

$$\text{Stable if } \left| \frac{D}{(1-\ell)} \right| < 1, \quad (5.4)$$

which is weaker than the result for semelparous population models, where $|D| < 1$ is the necessary and sufficient condition for local stability. Necessary conditions for local stability of (5.2) are available for specific values of age of recruitment, r , in Clark (1976b), Deriso (1978), and Bergh and Getz (1988). Some results on global stability are given in Deriso (1978) and Fisher and Goh (1984).

Fishery exploitation can be introduced into the delay-difference model (5.2) in a number of ways, as discussed by Schnute (1985), but we shall confine our presentation to the structure given by Clark (1976b) which also will be followed later in the derivation of biomass models. Assume that fishing occurs during the first part of a year and that natural mortality is negligible during that part of the year but occurs during the rest of the year. Spawning is assumed to occur after fishing. Let $S_t = N_t - C_t$, the escapement of adults from the fishery; C_t = be the catch in number of individuals in year t ; and ℓ = be the annual survival from natural sources. Note here that ℓ is redefined to be survival only from natural sources, not total annual survival from all sources. Annual survival is $\ell_t = \ell S_t / N_t$, the product of natural survival and survival from harvesting (ℓ_t is often written S_t in other chapters). Equation (5.2) is then modified to be

$$N_{t+1} = \ell S_t + \mathcal{F}(S_{t+1-r}). \quad (5.5)$$

Maximum sustainable yield (MSY) can be found at equilibrium,

$$\begin{aligned}\text{MSY} &= \max_S C_* \\ &= \max_S N_* - S \\ &= \max_S \ell S + \mathcal{F}(S) - S,\end{aligned}$$

which, by differentiation and setting to 0, implies

$$\mathcal{F}'(S_m) = 1 - \ell, \quad (5.6)$$

where S_m is the optimal escapement at MSY. This result is analogous to the necessary condition for MSY found in section 3.3 for semelparous population models [$\mathcal{F}'(S_m) = 1$].

A simple generalization of the result in (5.6) to stochastic delay-difference models is possible for the calculation of optimal fixed escapement policies. Let the stochastic population model with a fixed escapement policy be written as

$$N_{t+1} = \ell S_t + \mathcal{F}(S_t) e^{\epsilon_{t+1-r}},$$

where the model is the same as that given in (5.5), except a normal random variable, $\epsilon_{t+1-r} \sim N(0, \sigma^2)$, has been added in a log normal multiplicative manner to the spawner-recruitment function, which is a common assumption about stochasticity. In this model, maximum expected yield occurs by choosing a fixed escapement, S_* , which approximately satisfies the condition

$$\max_{S_*} [\ell S_* + \mathcal{F}(S_*) e^{\sigma^2/2} - S_*].$$

This leads to an approximate necessary condition similar to (5.6), except for the addition of a variance correction factor:

$$\mathcal{F}'(S_m) = (1 - \ell) e^{-\sigma^2/2}.$$

Example 5.1. Antarctic fin whales

Clark (1976b) applied delay-difference model (5.5) to Antarctic fin whales. Recruitment was taken to be the quadratic function

$$\mathcal{F}(S) = rS \left(1 - \frac{S}{K}\right).$$

Parameter values used in the model (5.5) are $r = 0.12$, $K = 600,000$, and $\ell = 0.96$. The unfished equilibrium population is found by solving (5.3) to get

$$\begin{aligned}N_* &= K \left(1 - \frac{1 - \ell}{r}\right) \\ &= 400,000.\end{aligned}$$

Stability is not confirmed by applying the sufficient criterion (5.4) because $D = r(1 - 2N_*/K) = -0.04$ and hence $D/[1 - \ell] = -1$, which lies on the border of the stability criterion. Clark (1976b) showed that this model is stable, however, for specific values

of the age of recruitment, $r > 1$. Maximum sustainable yield can be found by solving for the optimal escapement in (5.6)

$$r(1 - 2S_m/K) = 1 - \ell,$$

so that $S_m = 200,000$.

More generally, the model (5.5) with quadratic spawner-recruit function $\mathcal{F}(S) = rS(1 - S/K)$ always has optimal escapement occurring at one-half the unfished equilibrium population, which is a familiar result from the similar Graham-Schaefer production model (chapter 2). One caveat about using a quadratic function for whales is that the optimal escapement may in reality be higher than 50% of the pristine level.

■

5.2. DERISO-SCHNUTE BIOMASS MODELS

5.2.1. Deriso's Model

A limitation of the Allen-Clark delay-difference model is that it ignores the effects of individual growth on the dynamics of the stock. We consider next the model of Deriso (1980) in which the average weight of a catchable adult (of age $a > r$) is assumed to follow a special case solution (4.17) of the Ford growth equation described in section 4.2.2. Growth can be written in at least three equivalent forms: as a closed-form solution, as a first-order difference equation (one initial condition), or as a second-order difference equation (two initial conditions). The growth model presented by Deriso (1980) is a special case solution to the more general Ford model (4.18) in which the growth equation is constrained by an initial condition $W_{r-1} = 0$. The three equation forms, which describe growth of individuals older than recruitment age, $a > r$, are given, respectively, by

$$\begin{aligned} W_a &= W_r \frac{1 - \rho^{1+a-r}}{1 - \rho} \\ &= W_\infty(1 - \rho) + \rho W_{a-1} \\ &= (1 + \rho)W_{a-1} - \rho W_{a-2}, \end{aligned} \quad (5.7)$$

where $W_{r-1} = 0$ is an initial condition for the Deriso (1980) model; ρ = Ford growth parameter $\rho = \exp(-\kappa)$ (no units); r = age of recruitment of individuals to the fishery; and $W_\infty = W_r/(1 - \rho)$, asymptotic weight. Derivation of the Deriso (1980) delay-difference model requires two assumptions: (1) age-specific weight, W_a , is given by (5.7) for ages $a \geq r$ and (2) annual survival $\ell_{a,t} = \ell_t$ for ages $a \geq r$.

Total biomass of adults at the start of any given year can be written as the total biomass of adults that survive the previous year plus recruits. The three keys to the derivation are first, that weight, W_a , can be expanded into the second-order difference equation (5.7); second, that abundance can be written as

$$N_{a,t+1} = \ell_t N_{a-1,t} = \ell_t \ell_{t-1} N_{a-2,t-1} \quad \text{for ages } a \geq r + 2;$$

and third, that terms involving W_{r-1} are zero because of the initial condition constraint $W_{r-1} = 0$ in (5.7). Then,

$$\begin{aligned}
B_{t+1} &= \sum_{a=r}^{\infty} W_a N_{a,t+1} \\
&= W_r N_{r,t+1} + \sum_{a=r+1}^{\infty} \ell_t [(1+\rho)W_{a-1} - \rho W_{a-2}] N_{a-1,t} \\
&= W_r N_{r,t+1} + \sum_{a=r+1}^{\infty} \ell_t (1+\rho) W_{a-1} N_{a-1,t} \\
&\quad - \sum_{a=r+2}^{\infty} \rho \ell_t \ell_{t-1} W_{a-2} N_{a-2,t-1} \\
&= (1+\rho) \ell_t B_t - \rho \ell_t \ell_{t-1} B_{t-1} + W_r N_{r,t+1}. \tag{5.8}
\end{aligned}$$

Equation (5.8) states that the biomass at the start of year $t+1$ is the sum of exponential growth of surviving adults in year t minus a growth correction term to dampen exponential growth plus biomass of recruits. If we further assume that recruitment is a function of adult biomass present at the time of their birth, then

$$B_{t+1} = (1+\rho) \ell_t B_t - \rho \ell_t \ell_{t-1} B_{t-1} + \mathcal{F}_B(B_{t+1-r}), \tag{5.9}$$

where $\mathcal{F}_B(\cdot)$ is a spawner-recruit function between the biomass of fish in the adult catchable population and the biomass of recruits.

At equilibrium, we have the relationship

$$B_* = \frac{1}{(1-\rho\ell_*)(1-\ell_*)} \mathcal{F}_B(B_*). \tag{5.10}$$

Linearization of (5.9) about equilibrium (5.10) yields a criterion to determine stability. We show results for the case for which adult survival fraction is constant, $\ell_t = \ell$. As in the derivation of (5.4), we let $z_t = B_t - B_*$ and then expand the right side of (5.9) in a Taylor series. By neglecting high order terms and replacing z_t by y^t , the characteristic equation for (5.9) is

$$y^r - (1+\rho)\ell y^{r-1} + \rho\ell^2 y^{r-2} - D = 0,$$

where $D = \mathcal{F}'_B(B_*)$. The solution z_t is locally stable if and only if all roots of the characteristic equation have modulus $|y| < 1$. A sufficient condition for stability is given by Deriso (1978) as

$$\text{Stable if } |(1+\rho)\ell| + |\rho\ell^2| + |D| < 1, \tag{5.11}$$

which reduces to the same inequality as given for the Allen-Clark model in (5.4) when $\rho = 0$, such as when growth is zero for the catchable adults. Necessary and sufficient conditions for local stability for the model (5.9) are given for low values of r by Deriso (1978) and by Bergh and Getz (1988). Some results on global stability are given by Deriso (1978).

Fishery exploitation can be introduced in the biomass delay-difference model in the same way as done previously for the abundance model (5.5). Assume that fishing occurs

during the first part of a year and natural mortality occurs only for the remainder of the year. Spawning is assumed to occur after fishing. Let $\mathcal{S}_t = B_t - Y_t$, the escapement in biomass from the fishery; Y_t be the yield in biomass; $\mathcal{F}_B(\mathcal{S}_{t+1-r})$ be the recruit biomass as a function of spawning biomass; and ℓ be the annual survival from natural sources. Then total annual survival can be written $\ell_t = \ell \mathcal{S}_t / B_t$. Hence, the version of (5.8) with harvesting is

$$B_{t+1} = (1 + \rho) \ell \mathcal{S}_t - \rho \ell^2 \frac{\mathcal{S}_t}{B_t} \mathcal{S}_{t-1} + \mathcal{F}_B(\mathcal{S}_{t+1-r}). \quad (5.12)$$

Maximum sustainable yield can be found at equilibrium:

$$\begin{aligned} \text{MSY} &= \max_{\mathcal{S}} Y_* \\ &= \max_{\mathcal{S}} B_* - \mathcal{S} \\ &= \max_{\mathcal{S}} (1 + \rho) \ell \mathcal{S} - \rho \ell^2 \frac{\mathcal{S}^2}{B_*} + \mathcal{F}_B(\mathcal{S}) - \mathcal{S}, \end{aligned}$$

which, as shown by Deriso (1980), implies

$$R_r \mathcal{F}'_B(\mathcal{S}_m) = 1 - R_r \rho \ell^2 \left(1 - \frac{\mathcal{S}_m}{B_m}\right)^2 \quad (5.13)$$

where \mathcal{S}_m = optimal escapement at MSY, and $R_r = 1 / [(1 - \rho \ell)(1 - \ell)]$. The function R_r is the lifetime reproduction of a unit biomass of recruits in the unexploited population. The result in (5.13) is similar to the necessary condition for MSY found in section 5.1 for the Allen-Clark abundance model, except that the effect of continuing growth of adults is to lower the slope of the spawner-recruit function at MSY, which reflects a trade-off between yield-per-recruit optimization and spawner-recruit optimization. Deriso (1980) showed that the inclusion of a discount factor into the objective function for harvesting works in the opposite direction—that is, future growth does not count as much. Note in (5.13) that the term $(1 - \mathcal{S}_m / B_m)$ is just the exploitation rate, μ_m , so there is a connection between optimal exploitation rate and the slope of the spawner-recruit curve at the optimal escapement level.

Example 5.2. Yellowfin tuna in the eastern tropical Pacific Ocean

In many applications, a simple method of estimating MSY is to plot equilibrium yield, Y_* , for various levels of equilibrium fishing effort. There are two steps needed for such an approach. First, an equation is needed that relates annual yield to annual fishing effort and biomass of the population. A simple relationship is $Y_t = (1 - e^{-qE_t}) B_t$, which corresponds to the assumption that fishing takes place during each time period before any natural mortality occurs (see section 5.3.4). In the case of quarterly data on yellowfin catch and effort, such a sequence of events (fishing then natural mortality) is an approximation to continuous occurrence of both events.

An equation is needed where equilibrium biomass is given as a function of fishing effort. A Beverton-Holt spawner-recruit function (3.6) was used in this application with the additional assumption that spawning takes place prior to the fishery in each time period. An equation for equilibrium biomass is obtained by solving for B_* in (5.10) to get

$$B_* = \frac{1}{\beta} \left[\frac{\alpha}{(1 - \rho \ell_*)(1 - \ell_*)} - 1 \right],$$

where $\ell_* = e^{-qE_* - M}$. Figure 5.2 was generated by calculating Y_* for various values of E_* . The two curves shown in figure 5.2 correspond to a lower equilibrium yield for yellowfin before 1983 (where $\beta = 2.72 \times 10^{-5}$) versus after 1983 (where $\beta = 1.67 \times 10^{-5}$). Maximum sustainable yield occurs at roughly 6,000 days per quarter of standard purse seine fishing. Parameter values used for the figure are as follows: $\rho = 1.1$, $M = 0.2$, $\alpha = 0.711$, and $q = 2.31 \times 10^{-5}$; these latter two values are maximum likelihood estimates obtained in example 5.4 later. ■

5.2.2. Schnute's Extension

The biomass delay-difference model (5.8) contains a two-parameter growth model primarily for the sake of parsimony, which may fit some data on fish weights rather poorly. Schnute (1985) showed how to derive a more general three-parameter growth model by relaxing the assumption of $W_{r-1} = 0$, made for the derivation of (5.8). In particular, if a more general solution of the Ford growth equation is sought for which W_{r-1} can take on arbitrary values, then the closed-form solution from (4.18) is

$$W_a = W_{r-1} + (W_r - W_{r-1}) \frac{1 - \rho^{1+a-r}}{1 - \rho}, \quad (5.14)$$

instead of the first equation in (5.7). The first-order and second-order difference equations in (5.7) are still valid under this more general growth model, although asymptotic weight in the model (5.14) is given by $W_\infty = W_{r-1} + (W_r - W_{r-1})/(1 - \rho)$. Because W_{r-1} is nonzero here, the term $W_{r-1}N_{r,t}$ does not drop out in the third line of the derivation leading to (5.8), which leads to the delay-difference model:

$$B_{t+1} = (1 + \rho)\ell_t B_t - \rho \ell_t \ell_{t-1} B_{t-1} + W_r N_{r,t+1} - \rho \ell_t W_{r-1} N_{r,t}. \quad (5.15)$$

As in (5.12), introduction of a spawner-recruit function and harvest (with $\ell_t = \ell S_t / B_t$) into (5.15) leads to

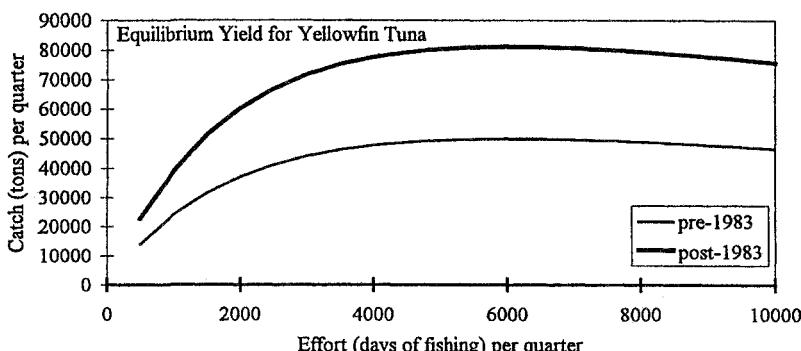


Figure 5.2. Equilibrium yield as a function of fishing effort for yellowfin tuna in the eastern tropical Pacific Ocean from the Deriso delay-difference model. Different curves are shown for the population before 1983 and after 1983.

$$\begin{aligned} B_{t+1} = & (1 + \rho)\ell S_t - \rho\ell^2 \frac{S_t}{B_t} S_{t-1} + \mathcal{F}_B(S_{t+1-r}) \\ & - \rho\ell \frac{S_t}{B_t} \frac{W_{r-1}}{W_r} \mathcal{F}_B(S_{t-r}). \end{aligned} \quad (5.16)$$

Other extensions of this approach are given in section 5.3.

5.2.3. Moments of the Weight Distribution of Adults

The biomass delay-difference model framework can be generalized to provide information about the moments of the distribution of weight of adults. Because the moments (particularly higher-order ones) generally require information on the size frequency of catch, the theory in this section is not often used in practice; instead, the catch-at-age and catch-at-size methods of chapters 8 and 9 are applied to such data.

We begin with an alternative representation to (5.16), as given by Fournier and Doonan (1987), where they derived that delay-difference model using the first-order growth model above (5.7), again with the generalization that W_{r-1} is not constrained to zero. This leads to a coupled set of equations with an abundance delay-difference model coupled to a biomass predictor equation:

$$\begin{aligned} N_{t+1} &= \ell_t N_t + N_{r,t+1} \\ B_{t+1} &= \rho\ell_t B_t + W_\infty(1 - \rho)\ell_t N_t + W_r N_{r,t+1}. \end{aligned} \quad (5.17)$$

These equations provide a framework for the inclusion of additional information into an estimation procedure for delay-difference models because both numbers of fish in the catch and biomass of fish in the catch can be accommodated.

A convenient way to interpret abundance and biomass of a population is in relationship to the moments of the distribution of weights of individuals in the adult population. Define the unnormalized n th moment of weight as

$$T_t^{[n]} = \sum_{a=r}^{\infty} W_a^n N_{a,t}, \quad (5.18)$$

then we have

$$\begin{aligned} T_t^{[0]} &= N_t \\ T_t^{[1]} &= B_t. \end{aligned}$$

Higher-order moments can be derived by applying the binomial theorem to the first-order Ford growth equation, as shown in Fournier and Doonan (1987) and in Schnute (1987). The binomial theorem states that

$$(a + b)^n = \sum_{j=0}^n \binom{n}{j} a^{n-j} b^j,$$

which applied to the first-order Ford growth equation above (5.7) yields

$$W_a^n = \sum_{j=0}^n \binom{n}{j} [W_\infty(1-\rho)]^{n-j} (\rho W_{a-1})^j.$$

By multiplying the expression above by $N_{a,t} = \ell_{t-1} N_{a-1,t-1}$ and summing over ages $a > r$, we find

$$\begin{aligned} \sum_{a=r+1}^{\infty} W_a^n N_{a,t+1} &= \ell_t \sum_{j=0}^n \binom{n}{j} [W_\infty(1-\rho)]^{n-j} \rho^j \sum_{a=r+1}^{\infty} W_{a-1}^j N_{a-1,t} \\ T_{t+1}^{[n]} - W_r^n N_{r,t+1} &= \ell_t \sum_{j=0}^n \binom{n}{j} [W_\infty(1-\rho)]^{n-j} \rho^j T_t^{[j]}. \end{aligned}$$

For example, the second unnormalized moment of weight can be written as a difference equation coupled to lower-order moments:

$$T_{t+1}^{[2]} - W_r^2 N_{r,t+1} = \ell_t [W_\infty(1-\rho)]^2 T_t^{[0]} + 2\ell_t W_\infty(1-\rho) \rho T_t^{[1]} + \ell_t \rho^2 T_t^{[2]}. \quad (5.19)$$

The central moments are functions of the $T_t^{[n]}$. The first two central moments, the mean and variance, are as follows:

$$\begin{aligned} \bar{W}_t &= T_t^{[1]} / T_t^{[0]} \\ \sigma_{W,t}^2 &= T_t^{[2]} / T_t^{[0]} - \bar{W}_t^2, \end{aligned} \quad (5.20)$$

where at the start of year t , \bar{W}_t is the mean weight of adults in the population; $\sigma_{W,t}^2$ is the variance of weight of adults in the population; and $T_t^{[n]}$ is the noncentral and unnormalized moment of weight of adults.

The moment equations (5.19) provide model structure to statistics that could be collected on the weight distribution in the adult population, as inferred by sampling the catch. There is information about recruitment in the changes in mean and variance of weight of the adult population. Figure 5.3 illustrates this fact by showing that mean weight and variance of weight both oscillate over time in response to a sinusoidal recruitment pattern. Because biomass of the adult population also oscillates in response to the sinusoidal recruitment, it is not clear how much additional information is provided by changes in the mean and variance of weight. Estimation of parameters in related delay-difference models for moments are dealt with by Fournier and Doonan (1987), Schnute (1987), Fournier and Warburton (1989), and Schnute et al. (1989a, b).

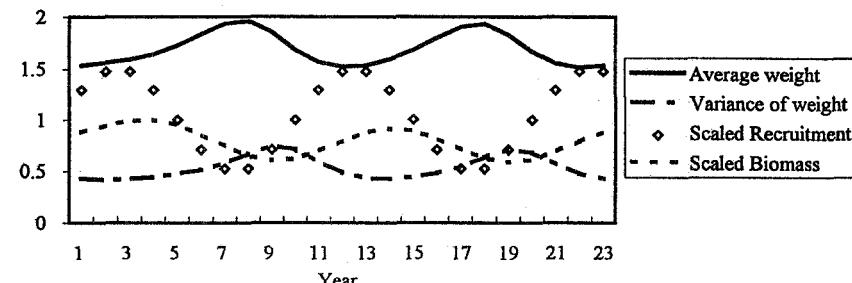


Figure 5.3. Mean and variance of weight of adults in response to a sinusoidal recruitment pattern. Also shown are scaled recruitment and adult biomass.

Without loss of generality, we could replace the definition of W_a as a weight measure by any other metric, for example length, and the derivations give us moments for the distribution of that metric. The key is the validity of the first-order linear model in (5.7). For example, logarithm of length may be a suitable metric, as suggested by Deriso and Parma (1988).

5.3. ALTERNATIVE MODELS AND REPRESENTATIONS

5.3.1. Use of a Net Growth Parameter

If measurements of the average weight of the total adult population are available, then alternative parameterizations of the delay-difference models may be advantageous. As shown in (5.17), the second lag term in (5.15) (the one with ℓ_{t-1}) can be replaced by a term with a lag of time t . We can write the model for biomass dynamics by substituting for N_t a term involving biomass, B_t , and mean weight, $\mu_{W,t}$, as defined in (5.20) and derived by Hilborn and Walters (1992), as

$$B_{t+1} = g_t \ell_t B_t + W_r N_{r,t+1}, \quad (5.21)$$

where

$$g_t = [\rho + W_\infty(1 - \rho)]/\bar{W}_t$$

is net growth of the adult population. By changing the definition of g_t , we can obtain other models. For example, if body growth were exponential, then, as shown by Fogarty and Murawski (1986), we obtain model (5.21) with $g_t = g$, a constant. We show below that (5.21) can be made representative of a much wider class of delay-difference models by generalizing the class of solutions to the net growth term, g_t .

5.3.2. Horbowy's Approach

Three alternate delay-difference models derived by Horbowy (1992) correspond to three different underlying growth models. We provide a trivial generalization of his approach to consider the wider problem of setting up delay-difference models that correspond to arbitrary growth models. Horbowy's approach is to set up the differential equations for growth and survival of adults and then approximate their solution to obtain alternatives for the growth term, g_t . Let $B_a(t)$, $N_a(t)$, and $W_a(t)$ be continuous functions of time t for biomass, numerical abundance, and mean weight of fish of age-category a ($> r$). The age category can be annual age, such as all 10-year-olds, or any other grouping as long as they are members of the adult population. We derive these equations for a single arbitrary time interval $t \in (0, 1)$ between recruitment dates (recruitment occurs at time points 0 and 1). Taking derivatives with respect to time (denote $\dot{x} = dx/dt$), we obtain

$$\dot{B}_a(t) = \dot{N}_a(t)W_a(t) + N_a(t)\dot{W}_a(t)$$

for $t \in (0, 1)$ for some i . We assume that mortality rate, Z , is independent of age for the adult population, so that $\dot{N}_a(t) = -ZN_a(t)$. By summing the differential equations over all fully recruited age categories and rewriting, we obtain

$$\dot{B}(t) = -ZB(t) + g(t)B(t),$$

where $g(t)$ can be seen to be the average growth rate of biomass in the adult population when written as

$$g(t) = \frac{\sum_{a \geq r} B_a(t) \dot{W}_a(t) / W_a(t)}{\sum_{a \geq r} B_a(t)}. \quad (5.22)$$

Integration of the differential equation for $B(t)$ from t to $t + 1$ yields

$$B_{t+1} = B_t \exp(-Z) \exp \left[\int_t^{t+1} g(x) dx \right] + W_r N_{r,t+1}.$$

This solution can be written as

$$B_{t+1} = g_t \ell_t B_t + W_r N_{r,t+1},$$

where $\ell_t = \exp(-Z)$ and we define the net growth term g_t as

$$g_t = \exp \left[\int_t^{t+1} g(x) dx \right].$$

Thus, we see that the delay-difference model (5.21) is generally applicable to a wide range of growth models.

The three growth models considered by Horbowy (1992) lead to three forms for the net growth term, g_t , in the delay-difference model (5.21). First, as shown in (4.21) in section 4.2.3, the von Bertalanffy growth model with an isometric weight-length relationship can be written as

$$\dot{W}/W = \eta_1 W^{-1/3} - \eta_2.$$

Using $B_a(t) = N_a(t)W_a(t)$, we solve for $g(t)$ in (5.22) as follows

$$\begin{aligned} g(t) &= \frac{\Sigma_a B_a(t)[\eta_1 W_a(t)^{-1/3} - \eta_2]}{\Sigma_a B_a(t)} \\ &= \frac{\Sigma_a N_a(t)[\eta_1 W_a(t)^{2/3} - \eta_2 W_a(t)]/\Sigma_a N_a(t)}{\Sigma_a N_a(t)W_a(t)/\Sigma_a N_a(t)} \\ &= \eta_1 \bar{W}^{2/3}(t)/\bar{W}(t) - \eta_2, \end{aligned}$$

where the means are taken over the adult population, such that

$$\bar{W}^p(t) = \Sigma_a W_a^p(t)N_a(t)/\Sigma_a N_a(t)$$

for a given coefficient p . Horbowy suggested approximating the integral solution for g_t by replacing all quantities involving means by their sample averages over the time interval $[0, 1]$. Let us denote such a sample average as $\bar{W}_t^p = \sum_i^n (W'_i)^p/n$ for a sample of size n of weights $\{W'_i\}$ from the population and use it as an estimate of the mean $\int \bar{W}^p(t) dt$. This leads to the approximation

$$g_t \simeq \exp(\eta_1 \bar{W}_t^{2/3} / \bar{W}_t - \eta_2)$$

for the von Bertalanffy equation with isometric weight-length.

A similar derivation leads to

$$g_t \simeq \exp[(W_\infty / \bar{W}_t - 1)\kappa]$$

for the Brody growth model, and

$$g_t \simeq \exp[(W_\infty - \bar{W}_t^2 / \bar{W}_t) \kappa']$$

for a logistic weight growth function of the form $\dot{W} = \kappa' W(W_\infty - W)$.

5.3.3. Some Generalizations

Age designation is somewhat artificial in delay-difference models because they are basically used for two purposes: first, age is used to describe a fixed interval of time, as, for example, in the growth model (5.7) and hence throughout the derivation of the biomass models; second, age r is used to quantify the lag time between spawning and subsequent recruitment. Schnute (1987) addressed both those points and showed first that the models above are valid as long as (5.7) describes growth over one time increment. For such a size-structured model, we assume that the initial conditions W_r, W_{r-1} are not age dependent, but rather specify a fixed recruitment size and the size of the individual one year earlier. This type of model is valid for continuous size distributions.

In regard to the point about the use of r as a fixed lag time, we can replace the fixed lag time by a fixed recruitment size, W_r , for which the subscript r no longer refers to age. When growth is variable during the prerecruitment life of animals, then one approach is to apply the recruitment hypothesis of Walters (1987), which specifies a type of continuous recruitment. Assume that the fraction π_a of the total recruitment of a given cohort reaches recruitment size W_r at age a , say from age $a \in [\min, \max]$. Then the number of recruits in year t is given by

$$N_{r,t} = \sum_{a=\min}^{\max} \pi_a \mathcal{F}(\mathcal{S}_{t-a}),$$

which should replace $N_{r,t}$ in (5.15) and (5.17).

5.3.4. Mortality Models

One salient feature of delay-difference models is that they implicitly account for age structure of the population without having to know it. The LVB form of the weight model is critical in obtaining explicit, closed-form equations. Nevertheless, this feature is preserved regardless of when fishing and natural mortality occur during the year, as shown by Schnute (1985). We now present several alternative mortality models and a summary of the pertinent difference equations from Schnute (1985) with some minor differences.

Assume that natural mortality, M_t , fishing effort, E_t , and catchability, q_t , are constant within a year but may vary across years $\{t = 1, \dots, T\}$. Let μ_t be the fraction

of the population at the start of the year that are caught in the fishery (the exploitation fraction), so that $C_{a,t} = \mu_t N_{a,t}$. Let ζ_t be the fraction of those not caught that do not die due to natural mortality, so that

$$N_{a+1,t+1} = \zeta_t (N_{a,t} - C_{a,t}) = \zeta_t (1 - \mu_t) N_{a,t}.$$

Then the survival fraction considering both fishing and natural causes is

$$\ell_t = \zeta_t (1 - \mu_t) \quad (5.23)$$

because $N_{a+1,t+1} = \ell_t N_{a,t}$. Schnute (1985) parameterized in terms of $\phi_t = 1 - \mu_t$, but we use the better-known exploitation fraction μ_t .

One option is for the Deriso-Schnute models of section 5.2 to assume $\mu_t = q_t E_t$ and $\zeta_t = e^{-M_t}$, where fishing mortality occurs at the start of the year after recruitment, spawning occurs after fishing with spawning stock, $S_t = B_t - Y_t$, and natural mortality occurs through the rest of the year. While this mortality model allows CPUE to be proportional to starting abundance ($C_{a,t}/E_t = q_t N_{a,t}$), it also allows the entire population to be caught with finite effort, $E_t = 1/q_t$, which is probably unrealistic for most fisheries. In these models, total survival, ℓ_t , is $e^{-M_t} (1 - q_t E_t)$ from (5.23).

For three alternative models, the timing of fishing varies throughout the year, but ℓ_t is

$$\ell_t = e^{-M_t - q_t E_t}.$$

From (5.23), natural survival for fish not caught is then

$$\zeta_t = e^{-M_t - q_t E_t} / (1 - \mu_t). \quad (5.24)$$

The first alternative model has fishing at the start of the year and lets $\mu_t = 1 - e^{-q_t E_t}$, which can be obtained from a stochastic model of fishing (see section 1.3.6) or a deterministic model of fishing with no natural mortality (see section 1.2.1).

The second alternative model has fishing at the end of the year prior to recruitment. Schnute (1985) showed that $\mu_t = e^{-M_t} (1 - e^{-q_t E_t})$.

The third alternative model has continuous fishing during the entire year. Schnute (1985) showed that $\mu_t = [q_t E_t / (M_t + q_t E_t)] [1 - e^{-(M_t + q_t E_t)}]$. This model is a simple recasting of the continuous fishing model in section 1.2.1 that leads to the Baranov catch equation (1.23).

Regardless of which mortality model is used, the dynamics of abundance, biomass, catch, and yield can be summarized in the following equations:

$$\begin{aligned} N_{a+1,t+1} - \ell_t N_{a,t} &= 0 & N_{t+1} - \ell_t N_t - R_{t+1} &= 0 \\ B_{a+1,t+1} - \ell_t B_{a,t} &= \rho \ell_t (B_{a,t} - \ell_{t-1} B_{a-1,t-1}) & C_t &= \mu_t N_t \\ B_{t+1} - \ell_t B_t - R_{t+1}^* &= \rho \ell_t (B_t - \ell_{t-1} B_{t-1} - \omega_{t-r} R_t^*) & Y_t &= \mu_t B_t \\ C_{a,t} &= \mu_t N_{a,t} & R_t^* &= W_{r,t} R_t = \mathcal{F}_B(S_{t-r}) \end{aligned}$$

where R is recruitment in numbers, R^* is recruitment in biomass, $W_{a,t}$ is average weight at age a in year t , ω_t is the ratio $W_{r-1,t} / W_{r,t}$ of prerecruit weight and recruit

weight in year t , and spawning stock is $S_t = B_t - Y_t$. Schnute referred to these equations as “conservation principles” for abundance and biomass. From these equations, expressions for biomass and yield become

$$\begin{aligned} B_{t+1} &= (1 + \rho)\ell_t B_t - \rho\ell_t\ell_{t-1}B_{t-1} + \mathcal{F}_B(S_{t+1-r}) \\ &\quad - \rho\ell_t\omega_{t-r}\mathcal{F}_B(S_{t-r}) \end{aligned} \quad (5.25)$$

$$\begin{aligned} \frac{Y_{t+1}}{\mu_{t+1}} &= (1 + \rho)\ell_t \frac{Y_t}{\mu_t} - \rho\ell_t\ell_{t-1} \frac{Y_{t-1}}{\mu_{t-1}} + \mathcal{F}_B \left[(1 - \mu_{t+1-r}) \frac{Y_{t+1-r}}{\mu_{t+1-r}} \right] \\ &\quad - \rho\ell_t\omega_{t-r}\mathcal{F}_B \left[(1 - \mu_{t-r}) \frac{Y_{t-r}}{\mu_{t-r}} \right]. \end{aligned} \quad (5.26)$$

Examination of the yield equation (5.26) shows that yield (catch) per unit mortality (CPUM instead of CPUE, catch-per-unit-effort) is the most appropriate measure of starting biomass in the delay-difference model. CPUM is a nonlinear function of fishing effort, E_t , for the three alternative models. Nevertheless, (5.26) can be viewed as prediction equation with dependent variable Y_{t+1} and nine independent variables, Y_t , Y_{t-1} , Y_{t+1-r} , Y_{t-r} , E_{t+1} , E_t , E_{t-1} , E_{t+1-r} , and E_{t-r} . For parameters constant in time, any of the mortality models, and the three-parameter Deriso-Schnute spawner-recruit function

$$\mathcal{F}_N(S) = \begin{cases} \alpha S(1 - \beta\gamma S)^{1/\gamma}, & \gamma > 0 \\ \alpha S e^{-\beta S}, & \gamma = 0 \text{ (Ricker)} \end{cases}$$

from section 3.1.4, there are seven parameters to be estimated in (5.26): M (or $\ell = e^{-M}$), q , ρ , αW_{r-1} , αW_r , β , and γ . In practice, growth parameters are usually obtained from other sources, and frequently M and at least one spawner-recruit parameter are fixed as well, to obtain parameter estimates with reasonably small standard errors and correlations (e.g., Quinn and Collie 1990).

The equilibrium yield solution can be obtained from (5.26) by dropping subscripts and solving for Y , which results in

$$Y_* = \begin{cases} \frac{\mu}{\beta\gamma(1-\mu)} \left\{ 1 - \left[\frac{(1-\tilde{\ell})(1-\rho\tilde{\ell})}{(1-\mu)(\alpha W_r - \rho\alpha W_{r-1}\tilde{\ell})} \right]^\gamma \right\}, & \gamma > 0 \\ -\frac{\mu}{\beta(1-\mu)} \ln \left[\frac{(1-\tilde{\ell})(1-\rho\tilde{\ell})}{(1-\mu)(\alpha W_r - \rho\alpha W_{r-1}\tilde{\ell})} \right], & \gamma = 0 \end{cases}, \quad (5.27)$$

where $\tilde{\ell} = \zeta(1-\mu)$ from (5.23). This relationship is a function of exploitation fraction, μ , and can be plotted to obtain the standard yield curve. Equilibrium biomass and spawning stock can be found from $B_* = Y_*/\mu$ and $S_* = B_* - Y_*$ and plotted as a function of μ . Equilibrium recruitment, R_* , can then be found from the spawner-recruit relationship. Equilibrium catch, C_* , can be found from (5.27) by replacing Y with C and setting ρ to 0 and W_{r-1} and W_r to 1, which effectively converts the yield equations to catch equations. Forecasting future biomass can be done for a given μ with (5.25).

An alternative parameterization is based on modeling the spawner-recruit biomass function directly as

$$\mathcal{F}_B(S) = \begin{cases} \alpha S(1 - \beta\gamma S)^{1/\gamma}, & \gamma > 0 \\ \alpha S e^{-\beta S}, & \gamma = 0 \text{ (Ricker)} \end{cases}.$$

The seven parameters to be estimated are M (or $\ell = e^{-M}$), q , ρ , α , ω , β , and γ . Equations (5.25) and (5.26) still apply for time-dependent biomass and yield. The equilibrium relationships in (5.27) also apply with the deletion of W_r and the substitution of ω for W_{r-1} .

Schnute (1985) presented a menu of options for mortality, growth, and recruitment submodels. He viewed the process of fitting delay-difference models as similar to that for time series models, for which identification, estimation, and forecasting are all important components of the process.

5.3.5. Stock Reduction Analysis

An application of delay-difference models called “stock reduction analysis” has been frequently used for stock assessment. A series of essays (Kimura and Tagart 1982, Kimura et al. 1984, Kimura 1985, 1988) describe its evolution. We present one version of the approach and note that alternative implementations can be found in the references mentioned above.

The primary data source used in stock reduction analysis is the series of yields $\{Y_t\}$ across years $t = 1, \dots, T$. It is assumed that yield is measured without error. If natural and fishing mortality occur continuously throughout the year, then $\ell_t = e^{-Z_t}$, $Z_t = M_t + F_t$, and the relationship between yield and biomass from the Baranov catch equation is

$$Y_t = B_t F_t (1 - \ell_t) / Z_t, \quad t = 1, \dots, T. \quad (5.28)$$

The dynamics of the stock are assumed to follow the deterministic delay-difference model (5.25). Up to time $t = 1$, the stock is assumed to be a pristine (unfished) population at equilibrium [this assumption can be relaxed; see Kimura et al. (1984)]; the pristine biomass is denoted B_0 . Growth parameter ρ and natural mortality parameters M_t are assumed known.

Any spawner-recruit relationship from chapter 3 can be used in (5.25); Kimura (1988) gave examples parameterized in terms of equilibrium recruitment, R_0 , at pristine biomass, B_0 . Note that $R_1 = R_0$ and $B_1 = B_0$. For example, the Cushing spawner-recruit model from section 3.1.3 is written

$$R_t = R_0 (B_{t-r} / B_0)^\gamma, \quad t \geq r, \quad (5.29)$$

where r is the recruitment age. (Alternatively, recruitment indices, p_t , can be used, such that $R_t = R_0 p_t$.) One or more parameters of the spawner-recruit model (e.g., γ) are assumed known. Kimura (1988) suggested hypothesizing the recruitment relative to R_0 when biomass is, say, one-half of B_0 . Such a hypothesis allows one parameter of the spawner-recruit model to be determined. From the delay-difference model (5.25) at equilibrium (omitting subscripts), it can be shown that

$$R_0 = B_0 \frac{1 - e^{-M_0} + \rho(e^{-2M_0} - e^{-M_0})}{1 - \rho \omega e^{-M_0}}. \quad (5.30)$$

Equilibrium relationships for constant fishing mortality, F , follow from the previous section with $\tilde{\ell} = e^{-(F+M)}$.

To implement this version of stock reduction analysis, one chooses a trial value for B_0 and notes that $B_1 = B_0$. Then F_1 is numerically solved from (5.28), $\ell_1 = e^{-Z_1}$,

and B_2 is calculated from (5.25). [If the Cushing spawner-recruit model is assumed, for example, then either (5.29) or (5.30), as appropriate, is used in (5.25).] This process is then repeated for the other times $t = 2, \dots, T$; the last biomass calculated is B_{T+1} .

One then chooses B_0 based on some criterion. Kimura et al. (1984) used $P = B_{T+1}/B_0$ as a criterion and inferred reasonable values of P from the ratio of CPUEs over time; they showed that this process is equivalent to solving a number of nonlinear equations with an equal number of parameters. The results of stock reduction analysis are highly dependent on the functional form of and the assumed parameter values used in the spawner-recruit model. Nevertheless, stock reduction analysis can minimally show which values of pristine biomass are inconsistent with the yield data given the assumptions made.

Other researchers (e.g., Fujioka 1993, Francis 1990) used an objective function with absolute or relative indices of biomass. An approach using minimum integrated average expected loss by Cordue (1993) is useful for performing risk analysis. Examples of stock reduction analysis are given in the papers cited above.

The major reason that stock reduction analysis has been used is that it gives an assessment of stock condition and production parameters using primarily yield data, which are usually available. The major caveat of the approach is that many parameter values must be assumed and cannot be estimated from yield data alone. The wide range of results from stock reduction analysis under different spawner-recruit models suggests that this approach should be used with caution because the estimated condition of the stock is subject to great uncertainty.

5.4. PARAMETER ESTIMATION

Data requirements for estimating parameters for delay-difference models include at a minimum a time series of catches (assumed without measurement error) and a time series of relative and absolute abundances or biomasses. For successful estimation, auxiliary information on growth, natural mortality, and/or the nature of the spawner-recruit relationship are needed as well, as explained below. Other types of auxiliary information include exploitation rates and relative or absolute recruitment indices.

5.4.1. Measurement Error Model

In a measurement error model, all error is assumed to be in measurement of abundance or biomass. The population dynamics are assumed to be deterministic, that is, there is no process error. Thus, for estimation purposes, the model parameters are ρ, ℓ , spawner-recruit parameters α, β, \dots , and initial abundances or biomasses. For the Allen-Clark model (5.5), the initial abundances are N_1, \dots, N_r . For the Deriso model (5.12), the initial biomasses are B_1, \dots, B_r . For the Schnute extensions (5.16) and (5.25), the initial biomasses are B_1, \dots, B_{r+1} . The recursive process in a delay-difference model has the consequence that once the r (or $r + 1$) initial biomasses (or abundances) are given, then subsequent predictions of biomass $\widehat{B}_{r+1}, \widehat{B}_{r+2}, \dots$ can be determined for as long as one likes from one of these equations. In the following development, the Deriso model (5.12) is presumed; adjustment of the time range or variable of interest for other models is straightforward.

If a time series of *absolute* biomass estimates $\{B'_t, t = 1, \dots, T\}$ is available, parameter estimates can be obtained from least squares or likelihood methods, as usual. For example, the residual sum of squares (RSS) criterion is

$$\text{RSS}_B = \sum_{t=1}^T (B'_t - \widehat{B}_t)^2, \quad (5.31)$$

which can be minimized as a function of the parameters.

If a time series of *relative* biomass estimates $\{U'_t, t = 1, \dots, T\}$ is available, an observation error submodel is needed. Walters (1987) and Zheng and Walters (1988) used the power model (1.56) with parameters $\alpha = 0$ and $\nu = \beta + 1$:

$$U'_t = U_t + \epsilon_t = q B_t^\nu + \epsilon_t, \quad (5.32)$$

where ϵ_t is an additive measurement error term. Then, two additional catchability parameters, q and ν , need to be estimated. The relevant residual sum of squares criterion is then

$$\text{RSS}_U = \sum_{t=1}^T (U'_t - \widehat{U}_t)^2, \quad (5.33)$$

where $\widehat{U}_t = q \widehat{B}_t^\nu$.

Walters (1987) noted that estimating initial biomasses along with the other parameters is difficult and suggested a simple procedure. Given starting values for q and ν , the r initial biomass parameters can be estimated by solving the observation error equation (and ignoring the error term), which results in estimates

$$\widehat{B}_p = (U'_p/q)^{1/\nu}, \quad p = 1, \dots, r. \quad (5.34)$$

These are then iteratively updated during the nonlinear search process. An additional enhancement in this algorithm is to use a moving average of observed biomasses to help smooth out measurement errors.

In practice, it is difficult to estimate all the other parameters from a single series of relative or absolute biomass. Estimates of various parameter combinations tend to be highly correlated; in particular, the combinations ρ and ℓ , ℓ and q , and β and q tend to have high negative correlations, and spawner-recruit parameters tend to have high correlations of both signs (Deriso 1980, Walters 1987). Sensitivity analysis suggests that the quality of the analysis depends on the amount of error in population parameters (Tyler et al. 1985), although biomass estimates can be robust in some situations.

Thus, reducing the number of estimated parameters is essential. The growth parameter ρ can usually be obtained from separate analyses of growth data, and various methods can be used to estimate natural mortality (see section 8.3). If separate analyses of the spawner-recruit relationship can be made as in chapter 3, then perhaps some of these parameters can be removed from the estimation. If an auxiliary set of recruitment indices is available, their deviations from predicted recruitment from the model can be incorporated into the sum of squares (Walters 1987).

Finally, a Bayesian-type approach might be used to restrict parameter estimates (Walters 1987). If $\tilde{\theta}$ is a prior estimate of parameter θ with prior variance $\tilde{\sigma}^2$, then a residual sum of squares criterion

$$\text{RSS}_\theta = \sum_\theta (\tilde{\theta} - \theta)^2 / \tilde{\sigma}^2 \quad (5.35)$$

can be included in the overall sum of squares, where the sum is taken over parameters for which prior information is available. A large value can be used for $\tilde{\sigma}^2$ to minimize the effect of the prior information, and vice versa.

5.4.2. Process Error Model

In a process error model, all error is assumed to be in the population dynamics; that is, there is no measurement error. Given r sequential observations of biomass, $B'_{t-r}, \dots, B'_{t-1}$ (without error), predicted biomass, \hat{B}_t , at the next time t can be obtained from one of the delay-difference models (Walters 1987). The deviation, $\hat{B}_t - B'_t$, from the corresponding observed biomass, B'_t , then represents process error. The parameters of the model are the same as for the measurement error model, except that initial biomasses B_1, \dots, B_r are not needed as they are known from the observations. Here, the sum of squares criterion is

$$\text{RSS}_B = \sum_{t=r+1}^T (\hat{B}_t - B'_t)^2. \quad (5.36)$$

If the biomass time series is relative (U'_t), the power model (1.56) still applies only without measurement error; thus

$$U'_t = U_t = q B_t^\nu. \quad (5.37)$$

Given starting values for q and ν , all biomasses can be estimated as

$$B'_t = (U'_t/q)^{1/\nu}, \quad t = 1, \dots, T. \quad (5.38)$$

The biomass residual sum of squares, RSS_B , is then minimized to estimate parameters. Alternatively, the delay-difference equation can be recast in terms of U , which leads to use of the criterion RSS_U . The same caveats about parameter confounding in the measurement error model apply here as well.

Example 5.3. Walleye pollock in the eastern Bering Sea

The eastern Bering Sea pollock fishery is one of the world's largest fisheries. It was prosecuted primarily by the Japanese from 1964 to 1985 (Quinn and Collie 1990, Wespestad 1993). Observers collected information on yield, CPUE, and other statistics (table 5.1). A joint venture fishery occurred between 1986 and 1988, and a domestic U.S. fishery has occurred since then, but a domestic observer program did not start up until 1990. As a consequence, CPUE data are not available after 1985. A joint hydroacoustic-bottom trawl survey has been conducted triennially by the National Marine Fisheries Service since 1979; estimates of pollock biomass $\{\tilde{B}_t\}$ from the survey are also shown in table 5.1.

A BASIC program, GENEST (Walters 1987), is a convenient tool for applying delay-difference models. It has a menu of items for data entry and editing, parameter estimation, determination of equilibrium relationships, and simulation of management strategies. The program uses model (5.25) for biomass in the alternative parameterization in section 5.3.4, which models the spawner-recruit biomass function directly. The power relationship (5.32) between CPUE (U) and biomass B is incorporated in

Table 5.1. Total yield, catch-per-unit-effort (CPUE) from Japanese trawlers, and survey biomass for wall-eye pollock in the eastern Bering Sea.

Year	Yield, Y_t (mmt)	CPUE U_t (t/0.1 ha)	Survey	
			biomass, \tilde{B}_t (mmt)	
1964	0.176	0.31		
1965	0.231	0.60		
1966	0.262	0.74		
1967	0.550	0.81		
1968	0.702	1.12		
1969	0.863	1.43		
1970	1.257	1.21		
1971	1.744	1.12		
1972	1.875	1.22		
1973	1.759	1.02		
1974	1.588	1.01		
1975	1.357	0.91		
1976	1.178	0.92		
1977	0.978	0.92		
1978	0.979	0.97		
1979	0.914	0.98	10.662	
1980	0.959	0.93		
1981	0.973	0.96		
1982	0.956	1.09	8.940	
1983	0.981	1.15		
1984	1.098	1.46		
1985	1.179	1.46	10.321	
1986	1.189			
1987	1.237			
1988	1.228		12.187	
1989	1.230			
1990	1.202			
1991	1.038		6.469	
1992	1.384			

The foreign fishery ended after 1985. Surveys have been conducted every three years since 1979. Data are from Wespestad (1993, 1995 personal communication); mmt, millions of metric tons.

the program. The first r biomass estimates can be smoothed by a running average to reduce measurement error effects.

Quinn and Collie (1990) applied delay-difference models to pollock data using GENEST; this example is an update of their work. Growth information was used to obtain parameters ρ , W_{r-1} , W_r , and their ratio, ω (table 5.2). Natural mortality for pollock is 0.3; consequently, annual survival, ℓ , is 0.74. By examining results from and comparison with catch-age analysis (described in chapter 8), Quinn and Collie obtained initial parameter values, given in table 5.2, for the Ricker spawner-recruit function ($a = \ln \alpha$ and β), the power relationship (5.32), and proportions recruiting at ages 2, 3, and 4 (π_a , $a = 2, \dots, 4$). This latter feature is described in section 5.3.3. Quinn and Collie found that a square-root relationship between CPUE and biomass was appropriate ($v = 0.5$).

Table 5.2. Fixed parameters and parameter estimates of q and β for walleye pollock in the eastern Bering Sea (after Quinn and Collie 1990). Estimates of productivity parameters are also given.

Fixed parameters:			
	M (n=29)	M (n=22)	P (n=22)
ρ	0.692		
ω	0.614		
ℓ	0.740		
v	0.500		
a	0.163		
π_2	0.127		
π_3	0.311		
π_4	0.562		
Estimated parameters			
	M (n=29)	M (n=22)	P (n=22)
\hat{q}	0.385	0.387	0.444
SE(\hat{q})	0.111	0.064	0.080
$\hat{\beta}$	0.161	0.161	0.025
SE($\hat{\beta}$)	0.006	0.003	0.296
corr($\hat{q}, \hat{\beta}$)	0.22	0.31	-0.98
Productivity parameters			
m	1.94	1.95	12.4
B_m	6.47	6.51	41.4
μ_m	0.3	0.3	0.3

M denotes measurement error, and P denotes process error. The first M model uses data from 1964 to 1992 and the second uses data from 1964 to 1985. The P model uses data from 1964 to 1985. For the measurement error models, smoothed estimates of early biomass were used in parameter estimation.

Given values for q and v shown in table 5.2, CPUE is converted into equivalent units of "observed biomass" using (5.34) and (5.38) (table 5.3). Given the first five observed biomasses, biomass in any subsequent year, t , is projected by (5.25). Then predicted CPUE \widehat{U}_t is calculated from (5.37). These calculations are shown in table 5.3 for data given in table 5.1 and the parameter values listed in table 5.2, along with intermediate quantities for exploitation fraction, $\widehat{\mu}_t = Y_t/\widehat{B}_t$, annual survival, $\ell_t = \ell(1 - \widehat{\mu}_t)$, and spawning stock, $\widehat{S}_t = \widehat{B}_t - Y_t$.

For the measurement error model, the residual sum of squares function used is $RSS = RSS_U + RSS_{aux}$. The term $RSS_{aux} = \sum(\tilde{B}_t - \widehat{B}_t)^2$ is a residual sum of squares term for the auxiliary survey information about biomass. This auxiliary sum of squares term includes a weight of 3 because the survey is conducted triennially, and enough weight was desired to be comparable to the annual sources of information. However, different weightings should be investigated because the magnitudes of the CPUE and biomass data are different. As an alternative, sums of squares for logarithms of CPUE and biomass could be used.

Parameter estimates for q and β , the two most uncertain parameters, are given in table 5.2 for two applications of the measurement error model: the first using data from 1964 to 1985 (as in Quinn and Collie 1990), the second using data through 1992. The calculations of predicted values shown in table 5.3 correspond to use of these

Table 5.3. Calculations of “observed” biomass, B' , and predicted biomass, \hat{B} , in millions of metric tons, and estimates of exploitation rate, μ , annual survival, ℓ , spawning stock, S , and catch-per-unit-effort (CPUE) using information from tables 5.1 and 5.2 for the M model with data from 1964 to 1992.

Year	Observed biomass, $B'_t = (U'_t / q)^2$	Predicted biomass, \hat{B}_t	Exploit. fraction, μ_t	Annual survival, ℓ_t	Spawning stock, S_t	Predicted CPUE, U_t
1964	0.649	0.649	0.271	0.539	0.473	0.310
1965	2.432	2.432	0.095	0.670	2.201	0.600
1966	3.699	3.699	0.071	0.688	3.437	0.740
1967	4.432	4.432	0.124	0.648	3.882	0.810
1968	8.473	8.473	0.083	0.679	7.771	1.120
1969	13.813	10.102	0.085	0.677	9.239	1.223
1970	9.890	10.681	0.118	0.653	9.424	1.257
1971	8.473	10.539	0.165	0.618	8.795	1.249
1972	10.054	9.912	0.189	0.600	8.037	1.211
1973	7.028	9.161	0.192	0.598	7.402	1.165
1974	6.891	8.653	0.184	0.604	7.065	1.132
1975	5.594	8.467	0.160	0.621	7.110	1.120
1976	5.717	8.592	0.137	0.639	7.414	1.128
1977	5.717	8.896	0.110	0.659	7.918	1.148
1978	6.356	9.327	0.105	0.662	8.348	1.175
1979	6.487	9.661	0.095	0.670	8.747	1.196
1980	5.842	9.949	0.096	0.669	8.990	1.214
1981	6.225	10.090	0.096	0.669	9.117	1.222
1982	8.026	10.135	0.094	0.670	9.179	1.225
1983	8.933	10.137	0.097	0.668	9.156	1.225
1984	14.399	10.085	0.109	0.659	8.987	1.222
1985	14.399	9.927	0.119	0.652	8.748	1.212
1986		9.729	0.122	0.650	8.540	1.200
1987		9.575	0.129	0.644	8.338	1.191
1988		9.440	0.130	0.644	8.212	1.182
1989		9.372	0.131	0.643	8.142	1.178
1990		9.345	0.129	0.645	8.143	1.176
1991		9.371	0.111	0.658	8.333	1.178
1992		9.544	0.145	0.633	8.160	1.189

parameter estimates. The estimates of q and β are stable with respect to the number of observations, and their estimated correlation is low. The standard error for \hat{q} is relatively much larger than that for $\hat{\beta}$. This result is probably a consequence of assuming that all error is in measurement, which leads to q being uncertain and constrains the spawner-recruit parameter β . The fit to the observed CPUE and survey biomass information (figure 5.4) reinforces this point. While the predicted CPUEs go through the middle of the data for each of the two data sets, the deterministic delay-difference model cannot capture the interannual variability present in the data. From catch-age analysis, it is known that large 1978, 1982, and 1984 year-classes occurred, which suggests that the interannual variability cannot be due to measurement error alone.

Nevertheless, the model should be applicable to average conditions over which the fishery occurred, so that equilibrium values should be fairly accurate. Indeed, the values in table 5.2 are similar to values using other methods (Quinn and Collie 1990). The relationship (5.27) can be used for equilibrium yield by omitting W_r and substituting

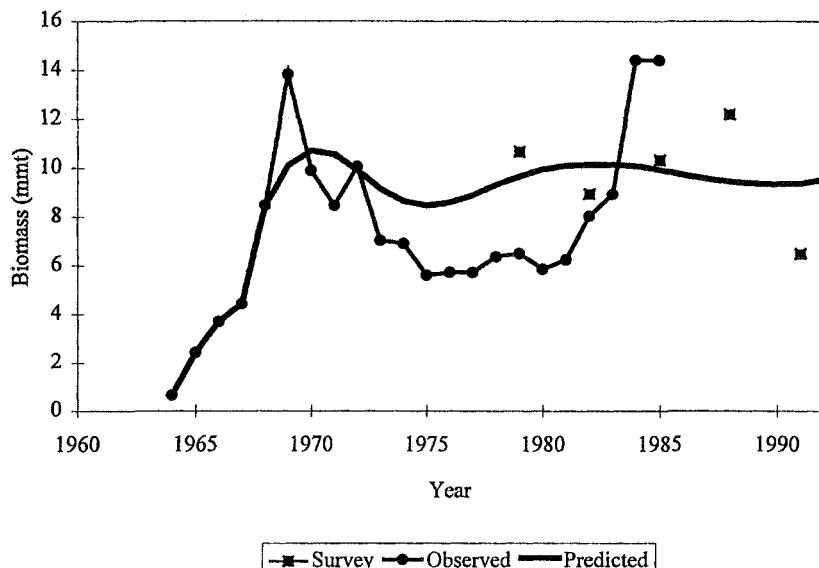


Figure 5.4. Survey estimates of biomass of walleye pollock in the eastern Bering Sea, estimates of biomass from extrapolation of observed CPUE, and predicted estimates of biomass from a delay-difference model with only measurement error. See example 5.3 for details.

ω_r for W_{r-1} . After calculation of equilibrium yield for several values of μ , equilibrium values of biomass and spawning stock are obtained, as explained in section 5.3.4. A plot of equilibrium yield versus biomass (figure 5.5) looks similar to the Graham-Schaefer parabolic curve from chapter 2 but is slightly skewed to the right. From this plot, one can obtain maximum productivity, m , biomass at maximum productivity, B_m , exploitation fraction at maximum productivity, μ_m , and pristine biomass, B_∞ . A plot of equilibrium biomass, spawning stock, and yield as a function of μ (figure 5.6) illustrates the relationship among these variables.

For the process error model, observed biomass, B'_t , is assumed to be measured without error, given values for q and v . Given the previous five values for observed biomass at times $t - 1$ to $t - r$, the biomass at time t is predicted from (5.25). The deviation between predicted and observed biomass at time t is then the process error. Predicted and observed biomass are then converted to CPUE using (5.37), as in the measurement error model, and the sum of squares function RSS_U is used. For walleye pollock, the process error model can only be applied to data from 1964 to 1985 because CPUE data are not available after 1985.

Results of applying the process error model (table 5.2) are quite different from those for the measurement error model, particularly in the estimate of spawner-recruit parameter β . The large standard error for this estimate and the high negative estimated correlation near -1 between \hat{q} and $\hat{\beta}$ suggest that this parameter cannot be estimated with confidence along with q . In contrast, the estimate of q has a low standard error because the CPUE data are treated as exact representatives of relative abundance. Of the productivity parameters (table 5.2), only parameter μ_m is robust to the specification of error; the other parameters are well out of line with published values. This result

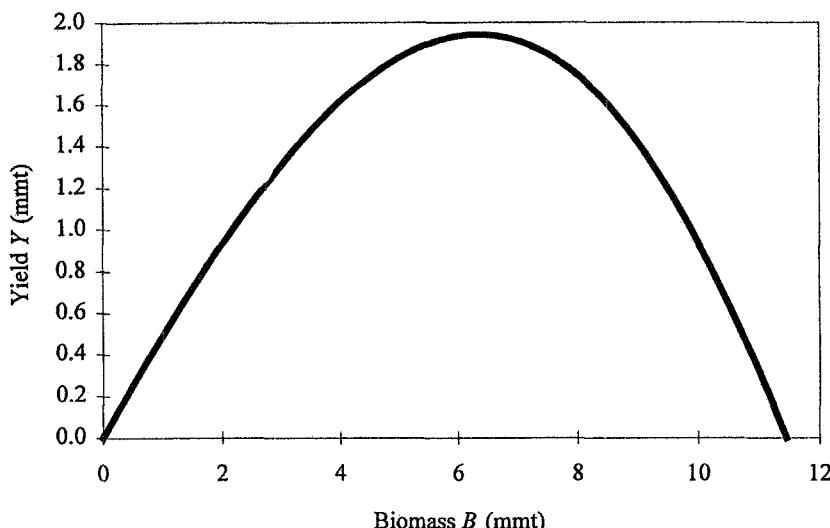


Figure 5.5. Equilibrium yield as a function of biomass for walleye pollock in the eastern Bering Sea.

suggests that the specification of error in the delay-difference model is quite important and interacts with the choice of parameters to be estimated. For confident application of delay-difference models, as many parameters as possible must be determined from auxiliary sources. ■

5.4.3. Combined Measurement and Process Error Model

The simple estimation procedures in sections 5.4.1 and 5.4.2 are often not successful for these models. Complications arise because of the intrinsic nonlinearity of the

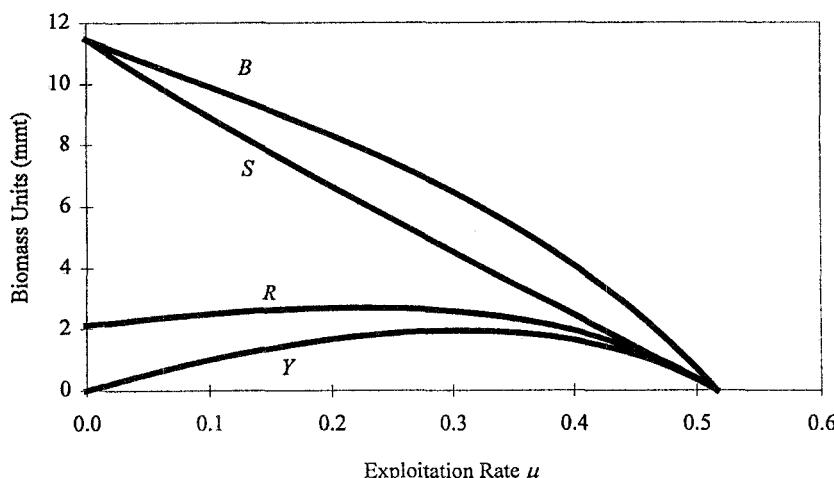


Figure 5.6. Equilibrium yield, recruitment, spawning biomass, and total biomass as a function of exploitation fraction μ for walleye pollock in the eastern Bering Sea.

models, the time series nature of the problem, and the presence of both measurement and dynamic process errors. Part of the practical difficulty also stems from the extensive number of computations required to perform such standard tasks as maximum likelihood estimation.

The estimation problem can be described for a reasonably general case as follows: let the population model be of the form

$$B_{t+1} = G(B_t, \mathbf{Y}, \mathbf{a}, \epsilon_t)$$

and the observation model be of the form

$$x_t \sim N[\ln(B_t), \sigma_x^2],$$

where $G(\cdot)$ indicates a function describing the population model; \mathbf{Y} is a vector of annual yields, $t = 1, \dots, T$; \mathbf{a} is a set of parameters to be estimated; $\epsilon \sim N(0, \sigma_\epsilon^2)$, a process error; and x_t is a measurement of abundance subject to measurement error.

One must deal with both process and measurement error. Maximum likelihood estimation requires the computation of the likelihood of the observations. Since we do not observe abundance, but only the measurements $\{x_t\}$, the likelihood of the observations is a marginal distribution, which must be integrated across the vector space of possible abundances, except for the first one, B_1 , which can be taken as an initial condition. That is,

$$\begin{aligned} p(\mathbf{x}|\mathbf{Y}, \mathbf{a}, B_1) &= \int_{B_2} \cdots \int_{B_T} p(x_1 \cdots x_T | B_1 \cdots B_T, \mathbf{a}, \mathbf{Y}) \\ &\quad \times p(B_2 \cdots B_T | \mathbf{a}, \mathbf{Y}, B_1) dB_2 \cdots dB_T, \end{aligned} \quad (5.39)$$

which, for example, with a moderate time series of 25 observations would require a 24-fold integral computation.

The two components in the right side of the integrand are (1) the conditional distribution of the measurements, \mathbf{x} , given the abundances, and (2) the distribution of the B 's. Because of the normal distribution assumptions above, we can write the conditional distribution of measurements as

$$p(x_1 \cdots x_T | B_1 \cdots B_T, \mathbf{a}, \mathbf{Y}) = (2\pi\sigma_x^2)^{-T/2} \exp \left[-\frac{1}{2} \sum_{t=1}^T \left(\frac{x_t - \ln(B_t)}{\sigma_x} \right)^2 \right],$$

and the distribution of the B 's, obtained by transformation of the known distribution of ϵ 's, as

$$\begin{aligned} p(B_2 \cdots B_T | \mathbf{a}, \mathbf{Y}, B_1) &= \prod_{t=2}^T p(B_t | B_1 \cdots B_{t-1}, \mathbf{a}, \mathbf{Y}) \\ &= (2\pi\sigma_\epsilon^2)^{-(T-1)/2} |\partial G/\partial \epsilon|^{-1} \exp \left[-\frac{1}{2} \sum_{t=2}^T \left(\frac{\epsilon_t}{\sigma_\epsilon} \right)^2 \right]. \end{aligned}$$

In some applications, reasonable estimates of parameters can be obtained by maximizing the integrand of (5.39), for which the ϵ 's (or equivalently the $B_2 \cdots B_T$) are

viewed as “nuisance parameters” and estimated along with the \mathbf{a} and B_1 parameters; we believe that the Jacobian of the transformation from \mathbf{B} to ϵ needs to be included in the objective. While this maximization objective is difficult to justify from a frequentist perspective, as Schnute (1994) shows, the rationale is clearer from a Bayesian perspective. We summarize his argument: suppose we define the complete parameter vector $\Theta = (\mathbf{B}_t, \mathbf{a})$ to include all unknown states (abundances) of the model. The posterior distribution for Θ is similar to the integrand of (5.39), and it is defined by the proportionality

$$p(\Theta | \mathbf{Y}, \mathbf{x}) \propto p(\mathbf{x} | \mathbf{Y}, \Theta) p(\mathbf{B} | \mathbf{Y}, \mathbf{a}) p(\mathbf{a}), \quad (5.40)$$

where the proportionality is the integral of the right side of (5.40) over the vector Θ . Note that the initial condition B_1 is part of \mathbf{B} . Two additional terms appear in (5.40) that are not listed in the integrand of (5.39): an additional term, $p(B_1 | \mathbf{Y}, \mathbf{a})$ for the addition of B_1 to \mathbf{B} , and a prior distribution, $p(\mathbf{a})$. Both the additional terms could be set to one if the prior distributions of the initial state(s) and parameter \mathbf{a} are assumed to be uniform distributions. From the Bayesian perspective, maximization of (5.40) with respect to Θ produces maximum posterior probability estimates of the joint distribution of \mathbf{a} and \mathbf{B} .

A unifying approach is possible in which estimators of \mathbf{a} are almost the same irrespective of whether one approaches the problem by maximum likelihood estimation, a frequentist perspective, or maximum posterior probability estimates, a Bayesian perspective. The unified approach is obtained by computing the marginal distribution of \mathbf{a} as obtained by integration of $p(\Theta | \mathbf{Y}, \mathbf{x})$ in (5.40) over the distribution of \mathbf{B} and with the assumption of uniform prior distributions on \mathbf{a} and B_1 . The resultant integral defines the posterior probability $p(\mathbf{a} | \mathbf{Y}, \mathbf{x})$. It is identical to (5.39), except for the normalizing constant in (5.40) and the treatment of initial conditions as parameters in (5.39) versus the integral averaging across initial conditions in (5.40).

Numerical methods for calculating marginal distributions, such as $p(\mathbf{a} | \mathbf{Y}, \mathbf{x})$, are described by Gelman et al. (1995) and in other references on Bayesian statistics. We described in section 3.4 the sampling, importance resampling algorithm for such calculations. In the example below, we illustrate one of the MCMC (Monte Carlo Markov chain) methods, the Metropolis algorithm.

Example 5.4. Yellowfin tuna in the eastern tropical Pacific Ocean

The delay-difference model (5.12) was fitted to yellowfin tuna catch and standardized purse seine effort data from each quarter of 1968–1992. A Beverton-Holt spawner-recruit relationship (3.6) was assumed with a four-quarter lag time between recruitment and date of spawning. An independent estimate of $\rho = 1.1$ was obtained by fitting weight versus age data, and quarterly $M = 0.2$ was assumed. Catch per unit standard effort (in units of tons per day of fishing by class-6 purse seine vessels) was assumed to be lognormally distributed with mean proportional to adult biomass. Two analyses were made. The first analysis assumes no process error and thus dynamics in (5.12) are a deterministic process. Results from that analysis were used to construct the equilibrium yield curve in example 5.2. In the second analysis, we maximize (5.40) and assume equal measurement and process error in which recruitment is lognormally distributed with mean given by the spawner-recruit model (3.6). Figure 5.7 shows observed logarithm of CPUE along with predicted values from the two analyses. Results are similar because only a small process error (standard deviation of 0.05) was esti-

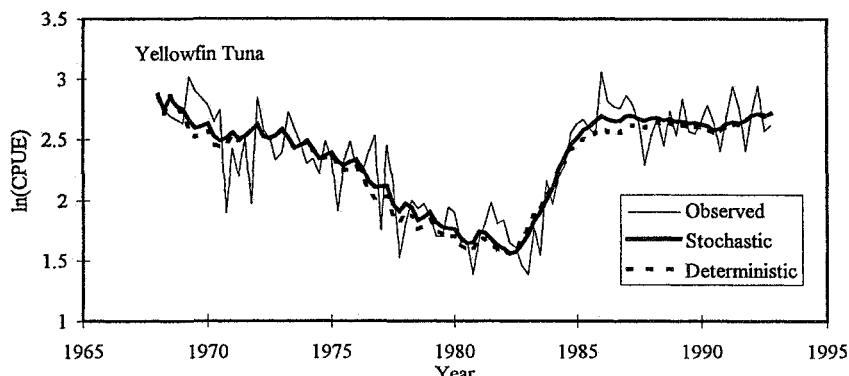


Figure 5.7. Observed and predicted $\ln(\text{CPUE})$ (catch per unit effort) over time from two versions of a delay-difference model fitted to data from yellowfin tuna in the eastern tropical Pacific Ocean. Both versions contain measurement error. Recruitment is deterministic (no process error) in one version and stochastic (process error) in the other.

mated; although the low process error estimate is suspicious and may be related to poor performance sometimes found in spreadsheet algorithms such as the one employed for this example.

A Metropolis algorithm was constructed to obtain random samples of the posterior probability of parameters. From those random samples, cumulative probability curves were constructed by calculating the equilibrium yield function given in example 5.2 for each random sample. A simple and, in our experience, reliable type of Metropolis algorithm was implemented similar to one described by Clifford (1994). The Metropolis algorithm produces a Markov chain with equilibrium density $p(\Theta|\mathbf{Y}, \mathbf{x})$ by stepping sequentially through the parameter indices either one at a time or in groups. The algorithm creates a sequence of samples $(\Theta^1, \dots, \Theta^n)$ by the following procedure.

1. Given the current i th sample Θ^i , choose a candidate $i + 1$ th sample by altering the k th parameter, θ_k^i . The candidate sample θ'_k is chosen by adding to θ_k^i an independent random variable uniformly distributed on the interval $(-\Delta_k, \Delta_k)$, subject to the constraint that the candidate value lie within a feasible range.
2. Compute the probability ratio $p(\Theta'|\mathbf{Y}, \mathbf{x})/p(\Theta^i|\mathbf{Y}, \mathbf{x})$. Note that the ratio does not depend on the normalization constant in (5.40).
3. If the probability ratio of step 2 exceeds u , where $u \sim U(0, 1)$ —a standard uniform—then the candidate sample is chosen as the $i + 1$ th sample; otherwise the parameter is unchanged.
4. Cycle to the next parameter $k + 1$ or 1 and return to step 1. Output Θ^i as a sample of the posterior probability after each, say fifth, complete cycle through the parameter indices and after discarding, say, the first 500 steps (an initial start-up).

Clifford (1994) recommended dynamic adjustment of Δ so that candidate samples are accepted about 50% of the time. Gelman et al. (1995) provided further guidance on the Metropolis and other MCMC algorithms. In our application, we adjusted the Δ by increasing (or decreasing) it by 5% each iteration if candidate samples for the

previous five cycles through the parameter indices had been accepted more (or less) than 50% of the time. The frequency of sample output and number of initial discards are probably too low if uncorrelated random samples are of importance. Our calculations of cumulative probability curves are not affected by such correlations. About 50,000 cycles are needed to produce stable results in our example. The initial sample Θ was set to the maximum posterior estimate.

Cumulative probability of equilibrium quarterly yield for three different levels of fishing effort are shown for deterministic and stochastic recruitment in figure 5.8. The two graphs show that qualitative features are similar. Both indicate a slightly flatter yield curve than the equilibrium yield curve (figure 5.2) based on maximum posterior parameter estimates. ■

5.4.4. Kalman Filters

An alternative approach to estimation of mixed error models is based on Kalman filter methods. Kalman filters are ideally suited to linear time series systems with both measurement and process error, but can often be applied to nonlinear systems by suitable

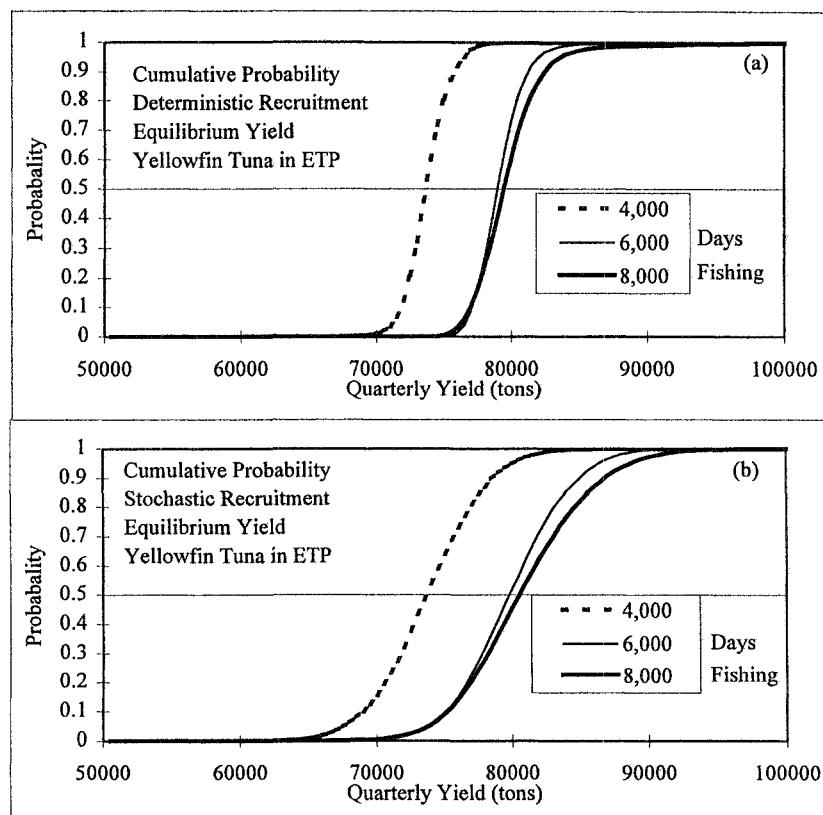


Figure 5.8. Cumulative probability of equilibrium quarterly yield for three different levels of fishing effort for yellowfin tuna in the eastern tropical Pacific Ocean. (a) Deterministic version, (b) stochastic version.

approximation. Another advantage of filters is that they are naturally suited to autocorrelated processes, such as would occur, for example, if catchability, q , was treated as a random walk process rather than as a constant. Kalman filters are recursive equations of the sufficient statistics of a normal distribution, which have been derived by applying Bayes theorem to recursively update linear combinations of normally distributed random variables. Applications of Kalman filters to fisheries problems include both theoretical treatments (Schnute 1994) and applications to specific models, such as to surplus production and spawner-recruit models (Pella 1993), delay-difference models (Pella 1996), catch-age models (Gudmundsson 1986, 1994; Mendelsohn 1988), and size-structured models (Sullivan 1992). As the research in quantitative fisheries methods progresses to wider acceptance of Bayesian statistics and autocorrelated time series processes, we anticipate wider use of filter methods. We include some recent theory to assist that progress.

Realizable minimum variance estimates

Significant advances have been made in filtering methodology. Liang and Christensen (1978) derived the realizable minimum variance (RMV) filter for discrete systems, which provides a rigorous method for generalizing the Kalman filter approach to nonlinear systems. Liang (1982a, b) shows that performance of the RMV filter is far superior to the extended Kalman filter in Monte Carlo experiments of a system with significant nonlinearities. The RMV filter uses a normal approximation to the probability density of nonlinear systems by matching their first and second moments at each step of a recursive algorithm; filter equations are chosen to provide minimum variance unbiased estimates of the state variables for approximating density functions. Other approaches based on more accurate representations of the posterior density can also be postulated for fisheries models (such as Gaussian sum filters; Anderson and Moore 1979), but they generally require much more elaborate computation schemes than the RMV filter. A simple explanation of the Kalman filter is given in Meinhold and Singpurwalla (1983).

The RMV filter equations are summarized below. Bold notation indicates vector and matrix quantities.

$$\begin{aligned} \text{System model: } & \mathbf{x}_k = \mathbf{g}(\mathbf{x}_{k-1}) + \boldsymbol{\epsilon}_k, \quad \boldsymbol{\epsilon}_k \sim N(0, \mathbf{Q}_k) \\ \text{Measurement model: } & \mathbf{z}_k = \mathbf{h}(\mathbf{x}_k) + \mathbf{v}_k, \quad \mathbf{v}_k \sim N(0, \mathbf{R}_k) \end{aligned} \quad (5.41)$$

where \mathbf{x}_k is the state vector $[x_{1k}, \dots, x_{nk}]^T$ for all n states of the system at step k , \mathbf{z}_k is the measurement vector $[z_{1k}, \dots, z_{mk}]^T$ for all m measurements of the system at step k , \mathbf{g} and \mathbf{h} are vector functions, and \mathbf{Q}_k and \mathbf{R}_k are covariance matrices for the system (of dimension $n \times n$) and measurements (of dimension $m \times m$), respectively. As written above, the vectors of random variables $\boldsymbol{\epsilon}_k$ and \mathbf{v}_k are serially uncorrelated, and $\mathbf{E}[\boldsymbol{\epsilon}_k \mathbf{v}_k^T] = 0$. Equations (5.41) are somewhat simplified from the general model given by Liang and Christensen (1978).

The RMV estimate $\hat{\mathbf{x}}_k$ of the state vector is given recursively in two steps: by a state estimate extrapolation (denoted by a minus sign) and by a state estimate update (denoted by a plus sign). The error covariance, \mathbf{P}_k , associated with $\hat{\mathbf{x}}_k$ is given by similar recursive updates. The estimation scheme is Bayesian in nature (as explained below), and $\hat{\mathbf{x}}_k$ and \mathbf{P}_k are the approximate expectation and covariance of $(\mathbf{x}_k | \mathbf{z}_1, \dots, \mathbf{z}_k)$. Filter equations are shown below:

State estimate extrapolation	$\hat{\mathbf{x}}_k^{(-)} = \mathbf{E}[\mathbf{g}(\hat{\mathbf{x}}_{k-1}^{(+)})],$
Error covariance extrapolation	$\mathbf{P}_k^{(-)} = \mathbf{E}[\tilde{\mathbf{g}}\tilde{\mathbf{g}}^T] + \mathbf{Q}_{k-1},$
State estimate update	$\hat{\mathbf{x}}_k^{(+)} = \hat{\mathbf{x}}_k^{(-)} + \mathbf{K}_k \{\mathbf{z}_k - \mathbf{E}[\mathbf{h}(\hat{\mathbf{x}}_k^{(-)})]\},$
Error covariance update	$\mathbf{P}_k^{(+)} = \mathbf{P}_k^{(-)} - \mathbf{K}_k \mathbf{E}[\tilde{\mathbf{h}}\tilde{\mathbf{h}}^T],$
Gain matrix	$\mathbf{K}_k = \mathbf{E}[\tilde{\mathbf{x}}_k \tilde{\mathbf{h}}^T] (\mathbf{R}_k + \mathbf{E}[\tilde{\mathbf{h}}\tilde{\mathbf{h}}^T])^{-1}. \quad (5.42)$

where the tilde notation (such as $\tilde{\mathbf{x}}$) indicates the difference between a random variable and its expected value at step k , conditioned on measurements $\mathbf{Y}_{k-1} = (\mathbf{z}_1, \dots, \mathbf{z}_{k-1})$ taken up to that step. Expectations are all conditional expectations, which are evaluated with respect to distributions of the form $N(\hat{\mathbf{x}}_t, \mathbf{P}_t)$, where $t = k-1$ and a superscript $(+)$ is added for extrapolation equations and where $t = k$ and a superscript $(-)$ is added for the update equations. Those distributions are Bayesian in nature: for linear Kalman filters, our state of knowledge about \mathbf{x}_k , say, at the $(+)$ stage after observing \mathbf{z}_k , is captured in the following probability statement (cf. Meinholt and Singpurwalla 1983),

$$(\mathbf{x}_k^{(+)} | \mathbf{Y}_k) \sim N(\hat{\mathbf{x}}_k^{(+)}, \mathbf{P}_k^{(+)})$$

For example, the expectation $\mathbf{E}[\mathbf{g}(\hat{\mathbf{x}}_{k-1}^{(+)})]$ is the expected value of $\mathbf{g}(\mathbf{x})$ in which $\mathbf{x} \sim N(\hat{\mathbf{x}}_{k-1}^{(+)}, \mathbf{P}_{k-1}^{(+)})$. The expectations of the outer products $\mathbf{E}[\tilde{\mathbf{g}}\tilde{\mathbf{g}}^T]$ and $\mathbf{E}[\tilde{\mathbf{h}}\tilde{\mathbf{h}}^T]$ are the covariance matrices at each step for the conditional densities of $\mathbf{g}(\mathbf{x})$ and $\mathbf{h}(\mathbf{x})$, respectively. Initial conditions for the filter are an initial estimate of state vector $\hat{\mathbf{x}}_0^{(-)}$ and an initial error covariance \mathbf{P}_0 .

Some simplifications are possible in the calculation of the cross product expectations in (5.42), since for normally distributed variables, we have

$$\mathbf{E}[\tilde{\mathbf{x}}_k \tilde{\mathbf{h}}^T] = \mathbf{P}_k^{(-)} \mathbf{E}[\partial \mathbf{h}^T / \partial \mathbf{x}],$$

where the (i, j) element of the expectation of the \mathbf{h}^T vector gradient is $E[\partial h_j / \partial x_i]$.

The likelihood of the observations, given a set of parameters Θ , is given approximately in the nonlinear case, but exactly in the linear case, as a product of multinormal distributions of the form

$$(\mathbf{z}_k | \mathbf{Y}_{k-1}, \Theta) \sim N(\mathbf{E}[\mathbf{h}(\hat{\mathbf{x}}_k^{(-)})], \{\mathbf{R}_k + \mathbf{E}[\tilde{\mathbf{h}}\tilde{\mathbf{h}}^T]\})$$

which can be maximized with respect to Θ to produce maximum likelihood estimates. If some of the parameters are thought to be random walk processes rather than constants, it is better to treat them as state variables rather than as parameters. For example, let $x_{1,t} = q_t$ be the catchability in year t , then $x_{1,t}$ is the first state variable, whose dynamic equation could be a simple random walk process. In delay-difference models, it is sometimes simpler, yet consistent with observed fisheries data, to treat recruitment as a state variable with a random walk process rather than being dependent on spawner biomass—at least in terms of obtaining accurate estimates of recent abundance.

Stochastic linearization estimates

This type of filter is derived by choosing the linear approximation of a given function, \mathbf{g} , to be that which minimizes the mean square error of the approximation. The stochastic

linearizations for the state and measurement functions of normally distributed variables are given, respectively, by

$$\begin{aligned} \mathbf{g}(\mathbf{x}) &\approx \mathbf{E}[\mathbf{g}(\mathbf{x})] + \mathbf{G}\tilde{\mathbf{x}} \\ \mathbf{h}(\mathbf{x}) &\approx \mathbf{E}[\mathbf{h}(\mathbf{x})] + \mathbf{H}\tilde{\mathbf{x}} \end{aligned}$$

where the tilde notation (such as $\tilde{\mathbf{x}}$) indicates the difference between a random variable and its expected value at its most recent update, and \mathbf{G} and \mathbf{H} are the expected values of vector gradients. The (i, j) element of the matrix \mathbf{G} is $E[\partial g_i / \partial x_j]$ and the (i, j) element of \mathbf{H} is $E[\partial h_i / \partial x_j]$.

For many nonlinear functions, the stochastic linear filter provides an accurate approximation to the RMV filter. Its principal advantage lies in ease of implementation. Filter equations are listed below:

State estimate extrapolation	$\hat{\mathbf{x}}_k^{(-)} = \mathbf{E}[\hat{\mathbf{x}}_{k-1}^{(+)})],$
Error covariance extrapolation	$\mathbf{P}_k^{(-)} = \mathbf{G}_{k-1}\mathbf{P}_{k-1}^{(+)}\mathbf{G}_{k-1}^T + \mathbf{Q}_{k-1},$
State estimate update	$\hat{\mathbf{x}}_k^{(+)} = \hat{\mathbf{x}}_k^{(-)} + \mathbf{K}_k(\mathbf{z}_k - \mathbf{E}[\mathbf{h}(\hat{\mathbf{x}}_k^{(-)})]),$
Error covariance update	$\mathbf{P}_k^{(+)} = \mathbf{P}_k^{(-)} - \mathbf{K}_k\mathbf{H}_k\mathbf{P}_k^{(-)},$
Gain matrix	$\mathbf{K}_k = \mathbf{P}_k^{(-)}\mathbf{H}_k^T \{ \mathbf{R}_k + \mathbf{H}_k\mathbf{P}_k^{(-)}\mathbf{H}_k^T \}^{-1}. \quad (5.43)$

where the notation \mathbf{G}_{k-1} indicates conditional expected values are taken at the $[(k-1), (+)]$ stage, and \mathbf{H}_k indicates conditional expected values are taken at the $[k, (-)]$ stage.

Age-structured Models: Per-Recruit and Year-Class Models

Age-structured (also called *dynamic pool*) models explicitly represent a population as a group of different year-classes or cohorts. Dynamic models for such a population contain three basic components: growth, mortality, and recruitment. In a year-class model, we focus on the first two components—growth and mortality—by tracking the fate of a cohort from the length, l_r (> 0), or age, t_r , of recruitment through its fishable life span. For our purposes, recruitment is the year-class abundance at the first possible age of exploitation, given by $N_r = N(t_r)$. However, t_r can be defined as any age of interest. Generally, N_r is chosen to be some value, such as 1 or 1000, so that all quantities are calculated on a relative or “per recruit” basis. Our goal is to develop a quantitative framework for examining the effects of fishing mortality rate, F , and length of entry, l_c , into the fishable stock on yield from a year-class of any given initial abundance.

The classical yield-per-recruit problem (analyzed extensively by Beverton and Holt, 1957) is to exploit a given cohort in such a way that its full yield potential is realized. The models in this chapter are all simplifications of fish dynamics. We generalize some of the more traditional approaches in yield theory, while keeping a close eye to maintaining equations whose parameters can reasonably be estimated from typical data. In chapter 7, we link the progeny reproduction process to year-class models.

As a starting point, we first examine the dynamics of an unfished cohort. Let

$N(t)$ = number of fish of a given cohort alive at age t

$L(t)$ = mean length of a fish at age t

$W(t)$ = mean weight of a fish at age t

$B(t)$ = biomass of the cohort at age t

t_∞ = maximum age of the cohort

M = natural mortality rate.

Natural mortality is assumed to be constant for all ages $t \geq t_r$. It is often difficult to

estimate M as anything other than a constant independent of age and year (section 8.3). Nevertheless, the generalization to age-specific $M(t)$ is trivial.

Cohort abundance from section 1.2 is

$$N(t) = N_r e^{-M(t-t_r)}, \quad (6.1)$$

which is an exponentially declining function of initial cohort abundance, N_r . Average weight, $W(t)$, is usually modeled by one of the size-age models from chapter 4. Cohort biomass, $B(t) = N(t)W(t)$, is almost always a dome-shaped curve. The peak of this curve occurs at what is called the critical age, t^* , which is found by solving the following equation:

$$\frac{dB}{dt} = N \frac{dW}{dt} + W \frac{dN}{dt} = 0.$$

For the LVB allometric model (4.20), the solution is

$$t^* = t_0 + \frac{1}{\kappa} \ln \left(1 + \frac{\beta}{m} \right), \quad (6.2)$$

where $m = M/\kappa$. This ratio of natural mortality to growth will occur frequently and can be thought of as a fundamental life-history parameter. Corresponding to t^* are parameters $L^* = L(t^*)$, $W^* = W(t^*)$, and so on.

Example 6.1. Gulf of Alaska sablefish

Female sablefish in the Gulf of Alaska experience natural mortality, M , of 0.10 and follow an isometric LVB model ($\beta = 3$) with parameters given in table 6.1 (M. Sigler, NMFS, Juneau, AK, personal communication, 1987). Age of recruitment is $t_r = 1$. Starting with $N_r = 1000$ recruits, the curves for $N(t)$, $W(t)$, and $B(t)$ for an unfished cohort are shown in figure 6.1. The peak of cohort biomass occurs at critical age $t^* = 8.36$ from (6.2). Corresponding statistics are $L^* = 67$, $W^* = 3.40$, $N^* = 479$, and $B^* = 1627$, summarized in table 6.1. ■

A discrete time model can also be constructed, which will be the basis of a generic approach described in section 6.3. Let N_t be the number of fish of a given cohort alive at the start of age t . Cohort abundance from section 1.2 is

Table 6.1. Population and critical age parameters for female sablefish in the Gulf of Alaska.

Population parameters	Value	Critical age parameters	Value
M	0.1 year ⁻¹	t^*	8.36 years
L_∞	82 cm	E^*	1.00
K	0.15 year ⁻¹	F^*	∞ year ⁻¹
t_0	-3 years	L^*	67 cm
W_∞	6.20 kg	W^*	3.40 kg
$m=M/K$	0.67	N^*	479
t_r	1 year	B^*	1627
N_r	1000	c^*	0.82
		y^*	17.6%
		Y^*/R	1.63 kg

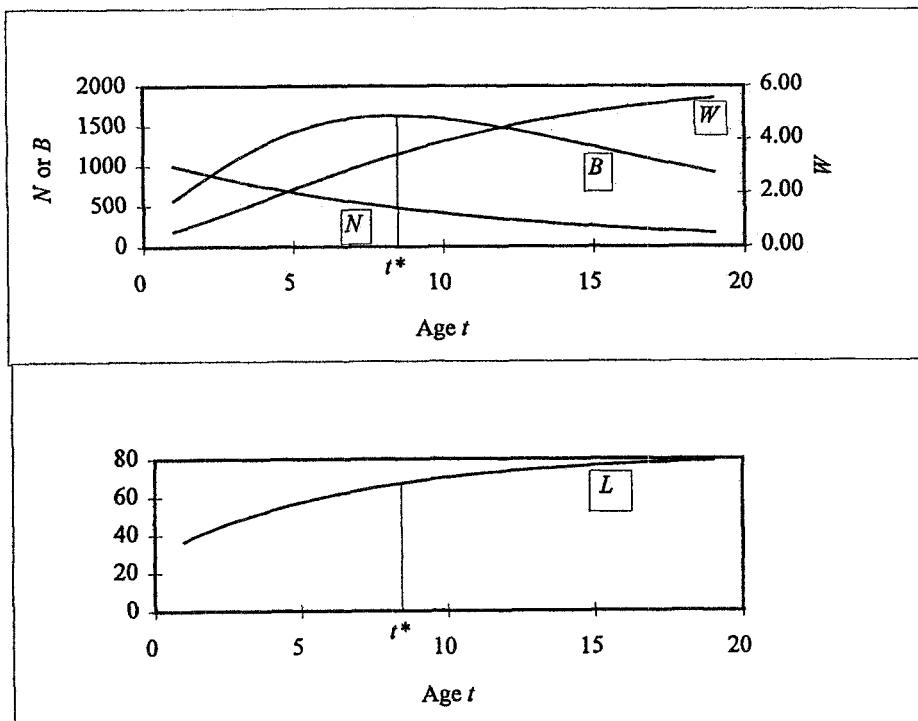


Figure 6.1. Abundance, N , average weight, W , biomass, B , and length, L , as a function of age, t , for the unfished Gulf of Alaska sablefish population in example 6.1. Critical age, t^* , occurs at the maximum of the biomass curve.

$$N_t = N_{t-1} e^{-M} = N_r e^{-M(t-t_r)}, \quad t = t_r, \dots, t_\lambda, \quad (6.3)$$

which is an exponentially declining function of initial cohort abundance N_r . Other equations follow analogously.

6.1. BEVERTON-HOLT MODELS

We first develop models for the classical situation where all members of a cohort reach fishable size at the common age t_c (or equivalently, length l_c). They are then fully vulnerable to the fishery; all have equal and constant F for ages $t > t_c$. The recruitment assumption is also referred to as *knife-edge selectivity*. Constant fishing mortality implies that our yield-per-recruit results will be applicable to all recruited cohorts in a given population because each cohort at each age above t_c is subjected to the same F . Constant F is not practical in most fishery situations, even when it is a management goal—fluctuating gear efficiency, uncertain stock abundance, and variable fishing effort, especially within a year, all cause F to vary. Even if we were to keep annual F constant, fishing mortality would probably vary by age due to size selectivity of fishing gear (see chapters 1, 8, 9). Despite these problems, the constant annual F assumption has given fishery agencies a practical means for evaluating current catch quotas (see chapter 11). The knife-edge selectivity assumption is another matter, which we relax in section 6.3.

We begin with some definitions. For a given cohort, let $C(t)$ be the cumulative catch (in numbers of fish) from age t_c to age t ; $Y(t)$ be the cumulative yield (in biomass) from age t_c to age t ; and Z be the total mortality rate, $Z = F + M$. Per capita mortality rate of a cohort is one of two constants in the simple yield model of Beverton and Holt (1957):

$$\frac{dN(t)}{N(t)dt} = \begin{cases} -M, & \text{for } t_r < t < t_c \\ -Z, & \text{for } t \geq t_c. \end{cases}$$

The solution of those differential equations gives us cohort abundance, *viz.*,

$$N(t) = \begin{cases} N_r e^{-M(t-t_r)}, & \text{for } t_r < t < t_c \\ N_r e^{-M(t_c-t_r)} e^{-Z(t-t_c)} = N_c e^{-Z(t-t_c)}, & \text{for } t \geq t_c, \end{cases} \quad (6.4)$$

where $N_c = N(t_c)$. Year-class abundance declines exponentially, where the decline is initially governed by natural mortality rate, M . At age t_c , total mortality rate increases to $Z = F + M$, which increases the rate of cohort decline. These declines are illustrated in figure 6.2, which uses parameters for sablefish from example 6.1, along with a fishing mortality, F , of 0.1 and knife-edge selectivity at a particular entry age $t_c = 5$.

The rate of increase in catch is that portion of $dN(t)$ taken by the fishery, $dC(t) = FdN(t)$. By integrating $dC(t)$ (as in section 1.2), we see that

$$\begin{aligned} C(t) &= \int_{t_c}^t FN(x)dx \\ &= N_c \frac{F}{Z} \left[1 - e^{-Z(t-t_c)} \right] \\ &= N_r e^{-M(t_c-t_r)} \frac{F}{Z} \left[1 - e^{-Z(t-t_c)} \right], \end{aligned} \quad (6.5)$$

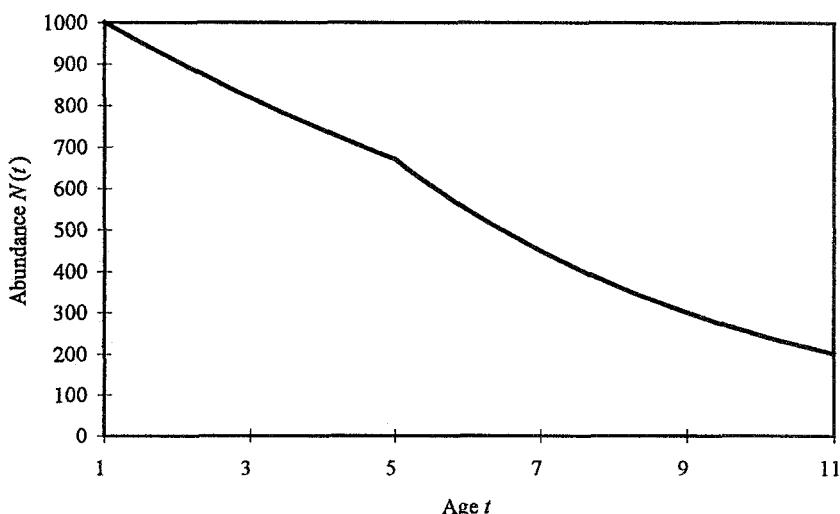


Figure 6.2. Abundance $N(t)$ as a function of age t for a fished Gulf of Alaska sablefish population. Only natural mortality occurs before age 5, and both natural and fishing mortality occur after age 5.

the Baranov catch equation. As $t \rightarrow \infty$, catch per recruit can be expressed simply as

$$C_\infty/N_r = E e^{-M(t_c - t_r)},$$

where $E = F/Z$ is called *exploitation rate*.

For a given t_c , catch per recruit, C/N_r , increases linearly as a function of E , reaching N_c/N_r at $E = 1$ or equivalently at $F = \infty$. Thus, the maximum catch per recruit is obtained by harvesting the entire cohort at age t_c . Choosing $t_c = t_r$ provides maximum catch per recruit as a function of t_c . This solution is obviously not practical, but it illustrates the importance of having a meaningful harvest objective. For the sablefish parameters in table 6.1, the increasing catch per recruit as a function of E for various values of $L_c = L(t_c)$ is illustrated in figure 6.3. As L_c or t_c increases, fewer fish in the cohort are left to be harvested due to losses from natural mortality.

Annual catch, C_t , for the year beginning at age t is

$$C_t = \mu N(t),$$

where the exploitation fraction, μ , is given by

$$\mu = \frac{F}{Z} (1 - e^{-Z}).$$

The rate $dY(t)$ is given by $F d[N(t)W(t)]$. Thus,

$$Y(t) = \int_{t_c}^t F N(x) W(x) dx, \quad (6.6)$$

which can also be written as

$$Y(t) = F N_r e^{-M(t_c - t_r)} \int_{t_c}^t e^{-Z(x - t_c)} W(x) dx \quad (6.7)$$

by substituting (6.4) for $N(x)$.

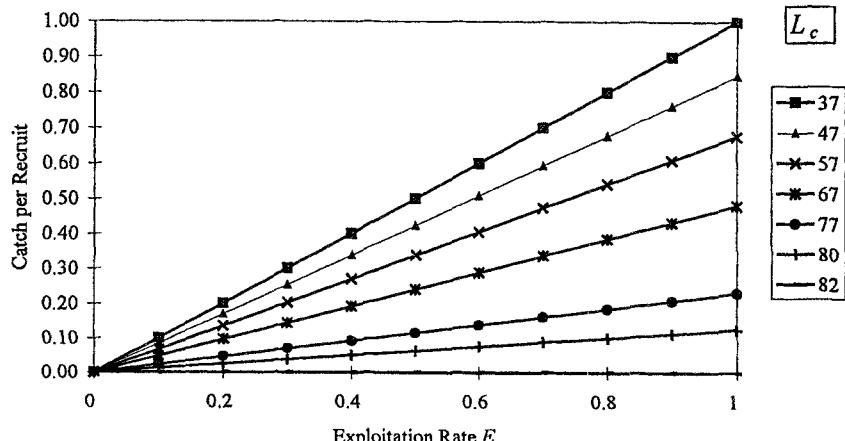


Figure 6.3. Catch per recruit, C_∞/N_r , as a function of exploitation rate, E , at several minimum sizes, L_c , for a fished Gulf of Alaska sablefish population.

The maximum yield per recruit is obtained by applying infinite fishing mortality ($F = \infty$) at age $t_c = t^*$, the critical age when the cohort achieves maximum biomass and has magnitude B^*/N_r . As shown in the next section, there are sometimes finite values of fishing mortality that provide for maximum yield per recruit for other choices of t_c .

6.1.1. LVB Isometric Weight–Age Model

There are several expressions for $W(x)$ that allow for easy integration of the yield equation above. Beverton and Holt (1957) showed how to solve for $Y(t)$ when weight at age is based on the LVB isometric weight–age relationship [(4.20) with $\beta = 3$], given by

$$W(t) = W_\infty [1 - e^{-\kappa(t-t_0)}]^3. \quad (6.8)$$

In the context of yield theory, this weight model can be regarded as a quantitative description of mean average weight as a function of age. Thus, the yield model developed in this section is most appropriate for average fish in the cohort; generalizations to more realistic, but more difficult to estimate situations are given in later sections (6.1.2, 6.2, 6.3) of this chapter.

To solve for $Y(t)$, expand the cubic expression in (6.8) to get

$$W(t) = W_\infty \sum_{n=0}^3 U_n e^{-n\kappa(t-t_0)}$$

where $U_n = +1, -3, +3, -1$ for $n = 0, 1, 2, 3$, respectively. Substitute this into (6.7) and integrate each term of the sum to find

$$Y(t) = FN_c W_\infty \sum_{n=0}^3 \frac{U_n}{Z+n\kappa} e^{-n\kappa(t_c-t_0)} [1 - e^{-(Z+n\kappa)(t-t_c)}]. \quad (6.9)$$

Equation (6.9) can also be expressed in terms of N_r by substituting the relationship

$$N_c = N_r \exp[-M(t_c - t_r)].$$

If (6.9) is evaluated at maximum age, t_∞ , the resultant $Y(t_\infty)$ is the total yield over the fishable life span of a cohort. If t_∞ is large enough for the last term in (6.9) to be negligible, then total yield is given by

$$Y_\infty = FN_r e^{-M(t_c - t_r)} W_\infty \sum_{n=0}^3 \frac{U_n e^{-n\kappa(t_c-t_0)}}{Z+n\kappa}. \quad (6.10)$$

Even though we have reached a considerable simplification in (6.10), there are still too many parameters ($t_r, t_c, F, M, \kappa, N_r, t_0$) in the yield equation to allow for easy graphical interpretation. Beverton and Holt (1964) gave a clever parameterization in dimensionless units for total catch and yield, which has the added benefit of completely removing age from the resulting equation.

The exploitation rate, $E = F/Z$, has dimensionless units and allows cumulative catch of the number of fish from a cohort from (6.5) to be written as

$$C(t) = E[N_c - N(t)], \quad (6.11)$$

which shows that the total deaths from a cohort for any period of time can be apportioned to the fishery with E and to other causes with $(1 - E)$. In particular, the lifetime catch from a cohort (for $t \rightarrow \infty$) is described by $C_\infty = EN_c$.

Define y as the lifetime yield from a cohort, expressed as a fraction of the maximum possible weight a cohort would reach if no mortality occurred after reference age t_0 . That is, let

$$y = \frac{Y_\infty}{N(t_0)W_\infty},$$

and then (6.10) can be written as

$$y = E \sum_{n=0}^3 \frac{U_n(1-c)^{n+m}}{1+n(1-E)/m}, \quad (6.12)$$

where $c = L_c/L_\infty$, the recruitment length as a fraction of asymptotic length, and $m = M/\kappa$, the natural mortality as a fraction of growth.

Derivation of (6.12) is a straightforward algebraic manipulation of (6.10) that makes use of the relationship $c = 1 - e^{-\kappa(t_c-t_0)}$. The reference age t_0 may be less than 0 if based on regression results. For this reason, we regard $N(t_0)$ as a reference prerecruit index, which is proportional to entry abundance, N_c , with proportionality constant $\exp[M(t_c - t_0)]$. That constant—and, in particular, the M rate—affects only the scaling of a yield curve. Thus, the shape of a y -versus- E (or versus c) graph will not be altered by a change in M , as long as the same change is made to κ so that m is constant. In particular, maxima and slopes for a y curve correspond directly to the Y_∞ curve. However, confidence intervals around yield per recruit depend on M when it is a component in the uncertainty of yield. For such calculations, it is better to return to the original scaling of yield per recruit given by

$$\frac{Y_\infty}{N_r} = ye^{M(t_r-t_0)}W_\infty. \quad (6.13)$$

Example 6.2. Sablefish in the Gulf of Alaska

The calculations of lifetime percentage yield, y , and yield per recruit, Y/R , are given in table 6.2 for the sablefish parameters in table 6.1. Parameters E^* , F^* , $c^* = L^*/L_\infty$, y^* , and Y^*/R corresponding to critical age, t^* , are given in table 6.1. The maximum yield per recruit of 1.63 kg (a percentage lifetime yield of 17.6%) can be obtained by harvesting all fish at length 67 cm at critical age 8.4 years. ■

The three parameters E , c , and m completely characterize the essential features of yield. Figure 6.4 shows the yield-per-recruit surface as a function of E and $L_c = L_\infty c$ for the values in table 6.2. Figure 6.5 shows the same values plotted as contours (isopleths) of yield. These figures show many features commonly found in yield curves: (1) Many pairs of E , c values produce the same yield per recruit. (2) The global maximum yield per recruit occurs at critical age, t^* , as $F \rightarrow \infty$ (or $E^* \rightarrow 1$). (3) For some fixed relative entry lengths (c), yield per recruit is a dome-shaped function of E with a peak at an intermediate E value, say E_{\max} . The locus of points E_{\max} for the fixed values of c (or L_c or t_c), called the line of cacometric fishing by Clark (1985),

Table 6.2. Calculation of percentage lifetime yield and yield per recruit as a function of exploitation rate and minimum size limit for sablefish in the Gulf of Alaska.

E	F	Minimum size limit, L_c (cm)						
		37	47	57	67	77	80	82
$c=L_c/L_\infty$		0.45	0.57	0.70	0.82	0.94	0.98	1.00
t_c		1.00	2.68	4.92	8.32	15.65	21.76	118.48
Percentage lifetime yield, y (%)								
0	0.00	0.0	0.0	0.0	0.0	0.0	0.0	0.0
0.1	0.01	3.4	3.3	3.1	2.6	1.4	0.8	0.0
0.2	0.03	6.5	6.4	6.0	5.0	2.9	1.6	0.0
0.3	0.04	9.0	9.1	8.7	7.4	4.2	2.4	0.0
0.4	0.07	11.0	11.3	11.1	9.6	5.6	3.2	0.0
0.5	0.10	12.4	13.1	13.1	11.7	7.0	4.0	0.0
0.6	0.15	13.0	14.3	14.8	13.5	8.3	4.8	0.0
0.7	0.23	12.7	14.7	16.0	15.2	9.5	5.6	0.0
0.8	0.40	11.3	14.3	16.5	16.4	10.7	6.4	0.0
0.9	0.90	9.0	12.9	16.3	17.3	11.8	7.1	0.0
1	∞	6.2	10.7	15.2	17.6	12.8	7.8	0.0
Yield per recruit Y/R^a (kg)								
0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.1	0.01	0.32	0.31	0.29	0.24	0.13	0.08	0.00
0.2	0.03	0.60	0.59	0.55	0.46	0.26	0.15	0.00
0.3	0.04	0.83	0.84	0.80	0.68	0.39	0.23	0.00
0.4	0.07	1.02	1.05	1.02	0.89	0.52	0.30	0.00
0.5	0.10	1.15	1.21	1.22	1.08	0.64	0.37	0.00
0.6	0.15	1.20	1.32	1.37	1.25	0.77	0.45	0.00
0.7	0.23	1.17	1.36	1.48	1.40	0.88	0.52	0.00
0.8	0.40	1.05	1.32	1.53	1.52	0.99	0.59	0.00
0.9	0.90	0.83	1.20	1.51	1.60	1.10	0.66	0.00
1	∞	0.57	0.99	1.41	1.63	1.19	0.72	0.00

^aFactor for converting between y and $Y/R = 9.25$.

is shown in figure 6.5. (4) For some fixed exploitation rates (E), yield per recruit is a dome-shaped function of c with a peak at an intermediate c value, say c_{\max} . The locus of points c_{\max} for the fixed values of E (or F), called the line of eumetric fishing by Clark (1985), is shown in figure 6.5.

"Cacometric" literally means "badly measured," which is probably not what was intended. This type of policy in terms of fishing mortality is known as an F_{\max} policy and has been widely used. A more accurate term might be " F_{\max} " fishing. Similarly, eumetric (meaning "well-measured") fishing might be called " $t_{c,\max}$ " fishing.

We discuss harvesting strategies that maximize yield per recruit further in section 11.4.3. As described in chapter 11, F_{\max} can frequently exceed sustainable harvest rates and is not considered a conservative policy. An improvement, called $F_{0.1}$, reduces the recommended F to a level where the marginal increase in the yield-per-recruit curve becomes small, as explained in section 11.4.5. Neither of these policies considers effects on spawning populations, which can be substantial. We consider these effects in section 6.4 and corresponding harvesting policies in section 11.4.6.

For some fishes, the cubic (isometric) curve relating length to weight is inadequate. One choice in such a situation is to view the weight model (6.8) for what it is: a

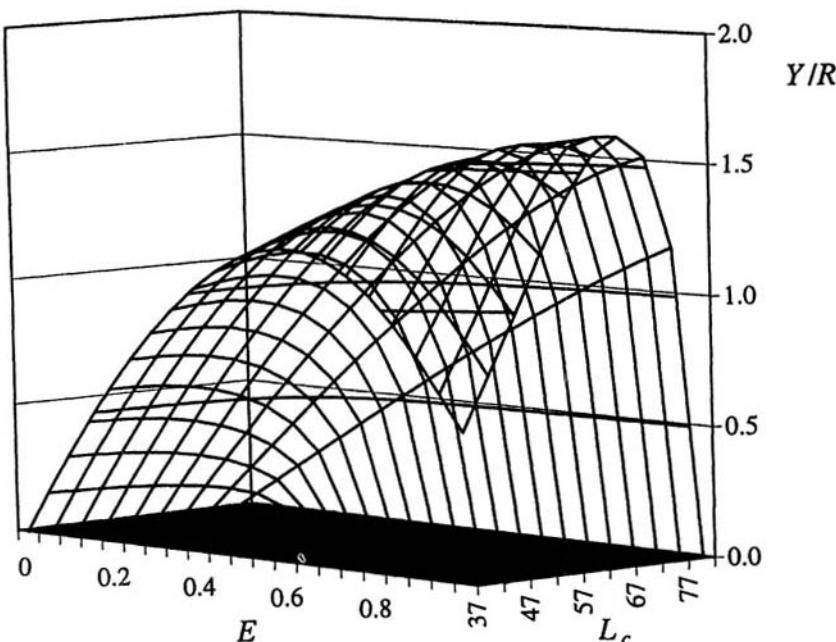


Figure 6.4. A three-dimensional graph of yield per recruit, Y/R , as a function of exploitation rate, E , and minimum size, L_c , for a fished Gulf of Alaska sablefish population (example 6.2).

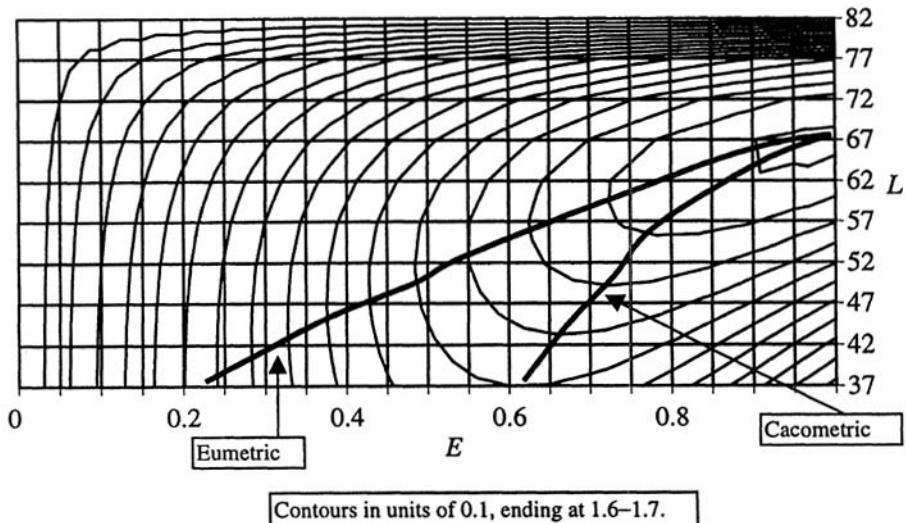


Figure 6.5. A contour plot of yield per recruit, Y/R , as a function of exploitation rate, E , and minimum size, L_c , for a fished Gulf of Alaska sablefish population (example 6.2). The lines of eumetric and cacometric fishing are also shown.

function relating age to weight. In this approach, we drop the two-step derivation of (6.8), which consisted of relating age to length and then relating length to weight. In its place, we view (6.8) strictly as a flexible three-parameter function relating weight to age. Estimation of those parameters is discussed in section 4.2.3. Yield equations of the previous section are still valid if we replace all expressions pertaining to length, $L(t)$, by the cube root of weight: replace L_c by $W(t_c)^{1/3}$ and L_∞ by $W_\infty^{1/3}$.

6.1.2. LVB Allometric Weight–Age Model

A closed-form solution for yield also occurs when growth is given by the LVB allometric weight–age relationship (4.20), given by

$$W(t) = W_\infty [1 - e^{-\kappa(t-t_0)}]^\beta. \quad (6.14)$$

There are now four parameters relating weight to age, which is not parsimonious with the single parameter F that describes fishing mortality. Another disadvantage of this $W(t)$ function is that the resultant yield equation is not integrable, although a table look-up procedure is available. Yield, $Y(t_\infty)$, can be written in terms of an incomplete beta function. Gulland (1973) showed for $t_\infty \rightarrow \infty$, that

$$Y_\infty = N_r W_\infty e^{M(t_r-t_0)} g(1-c)^{-g} B_{1-c}(m+g, \beta+1), \quad (6.15)$$

where $g = F/\kappa$, and the incomplete beta function is

$$B_x(p, q) = \int_0^x y^{p-1} (1-y)^{q-1} dy.$$

Modern spreadsheets have the incomplete beta function, and printed tables are also available.

6.1.3. Brody-LVB Weight–Age Model

Another weight–age model, commonly used in delay-difference population models (section 4.2.2 and chapter 5), is the Brody-LVB model. Instead of length, the assumption here is that

$$W(t) = W_\infty [1 - e^{-\kappa'(t-t'_0)}], \quad (6.16)$$

where κ' and t'_0 parameters are analogous to κ and t_0 defined previously.

Equation (6.16) is strictly concave [$\dot{W}(t) < 0$], so it is appropriate only for those situations where the inflection point in growth occurs before recruitment age t_c , if at all. The inflection point is not usually a problem, however, as many fishes are harvested at sizes above that point, as they should be; growth is nearly exponential before this point and higher yields can usually be obtained by letting them reach a larger size. We derive a rather thorough yield theory for (6.16), mainly because it lends itself to analytical expressions unavailable for more complex growth models. In our experience, we have found this model quite satisfactory for many fisheries analyses.

Substitution of (6.16) into (6.7) leads to a simple integral evaluation of yield as

$$Y(t) = FN_c W_\infty \left[\frac{1 - e^{-Z(t-t_c)}}{Z} - \frac{(1 - e^{-(Z+\kappa')(t-t_c)})e^{-\kappa'(t_c-t_0)}}{Z + \kappa'} \right], \quad (6.17)$$

which is similar to the first two terms in the yield equation (6.9). Total yield over the lifetime of a cohort, $Y(t_\infty)$, can be simplified further when t_∞ is sufficiently large, so that exponential terms raised to the power t can be ignored. Here we find

$$Y_\infty = FN_c W_\infty \left[\frac{1}{Z} - \frac{e^{-\kappa'(t_c-t_0)}}{Z + \kappa'} \right] \quad (6.18)$$

by analogy to (6.10). We can rewrite (6.18) in dimensionless quantities, analogous to (6.12), in a form which does not contain age-dependent variables, as

$$y = E(1 - c')^{m'} \left[1 - \frac{1 - c'}{1 + (1 - E)/m'} \right], \quad (6.19)$$

where $y = [Y(t_\infty)/N(t_0)W_\infty]$, the yield as a fraction of maximum possible cohort weight; $E = F/Z$, the rate of exploitation; $c' = W_c/W_\infty$, the recruitment weight as a fraction of asymptotic weight; and $m' = M/\kappa'$.

The yield formula in (6.19) can be differentiated (against E) so as to gain some insight into the influence of c and m on the properties of y . The slope of y as a function of E is given by

$$\begin{aligned} \frac{\partial y}{\partial E} &= (1 - c')^{m'} \left[1 - \frac{1 - c'}{1 + (1 - E)/m'} \right] \\ &\quad + E(1 - c')^{m'} \left[\frac{-(1 - c')/m'}{(1 + (1 - E)/m')^2} \right]. \end{aligned} \quad (6.20)$$

The maximum y value (as a function of E) is found by evaluating (6.20) at $\partial y/\partial E = 0$. The value, F_{\max} , at this maximum y value is given, after some algebra, as

$$F_{\max} = \frac{\kappa'}{\sqrt{(1 - c')(1 + \kappa'/M)} - 1} - M. \quad (6.21)$$

F_{\max} increases as either M , κ' , or c' increases.

We can generate confidence intervals around F_{\max} that reflect the effect of uncertainty in our estimates of the biological parameters. Suppose that upper and lower P percent confidence intervals, say (M_l, M_u) , have been computed for M , then the P percent confidence intervals for F_{\max} can be found. The lower confidence interval, say F_l , is calculated by substituting M_l for M in (6.21), and similarly for F_u . We write again to emphasize this useful result:

(F_l, F_u) confidence intervals for F_{\max} correspond to $(M_l \leq M \leq M_u)$.

Intervals about Y_∞ , as well as any other quantity, can be found with a similar procedure. We repeat the caution given in section 6.1.1: confidence intervals around y —as a function of M —are misleading, so it is better to set them around Y_∞ per recruit.

6.2. STOCHASTIC MODEL WITH RECRUITMENT BY SIZE GROUP

The yield equations discussed thus far do not capture the variability in size (for a given age) evidenced by the majority of fisheries studies. We now derive a class of models

based on the classical Beverton-Holt model that allows variable size. Furthermore, recruitment of individual fish into the fishery depends on their size—not on age—in these models; typically recruitment to the fishery will occur across several ages. Catches in such a year-class model show a pattern of increasing catches with increasing age up to some intermediate age followed by an exponential decline. Such model features are discussed further in chapter 9 with other size-structured models. Our purpose for including this material here is twofold: to show how easily we can build upon the models of the previous sections and, second, to show how the age-structured models given earlier extend naturally to size-structured models.

The principal assumption is that W_∞ and L_∞ are the only parameters in the Bertalanffy growth models that are not constant for all individuals in a cohort. That assumption implies that growth curves for individuals run parallel on a logarithm of weight-versus-age plot. To see this for the Brody-LVB weight model, take logarithms in (6.16):

$$\ln[W(t)] = \ln(W_\infty) + \ln[1 - e^{-\kappa'(t-t_0')}].$$

The $\ln(W_\infty)$ term is independent of age, and hence it is a constant term on a $\ln[W(t)]$ -versus- t graph. The right-hand side term in the above equation depends on age and hence sets the slope in the graph. Thus, growth rate (per unit body mass) is the same for all members of the cohort. But weight differs because some individuals start the first age at a size larger than other fish in the cohort.

For our model, we assume: (1) a cohort can be stratified into I groups; (2) the i th group has an asymptotic weight of $W_\infty^{(i)}$ and asymptotic length of $L_\infty^{(i)}$; (3) the proportion of individuals in the i th group is p_i at age t_r ; and (4) all groups have knife-edge selectivity at length L_c .

Starting with the LVB isometric weight model, we see that (6.12) remains valid for each size group in a cohort as long as we realize each of the parameters in that equation pertains only to that size group. Specifically, we define our replacements for terms in (6.12) as

$$\begin{aligned} N(t_0)^{(i)} &= p_i N(t_0), \\ c^{(i)} &= L_c / L_\infty^{(i)}, \\ \text{and } y^{(i)} &= \frac{Y(t_\infty)^{(i)}}{N(t_0)^{(i)} W_\infty^{(i)}}. \end{aligned}$$

We add the yield contributions from each size group to get total yield from the cohort, *viz.*,

$$Y(t_\infty) = \sum_{i=1}^I p_i y^{(i)} W_\infty^{(i)} N(t_0) \quad (6.22)$$

or, in terms of yield per recruit to the population,

$$\frac{Y(t_\infty)}{N_r} = \sum_{i=1}^I p_i y^{(i)} W_\infty^{(i)} e^{M(t_r - t_0)}. \quad (6.23)$$

Equation (6.22) is also appropriate when growth is represented by the Brody-LVB growth model (6.16), but relative yield, $y^{(i)}$, comes from equation (6.19) instead of (6.12).

We now show that exploitation fraction for a cohort is age specific in these yield models. First we sequence the groups in descending $W_\infty^{(i)}$ order; then $c^{(i)} \leq c^{(i+1)}$ for each i th group. For both growth models (6.8) and (6.16), c is related to recruitment age by the equation

$$t_c = t_0 - \frac{\ln(1 - c)}{\kappa}, \quad (6.24)$$

except that κ is replaced by κ' for (6.16). Therefore, age of recruitment is also sequenced in ascending order $t_c^{(i)} \leq t_c^{(i+1)}$. Size-groups recruit sequentially in time with another group joining the vulnerable adults after reaching its recruitment age. The largest size-group, which has the largest W_∞ value, joins first at the youngest recruitment age. At any age t in a cohort's life span, we calculate abundance of each group with (6.4) as in previous yield models, except that $N_r^{(i)} = p_i N_r$ and $t_c^{(i)}$ are the group-specific replacements for terms in (6.4). We can write total abundance of the cohort by summing the group abundances, as follows:

$$N(t) = e^{-M(t-t_r)} N_r \sum_{i=j+1}^I p_i + N_r \sum_{i=1}^j p_i e^{-M(t_c^{(i)}-t_r)} e^{-Z(t-t_c^{(i)})} \quad (6.25)$$

for $t_c^{(j)} < t \leq t_c^{(j+1)}$. The exploitation fraction for the entire cohort depends on age of the cohort, despite the fact that μ is constant for each size group within a cohort. We let μ_t denote the total exploitation rate for the t th year of the cohort's life. By applying the annual Baranov catch equation [given below (6.5)] to our current model, we see that

$$\mu_t = \frac{C_t}{N(t)}$$

where C_t is defined as the cumulative taken from the cohort during the t th year. The denominator in the μ_t formula is straightforward to calculate by applying (6.25). The numerator is more complicated. To simplify our presentation, we show C_t when the group ages of recruitment are successive integers—so that each group will recruit on successive annual birthdays. For $t = t_c^{(j)}$, say,

$$C_t = E \sum_{i=1}^j \left[N(t)^{(i)} - N(t+1)^{(i)} \right],$$

where abundance of each group is given by (6.4) with the use of group-specific parameters.

Some simplification of μ is possible. For example, when the first group is recruited at age $t = t_c^{(1)}$, annual catch is taken only from this group, *viz.*,

$$\begin{aligned} C_t &= E p_1 N(t)(1 - e^{-Z}) \\ &= p_1 \mu N(t) \\ &= \mu_t N(t). \end{aligned}$$

Hence, age-specific exploitation fraction is separable into a product of a full recruitment exploitation fraction, μ , and fraction p_1 describing the age selectivity of exploitation.

Furthermore, the age selectivity term is independent of F , which we shall see later (section 8.2) has particular significance for estimating parameters. For later ages, μ_t is not separable. Cohort abundance at the end of the second year of recruitment is given by

$$N(t+1) = N(t)e^{-M}[p_1e^{-F} + p_2 + \dots + p_I]$$

so that the exploitation fraction for the cohort at age $t+1$ after the second group is recruited can be shown to be

$$\begin{aligned} C_{t+1} &= \frac{p_1e^{-F} + p_2}{p_1e^{-F} + p_2 + \dots + p_I} \mu N(t+1) \\ &= \mu_{t+1} N(t+1). \end{aligned}$$

Here, age selectivity of exploitation depends on F . For the later years, say $t+j$, the exploitation fraction is given below; as a note, cohort abundance is the denominator multiplied by $e^{-Mj}N(t)$, while catch is the numerator multiplied by that same factor.

$$\mu_{t+j} = \frac{p_1e^{-Fj} + p_2e^{-F(j-1)} + \dots + p_{j+1}}{p_1e^{-Fj} + p_2e^{-F(j-1)} + \dots + p_{j+1} + \dots + p_I} \mu$$

Figure 6.6 shows the shape of μ_t versus age when there are five size groups, each with 20% of N_r ; we set $M = 0.2$ for this figure and let F take on a low value of 0.1 and a high value of 0.5. Note that exploitation increases roughly linearly for the small value and curvilinearly for the high value. This is no surprise because the age selectivity part of μ_{t+j} converges to $p_1 + \dots + p_{j+1}$ as $F \rightarrow 0$. Thus, when F is small, exploitation is roughly separable into a full recruitment exploitation, μ , and an age selectivity term (a sum of the p_i).

Yield formulae in this section are consistent with the assumption that W_∞ (or equivalently L_∞) is a random variable. This assumption makes it easy to apply (6.22)

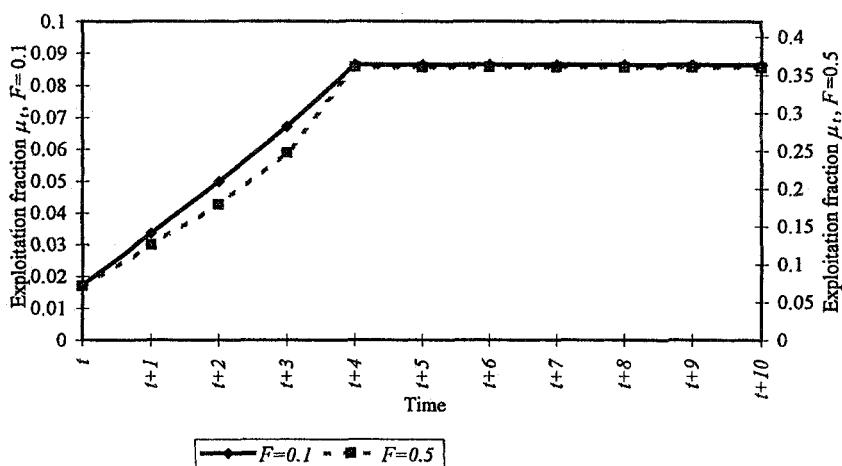


Figure 6.6. Exploitation rate, μ_t , versus age t for two values of F (0.1 and 0.5) for five size groups, each with 20% of N_r .

to most fish stocks. First we estimate the parameters of either LVB growth model (6.8) or (6.16) by a nonlinear regression of logarithm of weight using a multiplicative error structure (as discussed in section 4.2). The estimated residual variance from such a regression (say, $\hat{\sigma}^2$) can be interpreted as being the estimated variance for a normal probability distribution of the logarithm of asymptotic weight; that is, we assume

$$\ln(W_\infty) \sim N[\ln(\hat{W}_\infty), \hat{\sigma}^2].$$

Next we stratify the range for the normal distribution of $\ln(W_\infty)$ into I discrete groups. The midpoint of each group is the logarithm of that group's asymptotic weight. The probability density corresponding to the range for each group is p_i , the proportion of individuals in the cohort with that group's asymptotic weight. The groups should be sequenced in order of descending size so that the I th group has the smallest W_∞ value; therefore, it will have the largest t_c value.

Norris (1989) used the theory in this section to explore yield per recruit for a mixed-gear fishery on sablefish off the coasts of Washington, Oregon, and California. He extended the development to handle several gear types and selectivities for each gear type, as well as differences between males and females. The assumption of a log-normal distribution for length within age class was consistent with empirical evidence. He showed that the faster growing groups were underrepresented in population abundance due to being harvested sooner, but were overrepresented in contributions to egg production due to the greater fecundity of larger individuals. By using this approach he was able to make more realistic evaluation of the trade-off between yield and biomass per recruit in different fisheries.

Example 6.3. Sablefish off Washington, Oregon, and California

We illustrate the stochastic model by using a simpler version of the model of Norris (1989). We assume that the LVB isometric model applies to weight-age. Parameters for female sablefish are given in table 6.3, where we have substituted the value $\beta = 3$ for the allometric exponent (which is close to the value 3.12 estimated by Norris). Five groups of female sablefish were defined from an analysis of log length-versus-age data. The values for L_∞ by group are the transformed midpoints of five equal-probability regions (so that $p_i = 0.2$) from the probability density function of $\ln L_\infty$ with mean of $\ln(78.1)$ cm and $\hat{\sigma}$ of 0.092 (figure 6.7). Corresponding values of W_∞ come from the allometric weight-length model. Age of recruitment is arbitrarily chosen to be $t_r = 1$. Critical age, t^* , is about 7.6 for all groups, independent of L_∞ ; corresponding relative length, c^* , is 0.85. Other critical age statistics are given in table 6.3.

The stochastic model calculations are based on a knife-edge minimum size limit of $L_c = 50$ cm for all groups. Corresponding values of $c = L_c/L_\infty$ and t_c from (6.24) are given by group. Yield per recruit from (6.13) is shown in figure 6.8 by group as a function of exploitation rate. The yield per recruit pooled across groups is also shown, obtained by multiplying by p_i and then summing, as in (6.22) and (6.23). Yield per recruit is higher for faster growing groups and peaks slightly sooner than for slow-growing groups. The pooled yield per recruit is similar to that of the middle group but is not equal to the values due to the nonlinear relationships of growth. The variability in yield among groups is remarkable, which satisfies our goal of incorporating stochasticity into the harvest-per-recruit environment. Nevertheless, more elegant approaches are available for this task, as shown in chapter 9.

Table 6.3. Population parameters for female sablefish off the coasts of Washington, Oregon, and California used to construct a stochastic yield per recruit model.

Parameter ^a	Group				
	5	4	3	2	1
p	0.2	0.2	0.2	0.2	0.2
L_∞	87.9	82.0	78.1	74.4	69.4
W_∞	4.18	3.39	2.93	2.53	2.06
L_c	50	50	50	50	50
c	0.57	0.61	0.64	0.67	0.72
t_c	2.03	2.55	2.98	3.47	4.31
L^*	74.78	69.76	66.44	63.29	59.04
W^*	2.57	2.09	1.80	1.56	1.27
Y^*/R	1.33	1.08	0.93	0.81	0.65

^a $M = 0.10$; $\kappa = 0.19$; $t_0 = -2.40$; W-L $\alpha = 6.2E-06$; W-L $\beta = 3$; $t_r = 1$; $m = M/\kappa = 0.53$; $t^* = 7.61$; $E^* = 1$; $F^* = \infty$; $c^* = 0.85$; $y^* = 22.6\%$.

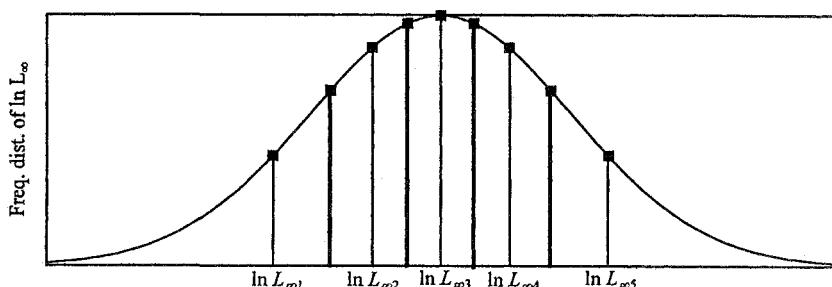


Figure 6.7. Illustration of the method of partitioning the $\ln L_\infty$ distribution into five subpopulations. L_∞ parameters for each subpopulation are determined by taking the antilog of the 10th, 30th, 50th, 70th, and 90th percentiles (weak lines) of the $\ln L_\infty$ distribution. The strong lines show the boundaries of the groups corresponding to the 20th, 40th, 60th, and 80th percentiles. (Redrawn from Norris 1989, figure 4.20.)

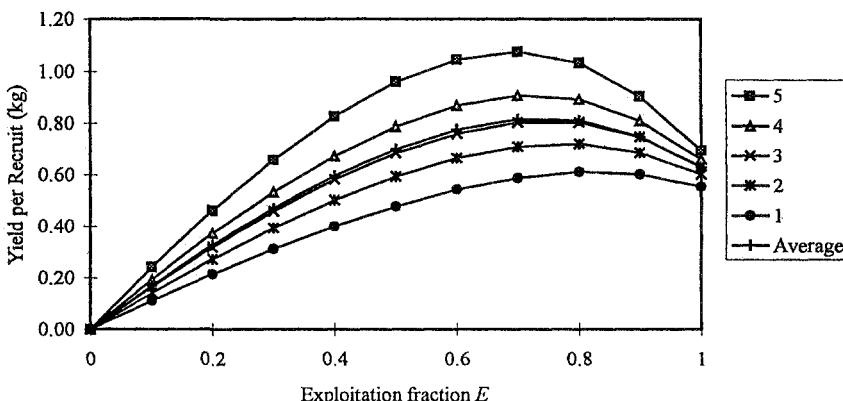


Figure 6.8. Yield per recruit, Y/R , for the five groups and averaged over groups for sablefish in example 6.3.

6.3. GENERIC PER-RECRUIT MODELS

The classical Beverton-Holt per-recruit models are based on knife-edge selectivity, constant fishing mortality and natural mortality across ages, and particular weight-age models. The main benefit, although not as important with today's computers, is the analytic simplicity of resultant abundance and yield equations. However, inapplicability of any of those characteristics renders those models useless. In this section, we develop a generic approach that can be adapted and extended to almost any typical fisheries application.

The continuous version of the generic model is a generalization of (6.5) and (6.6) for varying fishing mortality, $F(t)$, as a function of age, which results in equations for cumulative catch and yield as

$$Z(t) = M(t) + F(t) \quad (6.26)$$

$$N(t) = N_r \exp \left[\int_{t_r}^t -Z(x) dx \right] \quad (6.27)$$

$$C(t_\infty) = \int_{t_r}^{t_\infty} F(x) N(x) dx \quad (6.28)$$

$$Y(t_\infty) = \int_{t_r}^{t_\infty} F(x) N(x) W(x) dx, \quad (6.29)$$

where the specifications of $F(t)$, $N(t)$, and $W(t)$ are left to the user. Any of the variations in this and other chapters could be used for any of the three components. Numerical integration techniques are then used to obtain values.

The corresponding discrete version of the generic model is motivated by practical considerations when useful data are frequently only available on an annual basis. To allow the same feature of variable fishing mortality, the equations are expressed in terms for exploitation fractions $\mu_t = C_t/N_t$:

$$C(t_\infty) = \sum_{x=t_r}^{t_\infty} C_x = \sum_{x=t_r}^{t_\infty} \mu_x N_x \quad (6.30)$$

$$Y(t_\infty) = \sum_{x=t_r}^{t_\infty} Y_x = \sum_{x=t_r}^{t_\infty} \mu_x N_x W_x, \quad (6.31)$$

where the subscript notation is used to refer to discrete, annual quantities as usual. This pair of equations can alternatively be written in terms of cumulative survival. If S_a is annual survival at age a , usually determined as $\exp(-Z_a)$, then cumulative survival is

$$\mathcal{L}_x = \prod_{a=r}^{x-1} S_a.$$

The alternative formulations of catch and yield in their per-recruit versions are then

$$C(t_\infty)/N_r = \sum_{x=t_r}^{t_\infty} \mu_x \mathcal{L}_x \quad (6.32)$$

$$Y(t_\infty)/N_r = \sum_{x=t_r}^{t_\infty} \mu_x \mathcal{L}_x W_x. \quad (6.33)$$

One advantage to the generic, discrete formulation is its ability to use empirical weight-age data. Weight and age data are not typically as precise as assumed in the basic yield equation (6.7). Typical data are obtained during the course of the fishery and whole-integer ages assigned to sampled fish. Even special survey samples of weight data are not typically assigned precise fractional ages. This is not the kind of information that is consistent with the integration of weight by precise age performed in all the previous models. We assume here that the weight-at-age data really represent an integrated average of weight obtained during the course of the fishery. Thus, we interpret W_t as the integrated average weight of a t -year-old fish. We note in passing that this approach is directly transferable to any other fixed time step, such as a quarter of a year.

Yield in (6.31) will be approximately the same as in all previous models. The sole source of approximation is that W_t is fixed to an annual quantity. This is a minor source of error unless the values of μ used are very much different from the μ present when weight data were collected. Straight averages of the weight data by age can be used in (6.31), although it usually is better to smooth those averages first to reduce extraneous variability by fitting one of the growth models in chapter 4. As an alternative, Velleman's robust smoother (Velleman and Hoaglin 1981) works nicely here.

The annual exploitation fraction applied to (6.30) and (6.31) can take on a variety of forms. A list of some of the forms is given below, along with corresponding cohort abundance:

1. Assume knife-edge recruitment, then the Baranov catch equation implies full recruitment exploitation:

$$\begin{aligned}\mu_t &= \mu \\ &= \frac{F}{Z} (1 - e^{-Z}) \\ N_{t+1} &= N_t e^{-Z}.\end{aligned}$$

2. Assume recruitment by size group, as specified in the previous section, then

$$\begin{aligned}\mu_{t_c+j} &= \frac{p_1 e^{-Fj} + p_2 e^{-F(j-1)} + \cdots + p_j e^{-F} + p_{j+1}}{p_1 e^{-Fj} + p_2 e^{-F(j-1)} + \cdots + p_j e^{-F} + p_{j+1} + \cdots + p_I} \mu \\ N_{t_c+j} &= [p_1 e^{-Fj} + p_2 e^{-F(j-1)} + \cdots + p_{j+1} + \cdots + p_I] N_{t_c} e^{-Mj}.\end{aligned}$$

3. Assume age-specific fishing mortality rate, which occurs as a separable product of age-specific selectivity, s_t , and full-recruitment fishing mortality rate, F :

$$\begin{aligned}\mu_t &= \frac{F_t}{F_t + M} (1 - e^{-(F_t + M)}) \\ N_{t+1} &= N_t e^{-(F_t + M)} \\ F_t &= s_t F.\end{aligned}\tag{6.34}$$

This third model of fishing mortality is widely applied in fisheries stock assessment. Later in section 8.2, separable fishing mortality is shown to be the key assumption in some important parameter estimation methods. Estimates of age selectivity, s_t , from

those methods can be substituted directly into (6.34) to facilitate an easy method of yield-per-recruit analysis. An example is given below.

All the exploitation models itemized above contain the assumption that age-specific fishing mortality rate is constant within a year. That assumption is rarely true in practice, but it is convenient and widely applied in fisheries research. Nevertheless, the constant assumption captures two of the fundamental features of fishing: namely, competition between units of fishing effort for fish (lesser numbers of fish caught with an incremental increase in fishing effort), and the competition between natural mortality and fishing mortality for fish. Reduced catches occur because the next increment of fishing occurs on a cohort reduced in abundance by previous fishing.

For some fishes, such as Pacific halibut, the fishery was so intense that gear competition was compressed to a matter of days within each year. In such situations, it is more realistic to assume that fishing takes place over a short period of time each year. Aside from increasing realism, this assumption simplifies the model and facilitates easy parameter estimation [for example, the cohort analysis method of Pope (1972), or a simple modification of it, are appropriate, as discussed later in section 8.2].

Schnute (1987) discussed this type of model and assumed that the year can be broken into three parts with fishing occurring only during the second part. He assumed natural mortality does not occur, or is negligible, during the second part of the year when fishing occurs. Let ϕ be the fraction of a year before the start of the fishery. The fishing period is also assumed to occur over a small amount of time so that total natural mortality rate for the year is approximately M : $M\phi$ for the first period plus $M(1 - \phi)$ for the second period. The replacements for μ and N_{t+1} in the three exploitation models above are

$$\begin{aligned}\tilde{\mu} &= (1 - e^{-F})e^{-M\phi} \\ N_{t+1} &= N_t e^{-(F+M)},\end{aligned}\tag{6.35}$$

where F is the fishing mortality rate during the fishing period. For the third model, we replace F with F_t . When ϕ is set equal to 0.5, we get Pope's close approximation, used in cohort analysis in section 8.2. We have looked at that approximation and have found by setting $\phi = 0.45$, we get an even better approximation to the Baranov catch equation. For a seasonal fishery, ϕ should be set slightly earlier than the midpoint of the fishing season. The fraction is set before the midpoint because survival curves are skewed exponentially. For example, if the fishery occurs primarily for months 6–9, then ϕ can be set to 7.4/12.

Example 6.4. Rainbow trout in Blue Lake, Sitka, Alaska

This example illustrates the empirical calculation of yield-per-recruit parameters using form 3 above for the exploitation model and its corresponding set of equations (6.34). Table 6.4 contains growth, mortality, and selectivity parameters for rainbow trout in Blue Lake (DerHovanishan 1994), including estimates of current fishing mortality and exploitation rate. Full-recruitment fishing mortality, F , is the control parameter, and a value of twice the current level or 0.68 is used for contrast. Per-recruit statistics are given in table 6.4. First, fishing mortality at age is calculated as the product of age selectivity and F . Corresponding exploitation fractions follow from the Baranov catch equation. Abundance at age is then calculated using exponential decay, starting with an arbitrary 100 recruits. Catch and yield per 100 recruits are then calculated as a function

Table 6.4. Population parameters and per recruit statistics using the generic approach for rainbow trout in Blue Lake, Sitka, Alaska.

	Age, t						
F	3	4	5	6	7		
Mean length, L_t (mm)	238	286	329	368	400		
Mean weight, W_t (kg)	0.156	0.272	0.405	0.538	0.658		
Maturity, m_t	0.29	0.77	0.96	1	1		
Natural mortality, M_t	0.26	0.26	0.26	0.26	0.26		
Selectivity, s_t	0.61	0.92	1	0.6	0.6		
							Average
Fishing mortality, F_t	0.00	0.000	0.000	0.000	0.000	0.000	0.000
	0.34	0.207	0.313	0.340	0.204	0.204	0.254
	0.68	0.415	0.626	0.680	0.408	0.408	0.507
							Sum 3+ % of $F=0$
Abundance, N_t	0.00	100	77	59	46	35	318 100.0
	0.34	100	63	35	19	12	230 72.3
	0.68	100	51	21	8	4	184 58.0
							Average
Exploitation fraction, μ_t	0.00	0.000	0.000	0.000	0.000	0.000	0.000
	0.34	0.166	0.238	0.256	0.163	0.163	0.199
	0.68	0.302	0.415	0.441	0.298	0.298	0.349
							Sum
Catch, C_t	0.00	0	0	0	0	0	0
	0.34	17	15	9	3	2	46
	0.68	30	21	9	2	1	64
							Sum
Yield, Y_t	0.00	0.0	0.0	0.0	0.0	0.0	0.0
	0.34	2.6	4.1	3.7	1.7	1.3	13.3
	0.68	4.7	5.7	3.8	1.3	0.8	16.3
							Sum % of $F=0$
Spawning abundance, $S_{N,t}$	0.00	29	59	57	46	35	227 100.0
	0.34	29	48	34	19	12	143 63.0
	0.68	29	39	20	8	4	101 44.5
							Sum % of $F=0$
Spawning biomass, $S_{B,t}$	0.00	4.5	16.1	23.1	24.7	23.3	91.7 100.0
	0.34	4.5	13.1	13.7	10.4	8.0	49.8 54.4
	0.68	4.5	10.7	8.2	4.4	2.8	30.5 33.3

of full-recruitment fishing mortality using (6.32) and (6.33), respectively. Catch and yield per recruit are higher for the higher F . But the age composition of the population shifts to lower ages at the higher F . Optimal management strategies for this population are explored in chapter 11. ■

6.4. SPAWNING STOCK AND EGG PRODUCTION PER RECRUIT

One issue remaining in yield-per-recruit analysis is the effect that harvesting has on future recruitment. Such implications will become quite clear in chapter 7 when we

develop complete age-structured models. However, some common methods of assessing reproductive demands are based on yield theory. This section will also serve as a bridge between yield-per-recruit analysis and full age-structured models.

The definitions of spawning abundance, biomass, and egg production of a cohort for a continuous model are

$$\mathcal{S}_N(t_\infty) = \int_{t_r}^{t_\infty} m(x)N(x)dx \quad (6.36)$$

$$\mathcal{S}_B(t_\infty) = \int_{t_r}^{t_\infty} m(x)N(x)W(x)dx \quad (6.37)$$

$$N_0(t_\infty) = \int_{t_r}^{t_\infty} f(x)N(x)W(x)dx, \quad (6.38)$$

where $m(x)$ is maturity and $f(x)$ is net fecundity (see chapter 4). Further simplification occurs by assuming knife-edge maturity, so that $m(x) = 0$ for $x < t_s$ and $m(x) = 1$ for $x \geq t_s$. Then, when spawning commences after fishing, or $t_s \geq t_c$, the spawning biomass equation (6.37) becomes

$$\mathcal{S}_B(t_\infty) = \int_{t_s}^{t_\infty} N(x)W(x)dx = Y(t_s \rightarrow t_\infty)/F \quad (6.39)$$

where $Y(t_s \rightarrow t_\infty)$ is the yield equation (6.6) with t_c replaced by t_s .

6.4.1. Beverton-Holt Approach

For the LVB isometric model in section 6.1.1 under knife-edge spawning, abundance, N_s , at the earliest age of spawning, t_s , is

$$N_s = \begin{cases} N_r e^{-M(t_s - t_r)}, & \text{if } t_s < t_c, \\ N_r e^{-M(t_c - t_r)} e^{-Z(t_s - t_c)}, & \text{if } t_s \geq t_c. \end{cases}$$

Substitution of the yield equation (6.9) into (6.39) results in

$$\mathcal{S}_B(t_s \rightarrow t_\infty) = N_s W_\infty \sum_{n=0}^3 \frac{U_n}{Z + n\kappa} e^{-n\kappa(t_s - t_0)} [1 - e^{-(Z+n\kappa)(t_\infty - t_s)}], \quad (6.40a)$$

when $t_s \geq t_c$. When $t_s < t_c$, the integral (6.39) is separated into two parts, one from t_s to t_c and one from t_c to t_∞ . Using the notation in (6.40a), spawning biomass can be calculated as

$$\mathcal{S}_B(t_s \rightarrow t_\infty) = \mathcal{S}_B(t_s \rightarrow t_c) + \mathcal{S}_B(t_c \rightarrow t_\infty). \quad (6.40b)$$

If $t_s \geq t_c$, then, analogously to section 6.1.1, (6.40a) for $t_\infty \rightarrow \infty$ can be rewritten in terms of relative parameters $E = F/Z$, $s = L_s/L_\infty$, and $m = M/\kappa$. In terms of spawning biomass per fish of age t_s , the result is

$$\mathcal{S}_B/N_s = y_s e^{M(t_s - t_0)} W_\infty / F, \quad (6.41)$$

where

$$y_s = E \sum_{n=0}^3 \frac{U_n(1-s)^{n+m}}{1+n(1-E)/m}. \quad (6.42)$$

Spawning biomass per recruit becomes

$$\mathcal{S}_B/N_r = (\mathcal{S}_B/N_s)e^{-M(t_c-t_r)}e^{-Z(t_s-t_c)}. \quad (6.43)$$

Similar formulae can be obtained for spawning abundance and egg production.

Example 6.5. Sablefish in the Gulf of Alaska.

This example illustrates the closed-form calculation of spawning biomass per recruit using equations (6.41)–(6.43) for the LVB isometric model. Knife-edge selectivity is assumed to occur at the age of recruitment ($t_r = t_c = 1$), and knife-edge maturity is assumed to occur at $t_s = 5$. Values of y_s , \mathcal{S}_B/N_s , \mathcal{S}_B/N_r , and $\% \mathcal{S}_B/N_r$ are given in table 6.5 for selected values of E (and F). It is clear that higher exploitation results in lower spawning biomass per recruit. ■

6.4.2. Generic Approach

Generic per-recruit analyses can also be undertaken in a general age-structured setting as in section 6.3. Let \tilde{f}_t be the average fecundity of a mature female at age t ; m_t be the proportion of mature females at age t ; $f_t = m_t \tilde{f}_t$, the average net fecundity of a female at age t ; and $\mathcal{L}_t = \prod_{x=r}^{t-1} S_x$, the survival from age r to age t , where survival, S_x , is usually calculated as $\exp[-(M_x + s_x F)]$. The definitions of reproductive variables are:

$$\text{Spawning abundance per recruit } \mathcal{S}_N/N_r = \sum_t m_t \mathcal{L}_t \quad (6.44)$$

$$\text{Egg production per recruit } N_0/N_r = \sum_t f_t \mathcal{L}_t \quad (6.45)$$

$$\text{Spawning biomass per recruit } \mathcal{S}_B/N_r = \sum_t m_t \mathcal{L}_t W_t. \quad (6.46)$$

The N_0/N_r relationship is the expected lifetime egg production of a r -year-old. As cumulative survival, \mathcal{L}_t , is a monotonically decreasing function of F , it follows that

Table 6.5. Values of y_s , \mathcal{S}_B/N_s , \mathcal{S}_B/N_r , and $\% \mathcal{S}_B/N_r$ relative to $E = 0$ for Gulf of Alaska sablefish at various values of exploitation rate E .

E	F	y_s	\mathcal{S}_B/N_s	\mathcal{S}_B/N_r	$\% \mathcal{S}_B/N_r$
0.000	0.000	0.000	43.5	29.2	100.0
0.100	0.011	0.031	38.2	24.5	83.9
0.200	0.025	0.060	32.9	20.0	68.4
0.300	0.043	0.086	27.8	15.7	53.8
0.400	0.067	0.110	22.9	11.7	40.2
0.500	0.100	0.131	18.1	8.1	27.9
0.600	0.150	0.148	13.6	5.0	17.2
0.700	0.233	0.160	9.5	2.5	8.5
0.800	0.400	0.166	5.7	0.8	2.7
0.900	0.900	0.164	2.5	0.0	0.2
1.000	∞	0.153	0.0	0.0	0.0

these reproductive variables also decrease monotonically. These equations pose no special problems of calculation. The generic approach is further illustrated in section 11.4.6, when biological reference points related to reproduction are described.

Example 6.6. Rainbow trout in Blue Lake, Sitka, Alaska

This example illustrates the generic calculation of spawning abundance and biomass per recruit parameters, continuing from example 6.4. Table 6.4 also contains maturity parameters for rainbow trout in Blue Lake. Spawning abundance and biomass per an arbitrary 100 recruits are calculated in table 6.4 for the two values of full-recruitment fishing mortality previously used. Both spawning abundance and biomass are lower for the higher F with a greater effect on biomass. Optimal management strategies for this population are explored in chapter 11. ■

Implicit in the development of these equations is the principle that spawning is often not even close to a continuous process through the year, but rather occurs over a short period of the year. Our treatment supposes that spawning occurs early in the year—say, in a matter of weeks—so that we can approximate spawning as a pulse process, which occurs at the exact beginning of each year.

If maturity data are available but fecundity data are not, then it may be acceptable to use spawning biomass, S_B , as a surrogate for egg production, N_0 . The conditions required for this approximation are (1) $W(t)$ is proportional to fecundity of females at age t ; (2) the sex ratio is assumed to be 50/50; (3) the maturity coefficients, m_t , are assumed to be dependent only on age; and (4) t_∞ is assumed to be large enough to encompass the reproductive life span of the cohort.

6.4.3. Effects of Harvesting

Harvesting will not affect future recruitment if there is no relationship between spawners and future recruitment—within the range of actual spawning abundance that will occur in the future. Fishery scientists are not usually willing to make such an assumption, but rather prefer to evaluate the demands that harvesting places on the reproductive capability of the adult stock. This can be done quite conveniently along with yield-per-recruit analysis. Estimates of lifetime yield, $Y(t_\infty)$, are nearly proportional, in many cases, to the amount of eggs produced by a cohort over its life span; the proportionality factor is a monotonic function of fishing mortality. To develop this result, we consider first the simple yield model (6.6) where F is constant and recruitment is knife edge. A parsimonious model of the lifetime egg production by a cohort is based on similar assumptions: (1) that egg production occurs at a constant rate throughout the year and (2) that at every age above recruitment age, egg production is proportional to the biomass of the cohort.

Let \tilde{e} be the rate of egg production (per unit biomass per unit time); $N_0(t)$ be the cumulative eggs produced by a cohort to age t ; and $B(t)$ be the cumulative biomass produced by a cohort to age t . We can write this model of egg production as an equation similar to a yield model:

$$N_0(t) = \int_{t_c}^t \tilde{e} N(x) W(x) dx. \quad (6.47)$$

Factor the constant \tilde{e} out of the integral to show

$$N_0(t_\infty) = \frac{\tilde{e}}{F} Y(t_\infty) = \tilde{e} B(t_\infty), \quad (6.48)$$

because $N_0(t) = \tilde{e} B(t)$. Egg production is difficult to measure, so biomass is typically used instead. Yield is related to $B(t)$ by the simple but important equation

$$Y(t) = FB(t). \quad (6.49)$$

At population equilibrium, where all cohorts are of equal recruitment, cumulative cohort biomass equals fishable stock biomass. This equivalence is important for the evaluation of reproductive capability because it provides a sound basis for comparing analysis of a single cohort to results from the population as a whole. More generally, though, we can make such comparisons without appealing to equilibrium arguments. Instead, we appeal to an assumption of density-independent survival of the young. The idea is to calculate the amount of spawning biomass generated by a recruit over its life span and see if that amount of spawning biomass is large enough to produce a replacement progeny of recruitment age; survival of the progeny does not depend on population density in such a calculation.

There are several advantages to the use of fishable stock biomass as an index of egg production. One principal advantage is that a historical time series are usually available for estimates of stock biomass and recruitment. From that time series, estimates of reproductive capability can be made. One index of reproductive capability is the ratio of recruit abundance, N_c , to fishable stock biomass; stock biomass is evaluated t_c years earlier because it is an index of spawn size. The International Council for Exploration of the Sea (ICES, 1984) report suggested multiplying a maturity ogive to age-specific biomass to get a better index of spawning biomass. In chapter 3, we showed that an estimate of average reproductive capability is given by the slope of a line drawn through the average survival point on a spawner-recruit graph. The idea in either approach is to measure reproductive capability from historical data and compare those measurements to predictions from yield-per-recruit analysis. The advantage of these predictions is that they can all be done on proportions, without the need to know absolute recruitment abundance. Divide recruitment into both sides of (6.49) and take reciprocals to get

$$\frac{N_c}{B(t_\infty)} = F \frac{N_c}{Y(t_\infty)}, \quad (6.50)$$

the recruits per unit biomass produced by a cohort during its fishable life span. Recruits per unit biomass is a benchmark to compare to historical estimates of survival of progeny from birth to age of recruitment. With the simple egg production model (6.47), $N_0(t_\infty)$ is proportional to cumulative biomass, $B(t_\infty)$. Thus, for that simple egg production model, recruits per unit biomass [the left-hand side of (6.50)] is proportional, at equilibrium, to survival of progeny from birth to age of recruitment $N_c/N_0(t_\infty)$; the proportionality constant is \tilde{e}^{-1} .

The right-hand side of (6.50) depends only on growth and mortality parameters. Hence, predicted recruits per biomass is also a function only of those parameters. There is no guarantee that the stock has such reproductive capability. Only by comparing an expression like (6.50) to empirical estimates can this be evaluated. The ICES (1984) report proposes guidelines to be used in such a comparison, based on estimates of recruits per unit spawning biomass. First construct a plot of recruitment estimates (y-axis) against their parents' spawning biomass, then rank the recruit per biomass data.

Draw three lines on the plot, each originating at the origin; the first line separates the top 10% of the ranked recruit-per-biomass values; the second line is at the 50th percentile rank; the third line is at the 90th percentile rank. The ICES (1984) report suggests that (1) the slope of the 10% line represents a level of recruits per unit biomass which represent a significant danger of stock collapse; (2) the slope of the 50% line represents a level where the stock can reproduce itself comfortably; and (3) the slope of the 90% line represents a level where there is very little danger of stock collapse. A number of problems can be found in such a simple approach, yet it does attempt to address repercussions of yield per recruit results on reproduction. We discuss this further in section 11.4.7 in the context of optimal harvesting.

The equations developed above can be applied verbatim to all the yield models previously developed provided we use the forms where fishing mortality and spawning occur continuously. Total biomass, $B(t)$, is a better index of egg production when we use the yield models that assume recruitment occurs in discrete groups, either due to variability in size (6.22) or due to age-specific selectivity (6.34). We still apply equation (6.50) to predict recruits per unit biomass, but the denominator now is weighted more toward older and larger fish (owing to the discrete recruitment assumption) and to some extent reflects typical maturity ogives. This approach works nicely on Pacific halibut, for example, where the age selectivity estimates, s_t , from Deriso and Quinn (1983) which can be used in (6.34) are similar to the fractions, m_t , of sexually mature females at each age (Quinn 1981).

The effects of harvesting on spawning and reproduction quantities may often depend on the similarity of the fishery's selectivity and the fish population's maturity as a function of age or length. At low levels of exploitation, a fishery that harvests young fish probably will have little effect on the population even when maturity occurs at much older ages ($t_c < t_s$). However, it might be suspected that fish populations with $t_c < t_s$ are generally more vulnerable to overexploitation than when $t_c > t_s$. We now illustrate this point using the sablefish data from example 6.1 with the caveat that the validity of this vulnerability hypothesis is sensitive to the population parameters selected.

Example 6.7. Sablefish in the Gulf of Alaska

We contrast the sablefish per-recruit results based on $t_c = 1$ and $t_s = 5$ to a hypothetical population with the same population parameters but with $t_c = 5$ and $t_s = 1$ (earlier maturity, later fishery). In figure 6.9, yield and spawning biomass per recruit for the two populations are shown. For each population, there is the typical trade-off between increased yield but decreased spawning biomass as exploitation increases. Yield per recruit for the population with later maturity and an earlier fishery peaks at a lower value and at a lower exploitation rate than the other population. As expected, spawning biomass per recruit is lower for the population with later maturity, and it decreases faster than for the other population. Thus, the population with later maturity and earlier harvesting can be said to be more vulnerable. ■

6.5. MODEL VARIATIONS

6.5.1. Discard Mortality

The advantages of imposing a minimum size limit are clearly diminished if the mortality induced by discarding fish under this size is high. (If all discarded fish die, then the minimum size limit is totally ineffective.) Under knife-edge selectivity, discard

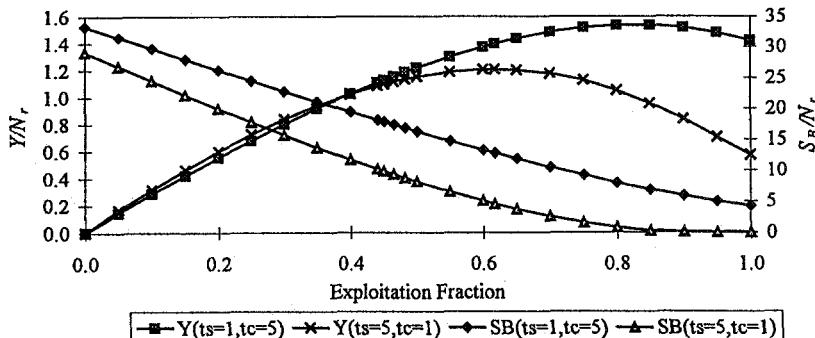


Figure 6.9. Yield per recruit, Y/R , and spawning biomass per recruit, S_B/N_r , for Gulf of Alaska sablefish in two hypothetical situations: $t_s = 1$, $t_c = 5$ (spawning before fishing) and $t_s = 5$, $t_c = 1$ (fishing before spawning). Other parameters are given in table 6.1.

mortality is readily incorporated into the yield-per-recruit model. The easiest way to do this is to replace natural mortality, M , between ages t_r and t_c with a total mortality parameter $M' = M + F'$ which includes discard mortality F' . The parameter F' can be varied between 0 and F to gauge the effects of discard mortality.

A more elegant approach is to separate the catch and mortality processes (Lowe et al. 1991). If F is instantaneous rate of catch, then $1 - \exp(-F)$ is the conditional annual catch rate in the absence of natural mortality. If H is the probability of dying after being caught, then the conditional annual survival and corresponding instantaneous fishing mortality rates are

$$S' = 1 - H(1 - e^{-F}) \quad \text{and} \quad F' = -\ln S'. \quad (6.51)$$

If discard death probability, H , is 0, then $S' = 1$ and $F' = 0$. If H is 1, then $S' = \exp(-F)$ and $F' = F$. Thus, equation (6.51) can be used to represent discard mortality between ages t_r and t_c and to represent fishing mortality for ages after t_c . Lowe et al. (1991) presented an example where the presence of discard mortality decreased yield per recruit as a function of an increasing size limit. In contrast, the absence of discard mortality increased yield per recruit. Thus, if discard mortality is present, it is important to include in yield-per-recruit analysis.

6.5.2. Trophy Fish and Slot Limits

Although the objective of yield maximization (biomass units) given either F or t_c is well-posed, the objective of catch maximization (abundance units) of interest in recreational fisheries is not. Given F , catch decreases as t_c increases because the number of fish decreases monotonically as a cohort ages. Given t_c , catch increases as F increases, with the asymptotic solution of applying infinite fishing mortality at the age of entry. One well-posed objective is to maximize catch of trophy fish, which are fish larger than a specified size or age.

Recall from (6.4) and (6.5) that catch for a given recruitment N_r (letting $t_\infty \rightarrow \infty$) is

$$C = \frac{F}{F + M} N_c = \frac{F}{F + M} N_r e^{-M(t_c - t_r)}. \quad (6.52)$$

If trophy fish are considered to be at ages greater than or equal to t_{tr} , then the catch of trophy fish is

$$C_{tr} = \frac{F}{F + M} N_{tr} = \frac{F}{F + M} N_r e^{-M(t_c - t_r) - (F+M)(t_{tr} - t_c)}. \quad (6.53)$$

Given t_c , trophy catch increases to a maximum and then decreases. By differentiating (6.53), Jensen (1987) showed that the maximum trophy catch occurs at fishing mortality

$$F = \frac{-M(t_{tr} - t_c) + \sqrt{M^2(t_{tr} - t_c)^2 + 4M(t_{tr} - t_c)}}{2(t_{tr} - t_c)}. \quad (6.54)$$

An alternative management approach is to introduce a slot limit, identified as $\{t_c, t_f, t_{tr}\}$. Retention of fish is illegal below age t_c , legal between t_c and t_f , illegal between t_f and t_{tr} , and legal above t_{tr} . Ignoring effects of handling mortality and assuming that fishing mortality is constant for legal ages, Jensen showed that nontrophy and trophy catches are

$$C_{nt} = \frac{F}{F + M} N_r e^{-M(t_c - t_r)} \left[1 - e^{-(F+M)(t_f - t_c)} \right] \quad (6.55)$$

$$C_{tr} = \frac{F}{F + M} N_r e^{-M(t_c - t_r) - (F+M)(t_f - t_c) - M(t_{tr} - t_f)}. \quad (6.56)$$

Given the slot-limit parameters, the maximum trophy catch occurs when

$$F = \frac{-M(t_f - t_c) + \sqrt{M^2(t_f - t_c)^2 + 4M(t_f - t_c)}}{2(t_f - t_c)}, \quad (6.57)$$

which holds for any $t_{tr} > t_f$. In the first management system, containing only a single age control parameter t_c , the maximization of trophy catch requires a great reduction in total catch. This effect is somewhat ameliorated in the second system with two age-control parameters, t_c and t_f , which can provide some catch at younger ages. Jensen suggested that unit values be determined for the two classes and that a reasonable objective for choosing control parameters would be to maximize total value.

6.5.3. Per-Recruit Models by Sex

For many species, growth, mortality, and maturity parameters differ by sex. Per-recruit models stratified by sex are easily constructed using the theory in previous sections. Let f be a subscript for females and m be a subscript for males. The number of females of age t at the start of the year is $N_{t,f}$, and the number of males is $N_{t,m}$. One simply starts with $N_{r,f}$ females and $N_{r,m}$ males at recruitment age t_r . Per-recruit calculations are done by sex and summed across sex if desired.

A more interesting situation is when fish can change sex, which occurs for a variety of reef fishes and shrimp species. Two examples of per-recruit models incorporating sex change are given by Punt et al. (1993) and Huntsman and Schaaf (1994). The main complication is that parameters need to be included for the proportion of the population changing sex.

Without loss of generality, we assume that fish start their life as females and change to males. If the opposite situation occurs, the subscripts are simply reversed. Let θ_t be the proportion of females that change to males. The values θ_t are assumed known and invariant under different fishing mortalities. It is presumed that all fish are females at the start of the age of first recruitment, r , so that the initial number of recruits is $N_{r,f}$, and the initial number of males $N_{r,m} = 0$. If θ_r is positive, sex change occurs just after reaching age r . The number of females and males at all other ages is calculated from recursion equations derived below.

We present one way to model the rate of sex change: the change occurs just after the start of the year. Models can also be constructed in which the change occurs at other times or continuously throughout the year. The latter situation is analogous to a two-area population model where individuals move from one area to the other and is developed in section 10.2.3.

Just after the start of the year, $\theta_t N_{t,f}$ females change to males, leaving $(1 - \theta_t)N_{t,f}$ females. After accounting for the mortality occurring throughout the year, the number of females at the start of the next year is

$$N_{t+1,f} = N_{t,f}(1 - \theta_t)e^{-Z_{t,f}}. \quad (6.58)$$

Just after the start of the year, an additional $\theta_t N_{t,f}$ males accrue due to the sex change of females. After accounting for the mortality occurring throughout the year, the number of males at the start of the next year is

$$N_{t+1,m} = (N_{t,m} + \theta_t N_{t,f})e^{-Z_{t,m}}. \quad (6.59)$$

The yield and reproductive equations are easily generalized for sex change by including a subscript x for sex. At this point, the proper objective function can be considered. One might wish to conduct the typical yield-per-recruit analysis, where yield, Y , would be maximized as a function of control variables F and s_t . This could be done either by combined sexes using $Y = Y_f + Y_m$ or individually by sex. Similarly, examining spawning abundance, spawning biomass, or eggs is desirable to maintain reproductive output on a per-recruit basis, as discussed in section 11.4.6.

Punt et al. (1993) extended this basic theory by allowing for cohort-specific growth. In their example, females change to males at a constant rate, and there is a growth spurt after sex change. Huntsman and Schaaf (1994) constructed simulation models that include various compensatory mechanisms to maintain reproductive capability. In both studies, there is suggestion that species with sex change are particularly vulnerable to fishing pressure because of the tendency to reduce the abundance of older age classes which will be primarily of one sex.

6.5.4. Per-Recruit Models for Multispecies and Multiple Fisheries

For many fisheries, a variety of different species is caught, each with their own growth, mortality, and maturity parameters. Per-recruit models for multispecies fisheries are easily constructed using the theory in previous sections. Let i be the subscript for species and the number of species i at age t be $N_{t,i}$. The major complication in this situation is that the number recruiting at age t_r is likely to differ by species. One starts with $N_{r,i} = N_r p_{r,i}$ fish of species i relative to a fixed number N_r , say 1000, of recruits

of all species, where $p_{r,i}$ is the relative abundance of species i . Per-recruit calculations are done by species and summed across species if desired. The proper objective in this case deserves attention. Maximizing total yield per recruit could lead to drastic reductions in abundance of some species with, for example, early selectivity to the gear and late maturity. On the other hand, keeping spawning biomass of each species above some reference level could require substantial reductions in catch and yield of dominant species. Applications of this approach are given by Murawski (1984), Pikitch (1987), and Gribble and Dredge (1994).

A different situation is where a single species is of interest, and multiple fisheries harvest this species. Let j be the subscript for a fishery, each with its own selectivity ($s_{t,j}$) and fishing mortality (F_j) parameters. The major complication in this situation is total fishing mortality, given by

$$F_t = \sum_j s_{t,j} F_j = \sum_j F_{t,j}, \quad (6.60)$$

which is a function of multiple control parameters for minimum size and fishing mortality. One starts with a fixed number N_r , say 1000, of recruits, and per-recruit calculations are done in the normal way. Catch and yield for fishery j are obtained by multiplying the total catch and yield for each age by the ratio of fishing mortality for the fishery to total fishing mortality and then summing over age, or

$$C_j = \sum_t \frac{F_{t,j}}{F_t} C_t \quad \text{and} \quad Y_j = \sum_t \frac{F_{t,j}}{F_t} Y_t. \quad (6.61)$$

An even more complicated model can be developed if average weight at age differs by fishery.

The objective usually considered in this case is maximizing total yield per recruit. The solution as a function of all control parameters usually selects one fishery that has selectivity properties close to the critical age, t^* . However, in many bioeconomic studies, the allocation by fishery is fixed, fishing mortality is fixed, the minimum size limit is fixed, and/or other objectives come into play. Per-recruit calculations are useful in these studies for examining the trade-offs in various policy alternatives.

Age-structured Models: Renewal Theory

In this chapter, the dynamics of an age-structured population partially developed in chapter 6 are completed by considering the regenerative process developed in chapter 3. The complete age-structured formulation has been studied by many authors. Pollard (1973) developed general theory with an elegant treatment of stochasticity and applied the methods to human populations. Keyfitz (1968) developed discrete and continuous theory, also with a view toward human demography. Getz and Haight (1989) described discrete age- and length-based models applicable to renewable resources and developed optimal harvesting results. Caswell (1989) considered a wide variety of age- and stage-structured models and provided extensive theory.

7.1. LESLIE MATRIX DISCRETE MODEL

Leslie (1945) showed how a linear discrete population model can be structured as a matrix equation, commonly referred to as the Leslie matrix population model. The matrix representation was derived independently by Bernardelli (1941) and Lewis (1942) as well. We follow the usual convention of considering only female individuals whose ages are not greater than some maximum age, A , chosen so as to include the bulk of reproduction. Females are represented in the model because it is their reproduction of female progeny that propagates the species. Implicit in this representation is the assumption that the number of males is not a constraint on fertility of females, which may not be true, in fact, for some species where only males are harvested, such as Alaskan red king crab. In this case, a more elaborate matrix model can be developed with both males and females (Caswell 1989, Zheng et al. 1995).

By assuming that population parameters remain constant over time, the Leslie matrix model can be written as

$$\mathbf{N}_{t+1} = \mathbf{M}\mathbf{N}_t \quad t = 0, 1, \dots, \quad (7.1)$$

where the population vector of female abundance \mathbf{N}_t in year t is multiplied by what is called the projection matrix, \mathbf{M} —of size A by A —to get the population vector of female abundance in year $t + 1$. The structure of (7.1) is given by

$$\begin{pmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ \vdots \\ N_{A,t+1} \end{pmatrix} = \begin{pmatrix} S_0 f_1 & S_0 f_2 & \dots & S_0 f_A \\ S_1 & 0 & \dots & 0 \\ 0 & S_2 & 0 \dots & 0 \\ \vdots & 0 & \vdots & \vdots \\ 0 & \dots & S_{A-1} & 0 \end{pmatrix} \begin{pmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ \vdots \\ N_{A,t} \end{pmatrix} \quad (7.2)$$

where

$N_{a,t}$ = number of females of age a at the beginning of year t

S_a = annual survival fraction for the a th age category

f_a = net fecundity of age a females.

As shown in section 4.8, net fecundity is the product of fraction of sexually mature females in an age category multiplied by the number of female fertile eggs produced by a mature female.

This Leslie matrix model is in a form that assumes spawning takes place at the beginning of a year, but other assumptions can be made. The top row of the matrix specifies the renewal part of the model; the subdiagonal S_a terms accommodate age-specific survival. Multiplication of the Leslie matrix by the abundance vector produces the following equations for the dynamics of abundance:

$$N_{1,t+1} = S_0 \sum_{a=1}^A f_a N_{a,t} \quad (7.3)$$

$$N_{a+1,t+1} = S_a N_{a,t} \quad \text{for } a \geq 1. \quad (7.4)$$

Keyfitz (1968) showed that (7.1) approximates linear population dynamics when birth rates are constant over time. He also provided an extensive analysis of the dynamics of (7.1).

Given initial abundance \mathbf{N}_0 , the solution of (7.1) is simply

$$\mathbf{N}_t = \mathbf{M}' \mathbf{N}_0. \quad (7.5)$$

This solution appears similar to the solution $N_t = R^t N_0$ to the simple difference equation $N_{t+1} = RN_t$ in section 1.1, and below we show that the similarity is not illusory.

Example 7.1. Hypothetical population

Consider the special case of a 3×3 Leslie matrix with the following element values: $f_1 = 0.0$, $f_2 = 1.0$, $f_3 = 2.0$, $S_0 = 0.576$, $S_1 = 0.8$, $S_2 = 0.8$. Table 7.1 shows the construction of the projection matrix from these parameters. Also shown are the calculations for the projection of the population for five years, starting with an initial population vector $\mathbf{N}'_0 = (100, 30, 50)$. A graph of abundance of each age over an expanded range of 30 years (figure 7.1) shows that after some initial irregularities, each age class grows exponentially, as does the total. ■

Analysis of population dynamics is accomplished through eigenanalysis of projection matrix \mathbf{M} . There are A eigenvalues, λ_i , and corresponding right (or column) eigenvectors \mathbf{k}_i (of size $A \times 1$) which obey the equation

Table 7.1. Construction of the Leslie matrix for example 7.1 and calculation of various population parameters, with $S_0 = 0.576$. Abundance is calculated using the projection equation (7.1). The empirical population change from $t = 29$ to $t = 30$ is shown, as well as the age distribution proportions and normalized age distribution. These quantities are compared with theoretical quantities corresponding to the stable age distribution. The necessary calculations are given, including that for the dominant eigenvalue found from the characteristic equation (7.10). Also shown are the calculations of mean generation length, T_0 , from (7.23) and abundance at time 30 using descriptive equation (7.26).

		Age, a									
		1	2	3							
f_a		0	1	2							
S_a		0.8	0.8	0.8							
\mathbf{M}		$\begin{pmatrix} 0 & 0.576 & 1.152 \\ 0.8 & 0 & 0 \\ 0 & 0.8 & 0 \end{pmatrix}$									
		Time, t									
a		0	1	2	3	4	5	...	29	30	
Abundance, $N_{a,t}$		1	100	75	74	108	89	104	557	597	
		2	30	80	60	59	87	71	416	446	
		3	50	24	64	48	47	69	310	333	
Total		Total	180	179	198	215	223	245	1283	1375	
		Population change			Age distribution			Normalized			
Empirical		1	1.071		0.434		1.000				
		2	1.072		0.324		0.747				
		3	1.072		0.242		0.557				
		Total	1.072		1.000						
a		f_a	S_a	\mathcal{L}_a	$f_a \mathcal{L}_a / \lambda_1^a$	k_{1a}	h_{1a}	$\sum_{j=a}^A f_j \mathcal{L}_j$	R_a	$a f_a k_{1a}$	$f_a k_{1a}$
Theoretical		0	0.576						1.198		
		1	0	0.800	1.000	0.000	1.000	1.000	2.080	2.080	0.000 0.000
		2	1	0.800	0.800	0.696	0.746	1.340	2.080	2.600	1.493 0.746
		3	2		0.640	1.040	0.557	1.075	1.280	2.000	3.343 1.114
Dominant Eigenvalue λ_1					1.072						
Right-hand side of characteristic equation					1.000						
						a	\mathbf{N}_{30}				
						1	597				
						2	446				
						3	333				
						Total	1375				

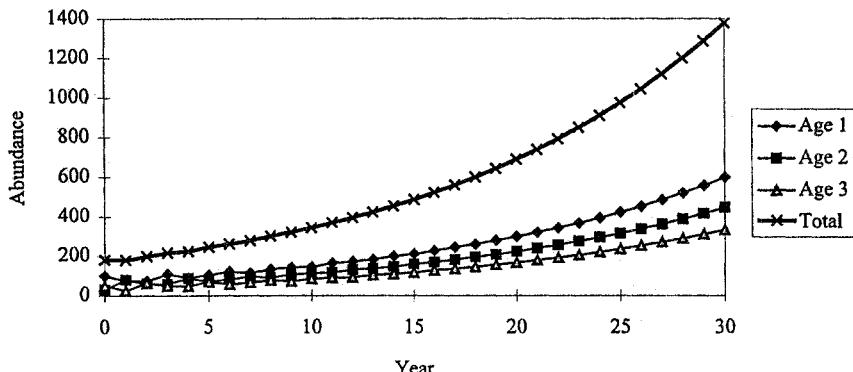


Figure 7.1. Abundance of each age and total abundance over time for the hypothetical population in example 7.1.

$$\mathbf{M}\mathbf{k} = \lambda\mathbf{k}, \quad (7.6)$$

Similarly, there are A corresponding left (or row) eigenvectors \mathbf{h}'_i (of size $1 \times A$) associated with the λ_i which obey the equation

$$\mathbf{h}'\mathbf{M} = \lambda\mathbf{h}'. \quad (7.7)$$

Eigenvalues can be found for the projection matrix by solving its characteristic equation for the A eigenvalues. The characteristic equation is obtained from (7.6) as follows:

$$\begin{aligned} \mathbf{M}\mathbf{k} - \lambda\mathbf{k} &= \mathbf{0} \\ (\mathbf{M} - \lambda\mathbf{I})\mathbf{k} &= \mathbf{0} \\ \Rightarrow |\mathbf{M} - \lambda\mathbf{I}| &= 0, \end{aligned} \quad (7.8)$$

where $|\mathbf{X}|$ is the determinant of any matrix \mathbf{X} . It can be shown that the characteristic equation can be written as the polynomial

$$\begin{aligned} \lambda^A - (S_0 f_1) \lambda^{A-1} - (S_0 S_1 f_2) \lambda^{A-2} - \dots - (S_0 S_1 \dots S_{A-1} f_A) &= 0 \\ \lambda^A - (S_0 f_1 \mathcal{L}_1) \lambda^{A-1} - (S_0 f_2 \mathcal{L}_2) \lambda^{A-2} - \dots - (S_0 f_A \mathcal{L}_A) &= 0, \end{aligned} \quad (7.9)$$

where \mathcal{L}_a = survival from age 1 to age a , that is $S_1 \dots S_{a-1}$. We use the convention that $\mathcal{L}_1 = 1$.

We can also write (7.9) as a polynomial in $1/\lambda$ as

$$1 = S_0 \sum_{a=1}^A f_a \mathcal{L}_a \lambda^{-a}, \quad (7.10)$$

which will be useful below. The positive root of (7.10) can be found quite easily numerically because it will have only one positive real root. Just evaluate the right-hand side of (7.10) for a grid of λ values from, say 0 to 3, and find the function evaluation closest to 1. Several simple upper and lower bounds can be computed for

the dominant root, which can be used to narrow the numerical search (Hearon 1976); Hearon showed that either $1 \leq \lambda_1 \leq R_0$ or $R_0 \leq \lambda_1 \leq 1$, where R_0 is the lifetime egg production of an age 0 female given by $R_0 = S_0 \sum_{a=1}^A f_a \mathcal{L}_a$ as described below.

We can write the eigenvector equations (7.6) and (7.7) in matrix form as

$$\mathbf{MK} = \mathbf{K}\Lambda \quad \text{and} \quad \mathbf{HM} = \mathbf{\Lambda H}, \quad (7.11)$$

where

Λ = diagonal matrix with eigenvalues λ_i , $i = 1, \dots, A$ down the diagonal

\mathbf{K} = matrix where the i th column is the right eigenvector \mathbf{k}_i

\mathbf{H} = matrix where the i th row is left eigenvector \mathbf{h}'_i .

By inverting appropriate matrices in (7.11), it follows that

$$\Lambda = \mathbf{HMH}^{-1} = \mathbf{K}^{-1}\mathbf{MK}.$$

This can be so only if $\mathbf{H} = \mathbf{K}^{-1}$; that is, the left eigenvector matrix is the inverse of the right eigenvector matrix. Hence, the projection matrix can now be written

$$\mathbf{M} = \mathbf{K}\Lambda\mathbf{H} = \mathbf{K}\Lambda\mathbf{K}^{-1}. \quad (7.12)$$

We now show that total abundance of the population over time depends only on the eigenvalues of \mathbf{M} found in Λ . By writing population abundance in year $t + q$ as

$$\mathbf{N}_{t+q} = \mathbf{M}^q \mathbf{N}_t, \quad (7.13)$$

it is clear that changes in the population depend on the projection matrix \mathbf{M} . The eigensystem representation of \mathbf{M} in (7.12) leads to

$$\mathbf{M}^q = \mathbf{K}\Lambda^q\mathbf{K}^{-1},$$

with the only time-dependent term being Λ^q .

The projection matrix \mathbf{M} has more nice algebraic properties.

1. \mathbf{M} has one and only one positive eigenvalue, say λ_1 , which is not exceeded by the modulus of any other eigenvalue of \mathbf{M} . Sykes (1969a) showed that λ_1 is dominant (greater than the other eigenvalues) when 1 is the greatest common divisor of the subscripts of the positive f_i values.
2. All remaining eigenvalues of \mathbf{M} are either negative or complex numbers.
3. The eigenvector \mathbf{k}_1 corresponding to λ_1 is proportional to the asymptotic ($q \rightarrow \infty$) age distribution, up to a multiplicative constant, if λ_1 is dominant.

The first property above assures that almost all Leslie matrix models for fish populations have a dominant eigenvalue. Possible exceptions to such models would include populations with a single fecund age or populations that exhibit skip-spawning (spawning at ages 2, 4, ...). The first property also comes from the Perron-Frobenius theorem (described in Caswell 1989), which applies to stage-structured populations as well.

We mainly restrict our attention to Leslie matrix models with a dominant eigenvalue. Long-term abundance will be determined solely by the value of λ_1 , which we later show is the *intrinsic growth fraction* for the population—the other eigenvalues affect only transient behavior. If $\lambda_1 > 1$, then abundance ultimately increases; if $\lambda_1 < 1$, then abundance ultimately decreases; if $\lambda_1 = 1$, then the population eventually becomes stationary.

Example 7.2. Hypothetical population

For the 3×3 Leslie matrix in example 7.1, consider three different values for early life survival, S_0 : 0.4, 0.481, and 0.576. Figure 7.2 shows projections of the total population for 20 years for these three values, starting with an initial population vector $\mathbf{N}'_0 = (100, 30, 50)$. After some initial irregularities, the population decreases exponentially, remains stable, or increases exponentially for each increasing value of S_0 . The dominant eigenvalues for the three values of S_0 are 0.932, 1.0, and 1.072, respectively. ■

Asymptotic ($q \rightarrow \infty$) abundance from (7.13) converges to

$$\mathbf{N}_{t+q} \rightarrow \lambda_1^q C \mathbf{k}_1. \quad (7.14)$$

C is a constant, which depends on both \mathbf{N}_t and \mathbf{M} . The constant C can be written in terms of the initial abundance vector and eigenvectors:

$$\begin{aligned} C &= \mathbf{h}_1^{*'} \mathbf{N}_t \\ &= \frac{\mathbf{h}_1' \mathbf{N}_t}{\mathbf{h}_1' \mathbf{k}_1} \end{aligned} \quad (7.15)$$

for arbitrarily scaled row eigenvectors, \mathbf{h}_1' . The first-row eigenvector $\mathbf{h}_1^{*'}$ is normalized by the h' and k vectors: $\mathbf{h}_1^{*'} = \mathbf{h}_1'/(\mathbf{h}_1' \mathbf{k}_1)$.

The ratio of any two successive ages of a year-class $N_{a+1,t+q+1}/N_{a,t+q}$ approaches λ_1 from (7.14), and thus the total population changes asymptotically according to λ_1 . This result is reminiscent of the difference equation $N_{t+1} = RN_t$ in section 1.1 for a simple population, where R is the intrinsic growth fraction. Hence the magnitude of $\ln \lambda_1$ is analogous to the instantaneous growth rate r in that section.

A *stable* population is defined as one which, for any given year, has a constant percentage of animals in each age category. A stable population can be increasing in

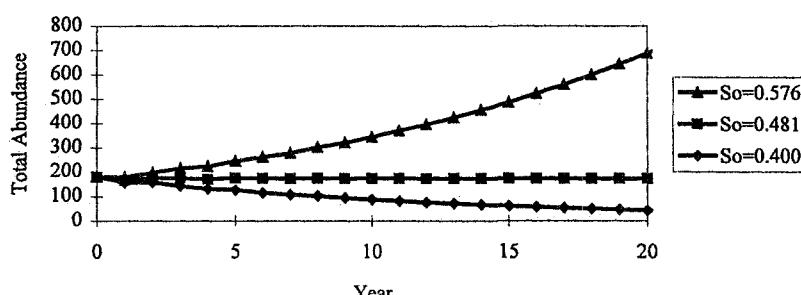


Figure 7.2. Total abundance over time for the hypothetical population in example 7.2 for three different values of early life survival, S_0 .

abundance, constant, or decreasing. Asymptotically, the percentage of fish in each age category (for a given year) is proportional to the components of \mathbf{k}_1 and are said to form a stable age distribution. When $\lambda_1 = 1$, abundance asymptotically trends to a constant (defined as *stationary*) abundance. Vector \mathbf{k}_1 has components (Caswell 1989)

$$k_{1a} = \mathcal{L}_a \lambda_1^{1-a} \quad a = 1, \dots, A, \quad (7.16)$$

where the vector is arbitrarily scaled so that $k_{11} = 1$ [since $\mathcal{L}_1 = 1$ in (7.16)].

The first-row eigenvector, \mathbf{h}_1 , has components

$$h_{1a} = \frac{S_0}{\lambda_1} \left(\sum_{j=a}^A f_j \frac{\mathcal{L}_j}{\mathcal{L}_a} \lambda_1^{a-j} \right) = \frac{S_0}{\lambda_1} \text{RV}_a, \quad (7.17)$$

where this vector is scaled so that $h_{11} = 1$. [Note that when $a = 1$, the summation term in (7.17) equals λ_1/S_0 using (7.10) and $\mathcal{L}_1 = 1$.] The components of h_{1a} are proportional (with proportionality S_0/λ_1) to the reproductive value RV_a , of an a -year-old, as shown later in this section. For the example of a population with 3 ages ($A = 3$), $h_{11} = 1$, $h_{12} = S_0 f_2 / \lambda_1 + S_0 f_3 S_2 / \lambda_1^2$ (since $\mathcal{L}_3 / \mathcal{L}_2 = S_2$), and $h_{13} = S_0 f_3 / \lambda_1$.

We can substitute the formula (7.16) for \mathbf{k}_1 into the right-hand-side of (7.10), evaluated at the real root, λ_1 , and rearrange terms to get a relationship between total annual egg production in a stable population, intrinsic growth fraction of the population, and survival of the young:

$$\frac{\lambda_1}{S_0} = \sum_{a=1}^A f_a k_{1a}. \quad (7.18)$$

Furthermore, when (7.10) is evaluated at this root, λ_1 , the right-hand side of (7.10) gives the total number of female offspring produced by a female over her entire life (defined as R_0 below), discounted by the intrinsic rate of natural increase, r , where $r = \ln(\lambda_1)$. This is a discrete version of Fisher's (1930) *reproductive value* of a newborn.

More generally, the reproductive value, RV_a , of an a -year-old female is defined for ages > 0 by

$$\text{RV}_a = \sum_{j=a}^A \frac{f_j \mathcal{L}_j}{\mathcal{L}_a} \lambda_1^{a-j}. \quad (7.19)$$

Comparing (7.17) and (7.19) shows that each element of the dominant row eigenvector, h_{1a} , is proportional to reproductive value; that is, $h_{1a} = (S_0/\lambda_1)\text{RV}_a$. Reproductive value curves (versus age) typically increase with age up to some intermediate age and then decrease for older ages (see e.g., Pianka 1974). As Fisher (1930) describes it (for a continuous model), reproductive value of an animal aged a is its contribution "to the ancestry of future generations." We add that this description is made for a population model with density-independent vital statistics.

Further insight into reproductive value can be obtained by examining life-time egg production of an individual of age a , which is defined as

$$R_a = \sum_{j=a}^A \frac{f_j \mathcal{L}_j}{\mathcal{L}_a}, \quad \text{for } a > 0, \quad (7.20)$$

$$R_0 = S_0 \sum_{j=1}^A f_j \mathcal{L}_j, \quad (7.21)$$

and is a useful notation for equilibrium analysis. If a population is at equilibrium ($\lambda_1 = 1$), then the lifetime egg production of a newborn individual (age 0; $R_0 = 1$, so that each individual reproduces just enough to replace itself. At equilibrium the element h_{1a} in (7.17) (which is now equal to $S_0 \text{RV}_a$) is also equal to $S_0 R_a$; that is, reproductive value and lifetime egg production are equivalent at equilibrium.

The characteristic equation (7.10) can be used to solve for survival of the young when λ_1 is fixed at a given value. Vaughn and Saila (1976) solved (7.10) for S_0 to get

$$S_0 = \left(\sum_{a=1}^A f_a \mathcal{L}_a \lambda^{-a} \right)^{-1}. \quad (7.22)$$

for a population with a given intrinsic growth fraction. Vaughan (1977) showed that (7.22) gives biased estimates when the Leslie matrix is stochastic, as we discuss further in the section 7.3.

The mean age of reproduction in a stable population, T_0 , is defined as

$$T_0 = \frac{\sum_{a=1}^A a f_a k_{1a}}{\sum_{a=1}^A f_a k_{1a}}. \quad (7.23)$$

By using (7.10) and (7.16), this equation simplifies to

$$T_0 = \sum_{a=1}^A a f_a S_0 \mathcal{L}_a \lambda_1^{-a}. \quad (7.24)$$

Parameter T_0 is commonly referred to in contemporary literature as the *mean generation length*. Other definitions of generation length have been employed in demography, especially in the older literature, but their usefulness is limited to stationary ($\lambda_1 = 1$) populations (Leslie 1966, Caughey 1967). We will find T_0 useful for stochastic matrices in section 7.3.

Another useful formula for mean generation length is

$$T_0 = \mathbf{h}'_1 \mathbf{k}_1. \quad (7.25)$$

This equation can be derived by substituting (7.16) and (7.17) into the right-hand side of (7.25) and simplifying to obtain (7.24). The result (7.25) is useful for determining the constant C in the asymptotic abundance formula (7.14), which can be written

$$\mathbf{N}_{t+q} \rightarrow (\lambda_1^q \mathbf{k}_1) \left(\frac{\mathbf{h}'_1 \mathbf{N}_t}{T_0} \right). \quad (7.26)$$

Thus, abundance at any future time, $t + q$, is dependent on reference abundance, \mathbf{N}_t , the dominant eigenvalue, λ_1 , and its eigenvectors \mathbf{k}_1 and \mathbf{h}_1 , and mean generation length, T_0 [which is a function of \mathbf{k}_1 and \mathbf{h}_1 in (7.25)].

Caswell (1989) gave an alternative asymptotic abundance formula that shows the importance of the other eigenvalues and eigenvectors:

$$\mathbf{N}_{t+q} = \tilde{c}_1 \lambda_1^q \mathbf{k}_1 + \tilde{c}_2 \lambda_2^q \mathbf{k}_2 + \cdots + \tilde{c}_A \lambda_A^q \mathbf{k}_A, \quad (7.27)$$

where the constants $\{\tilde{c}_i\}$ are functions of N_t . If the j th eigenvalue is written $a + bi$ (a complex number), then it can be decomposed as

$$\lambda_j = |\lambda_j|(\cos \theta + i \sin \theta), \quad \text{where } |\lambda_j| = \sqrt{a^2 + b^2} \text{ and } \theta = \tan^{-1}(b/a).$$

Essentially, the eigenvalues control the amount of oscillatory behavior in the approach to stability of the age distribution. The first eigenvalue λ_1 has the largest amount of influence, being the largest in magnitude (in most cases), and influences the population trajectory monotonically because $b = 0$ and $\theta = 0$.

A technique for estimating adult survival from estimates of T_0 and λ_1 is given in York (1987), which is a variation of the method in Chapman and Robson (1960). In these methods adult annual survival fractions are all assumed to be independent of age (i.e., $S_a = S$). Further aspects of age-structured models related to management strategies are discussed in chapter 11.

Example 7.3. Hypothetical population

Consider the special case of a 3×3 Leslie matrix with the following element values: $f_1 = 0.0$, $f_2 = 1.0$, $f_3 = 2.0$, $S_1 = 0.8$, $S_2 = 0.8$. The population is known to have doubled in abundance in the last 10 years but has had a stable age distribution.

1. First we calculate S_0 for this stable population. The abundance increase implies $\lambda_1^{10} = 2.0$ and, therefore, $\lambda_1 = 1.0718$. Substitute this lambda value into (7.22) to get $S_0 = 0.576$. (This is where S_0 in examples 7.1 and 7.2 came from.)
2. Next we find the eigenvalues of the Leslie matrix: the characteristic equation is

$$\lambda^3 - (0.576)(0.8)\lambda - (0.576)(2.0)(0.8)(0.8) = 0$$

in which we factor out $(\lambda - \lambda_1)$, where $\lambda_1 = 1.0718$ to get the quadratic $\lambda^2 + 1.0718\lambda + 0.6879 = 0$, which has roots $\lambda_2, \lambda_3 = -0.536 \pm 0.633i$. The imaginary components indicate oscillatory convergence to the stable population vector.

3. The stable population vector, \mathbf{k}'_1 , for this example is $(1.0, 0.746, 0.557)$. The reproductive value vector, \mathbf{h}'_1 , is $(1.0, 1.340, 1.075)$.
4. Various population parameters are shown in table 7.1. The population at year 30 is close to the stable age distribution, and its rate of increase is close to the dominant eigenvalue λ_1 by age and by total. Note that the reproductive value vector, \mathbf{h} , is not strictly proportional to lifetime egg production, \mathbf{R} , because the population is not stationary. The mean generation length, T_0 , is 2.6. Population abundance at year 30 calculated from (7.26) is identical to that obtained by projection. ■

Example 7.4. Bernardelli matrix

The Bernardelli matrix (Bernardelli 1941) is

$$\mathbf{M} = \begin{pmatrix} 0 & 0 & 6 \\ \frac{1}{2} & 0 & 0 \\ 0 & \frac{1}{3} & 0 \end{pmatrix}.$$

Its eigenvalues from the characteristic equation $\lambda^3 - 1 = 0$ are $\lambda_1 = 1$ and $\lambda_2, \lambda_3 = -\frac{1}{2} \pm \frac{\sqrt{3}}{2}i$ (which are the roots of $\lambda^2 + \lambda + 1 = 0$). The moduli of the eigenvalues

are all equal to 1; hence the condition of the Perron-Frobenius theorem for stability does not hold here [the greatest common divisor of the columns with positive first-row elements (only column 3) is 3, not 1]. The stable population vector for this example is $(1, \frac{1}{2}, \frac{1}{6})$, and a starting population following these fractions [e.g. (60,30,10)] is stationary. For any other initial condition, the population cycles over three years. For example, starting with a population of (30,30,40), the population becomes (240,15,10), then (60,120,5), and then returns to (30,30,40). The column eigenvector \mathbf{k}'_1 for this example is $(1, \frac{1}{2}, \frac{1}{6})$. The reproductive value vector \mathbf{h}'_1 is $(1, 2, 6)$, which corresponds to lifetime egg production, R_a , in this case because $\lambda_1 = 1$. The mean generation length T_0 is 3. ■

Example 7.5. Hypothetical oil spill

Here we consider application to calculating effects of a one-time loss of fish from a hypothetical oil spill. We consider two scenarios.

Suppose that a stable population has a one-time loss of a fraction p of young-of-the-year. We find the fractional reduction in stable population abundance. We can assume, without loss of generality, that the stable population has abundance $\mathbf{N}_0 = \mathbf{k}_1$ prior to being oiled because \mathbf{k}_1 defines the distribution of abundance in a stable population. Initially the oiled population $\tilde{\mathbf{N}}_0$ has the same abundance vector as \mathbf{k}_1 , except that now $(1 - p)$ is the first component; that is, $\tilde{N}_{0,1} = 1 - p$ and $\tilde{N}_{0,a} = k_{1a}$ for the older ages. The fractional reduction in abundance is given solely by the shift in the constant C between an unoiled population [here, $C = 1$ from (7.15)] and an oiled one. Asymptotically, the fractional reduction is

$$\begin{aligned}\frac{\tilde{N}_{a,t}}{N_{a,t}} &= \frac{\mathbf{h}'_1 \tilde{\mathbf{N}}_0}{T_0} \text{ from (7.26)} \\ &= \frac{\mathbf{h}'_1 \mathbf{k}_1 - p}{T_0} \\ &= 1 - \frac{p}{T_0} \text{ from (7.25)}\end{aligned}$$

for each age category a . Thus, the fractional reduction is inversely dependent on the mean generation length of the population.

For our second scenario, suppose there is a one-time loss of a fraction p_2 of all individuals older than the young-of-the-year and a one-time loss of a fraction p of the young-of-the-year. Here the asymptotic fractional reduction is

$$\begin{aligned}\frac{\tilde{N}_{a,t}}{N_{a,t}} &= \frac{\mathbf{h}'_1 \tilde{\mathbf{N}}_0}{T_0} \\ &= \frac{\mathbf{h}'_1 \mathbf{k}_1 - p - (\mathbf{h}'_1 \mathbf{k}_1 - 1)p_2}{T_0} \\ &= 1 - p_2 + \frac{p_2 - p}{T_0}\end{aligned}$$

for each age category a . ■

7.2. TIME-VARYING LINEAR MATRIX MODELS

For applications of fish populations, the projection matrix \mathbf{M} may be a function of time, or \mathbf{M}_t . The projection equation in this case is written

$$\mathbf{N}_{t+1} = \mathbf{M}_t \mathbf{N}_t \quad t = 0, 1, \dots, \quad (7.28)$$

and its solution is

$$\mathbf{N}_{t+q} = \mathbf{M}_{t+q-1} \mathbf{M}_{t+q-2} \cdots \mathbf{M}_{t+1} \mathbf{M}_t \mathbf{N}_t. \quad (7.29)$$

The stability properties of the projection matrix also change over time, avoiding the simplistic behavior of the constant-parameter matrix model.

An example of the empirical approach to the Leslie matrix for Pacific halibut may be found in the essay by Quinn (1981). Examination of data over time led to a Leslie matrix model where fecundity, early-stage survival fraction, S_0 , fishing mortality, and sex ratio were all functions of time. The Leslie matrix model provided a convenient summarization of the population's essential parameters and was used to project population trends based on observed trends in parameters. Deriso (1985), examining more recent data, showed a remarkable change in early-stage survival. The Leslie matrix approach was also used to show that observed sex ratio differences in surveys could be explained by differential mortality among the sexes (Deriso and Quinn 1983).

Example 7.6. Sinusoidal variation in S_0

Consider example 7.1 with sinusoidal variation in S_0 with a period of 10 years and a half-amplitude of 25% of $S_0 = 0.576$ [$S_{0,t} = 0.576 + 0.144 \sin(2\pi/10)t$]. Figure 7.3 shows the projection of the population and its age structure over three cycles. As expected, the oscillatory behavior in S_0 induces similar behavior throughout the age spectrum. That cyclical behavior can occur with both constant and time-varying matrices implies that confounding of underlying biological and physical processes can occur. ■

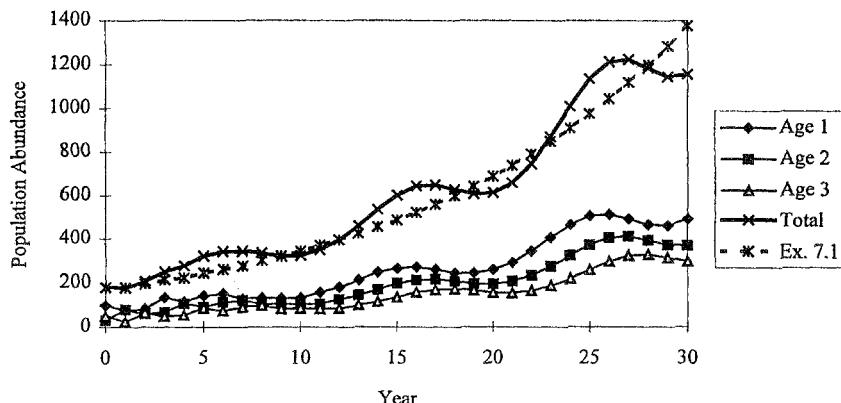


Figure 7.3. Abundance of each age and total abundance over time for the hypothetical population in example 7.6 with sinusoidal variation in early life survival, S_0 . The sinusoidal function has a half-amplitude of 0.144 (25% of the mean 0.576), a period of 10 years, and no phase shift. Total abundance with no sinusoidal variation from example 7.1 is shown for comparison.

7.3. STOCHASTIC LINEAR MATRIX MODELS

The models described thus far are all limited by their deterministic character, although time-dependent models do allow for changes over time. The easiest way to incorporate stochasticity into these models is by allowing for additive and independent variation in each year, t . We let δ_t represent such variation and assume its expected value is 0 and its variance–covariance matrix is \mathbf{V}_t . In analogy to (7.1), the population projection equation becomes

$$\mathbf{N}_{t+1} = \mathbf{M}\mathbf{N}_t + \delta_{t+1}. \quad (7.30)$$

The expected population size is the same as its deterministic counterpart because

$$E(\mathbf{N}_{t+1}) = \mathbf{M}E(\mathbf{N}_t).$$

Its variance–covariance matrix can be determined recursively as

$$\Sigma_{t+1} = \mathbf{M}\Sigma_t\mathbf{M}' + \mathbf{V}_{t+1}.$$

This model is analyzed extensively in Pollard (1973).

Alternatively, models with stochastic variation in population parameters can be constructed. Survival, growth, and reproduction dynamics all could contain random elements. However, it is the survival of the young in fish populations where stochasticity is most apparent. As was demonstrated in chapter 3, spawner-recruit graphs typically show a lot of scatter.

Tuljapurkar (1982) derived an elegant approximation for the median long-term growth rate of a population, specifically the logarithmic growth rate, for the special case where survival of the young, S_0 , is a random variable with no serial autocorrelation. The logarithmic growth rate, r' , is given by

$$\begin{aligned} r' &= \lim_{q \rightarrow \infty} \frac{1}{q} E[\ln(N_{t+q}/N_t)] \\ &\approx r - \frac{CV^2}{2T_0^2}, \end{aligned} \quad (7.31)$$

where N_t is total population abundance at time t , CV is the coefficient of variation in S_0 , and the other symbols are given in the previous section, as calculated with the average S_0 value in all formulae. The above approximation works nicely for small CV values—say, less than 0.3—we do not know how well the approximation works for larger values of CV .

The median growth rate, r' , is less than the average growth rate, r , because, for large t , N_{t+q}/N_t will be approximately lognormally distributed, which is a skewed distribution whose median is less than its mean. Cohen et al. (1983) discussed the different measures of population growth rate. Equation (7.31) is, by definition, the average of the growth rate of population size, whereas Cohen et al. (1983) showed that the growth rate of the average population size is given by r , the dominant eigenvalue of the average Leslie matrix:

$$r = \lim_{q \rightarrow \infty} \frac{1}{q} \ln[E(N_{t+q}/N_t)]. \quad (7.32)$$

Equation (7.31) shows that a stochastic Leslie matrix has a lower r' than the intrinsic rate of growth, $r = \ln \lambda_1$, calculated for deterministic models. One consequence of a lower growth rate in the stochastic model is that average survival of the young will need to be higher in order for median abundance to be at a stochastic equilibrium. By analogy with (7.22), average survival of the young is given by the equation

$$S_0 = \left(\sum_{a=1}^A f_a \mathcal{L}_a e^{-r' a} \right)^{-1} \quad (7.33)$$

for a population with median growth rate r' . Goodyear and Christensen (1984) demonstrated a numerical procedure for calibrating estimates of S_0 so as to ensure stochastic equilibrium.

Example 7.7. Hudson River striped bass

Estimates of average cumulative survival from age 0 to age 4, $S_0 \mathcal{L}_4$, and the effect of changes in $S_0 \mathcal{L}_4$ on r' for Hudson River striped bass are examined in table 7.2. Net fecundity is calculated as the fraction of females that are sexually mature times the number of viable eggs per mature female times 0.5 (assumes 50% sex ratio; data from Texas Instruments 1981). Annual survival is $S_a = 0.681$ for all ages $a \geq 4$, as given for female striped bass in Fletcher and Deriso (1979). The CV is set to 0.3 for this example, although that number is probably too low in reality. The growth rates r' and r do not differ much, which is due primarily to the large mean generation length for this long-lived species of fish. Survival fractions $S_0 \mathcal{L}_4$ listed in the table represent incremental changes of 20% around the equilibrium survival value along with survival fractions corresponding to $r' = 0$ and $r = 0$. ■

When several elements of the Leslie matrix contain stochastic components, the lognormal approximation to N_{t+q}/N_t can still be used, according to results given in Tuljapurkar and Orzack (1980). Alternatively, Gerrodette et al. (1985) investigated the following class of stochastic Leslie matrix models:

$$\mathbf{N}_{t+1} = (\mathbf{M} + \Delta_t) \mathbf{N}_t \quad t = 0, 1, \dots \quad (7.34)$$

where Δ_t is a matrix of random deviations with a specified covariance structure, which is assumed to be uncorrelated in time. By employing a lognormal approximation for population growth, Gerrodette et al. showed a series of equations for calculating the mean and variance of logarithmic growth rate. The equations are long and complicated, and we do not see any advantage to applying them rather than simply determining population statistics by Monte Carlo simulation. Gerrodette et al. (1985) showed, in fact, that for small to moderate time periods, q , the lognormal approximation is not accurate (compared to results they obtained with Monte Carlo simulation).

Assumptions for a Monte Carlo simulation of the stochastic population model are (1) initial population vector \mathbf{N}_t , (2) fecundity and survival elements of the matrix \mathbf{M} , and (3) probability distributions for the elements of Δ_t . Given these assumed quantities, the stochastic model is simulated forward in time. At each time period, a new set of stochastic elements is selected at random from respective probability distributions. After q time periods, results of the simulation are tabulated, which concludes the first trial of the Monte Carlo experiment. The simulation process is started anew at the

Table 7.2. Six selected estimates of average cumulative survival from age 0 to age 4, $S_0\mathcal{L}_4$, and the effect of changes in $S_0\mathcal{L}_4$ on the median growth rate, r' , for Hudson River striped bass. (Modified from ABM 1983)

Input parameters			Results			
Age	Net fecundity (10^{-4} eggs)	Case	Avg. survival, $S_0\mathcal{L}_4(10^6)$	Med. growth, $r'(10^3)$	Avg. growth, $r(10^3)$	Mean generation length, T_0
4	0.56	1	1.26	0.0	1.05	9.26
5	5.56	2	1.25	-1.04	0.0	9.27
6	20.58	3	1.01	-23.8	-22.8	9.48
7	37.35	4	0.76	-53.6	-52.7	9.77
8	54.20	5	1.52	19.8	20.9	9.09
9	72.55	6	1.77	36.8	38.0	8.95
10	83.81					
11	101.10					
12	115.05					
13	114.25					
14	117.10					
15	129.55					
16–17	129.55					
18+	150.95					

same initial population vector. The number of trials required to produce reliable results depends on the quantity of interest. Rare events, like 99% confidence intervals, can require 5000 or more trials, whereas reliable estimates of the mean take much fewer trials, perhaps 200 or less. Results from such a simulation study are presented below.

Example 7.8. Stochastic Leslie matrix

Results from Monte Carlo simulation of a stochastic Leslie matrix model are shown in table 7.3; 5000 trials of the model were made with the parameters given in the table. Elements of the Δ_t matrix are all assumed to be normal random variables. "Factor of increase" in the table refers to the realized rate of increase, $(N_{t+q}/N_t)^{1/q}$. The probability P is the probability that the final population size will be greater than the initial population size. Note how confidence intervals for total abundance increase as elapsed time in the simulation is increased from $q = 1$ to $q = 6$, whereas confidence intervals around the mean rate of population increase are smaller as q increases. ■

The addition of a stochastic matrix Δ_t to \mathbf{M} is but one of many possible ways to include stochasticity in a Leslie matrix. Even in more general situations, where \mathbf{M}_t denotes a stochastic transition matrix of arbitrary complexity, we can still easily find the time trajectory of expected population abundance, as long as elements of the matrix are uncorrelated in time. In this case, the matrix operation on \mathbf{N}_t is linear, and thus expected abundance depends on the expected value of the transition matrix:

$$E(\mathbf{N}_{t+1}) = E(\mathbf{M}_t)E(\mathbf{N}_t) \quad t = 0, 1, \dots$$

where $E(\cdot)$ denotes expected value of each element in parentheses. We reiterate here that the probability distribution for abundance is likely to be skewed so that mean abundance is not a good measure of central tendency of the population. Variance equations are nonrecursive and become very lengthy after a few iterations [see Sykes (1969b) for some variance equations].

Table 7.3. Results from Monte Carlo simulation of a stochastic Leslie matrix model with 5000 replications (after Gerrodette et al. 1985).

Age, a	Initial population size	Mean	Mean	Covariance matrix					
		$S_0 f_a$ value	S_a value	$S_0 f_1$	$S_0 f_2$	$S_0 f_3$	S_1	S_2	
1	100	0.1	0.7	$S_0 f_1$	0.0010	0.0020	0.0020	0.0005	0.0005
2	80	1.0	0.9	$S_0 f_2$		0.0050	0.0045	0.0010	0.0010
3	50	0.4	0.0	$S_0 f_3$			0.0050	0.0010	0.0010
				S_1				0.0050	0.0045
				S_2					0.0050
Results									
Elapsed time	Expected population size			Total population		Factor of increase			
	Age 1	Age 2	Age 3	Mean	95% CI	Mean	Lower 95% CI	Upper 95% CI	P
$q=1$	110	70	72	252	(215, 289)	1.096	0.934	1.258	.8764
$q=6$	121	83	73	277	(182, 400)	1.029	0.961	1.096	.7990

Formulae for abundance of a single cohort are much simpler. When stochastic survival is uncorrelated in time, expected abundance of a cohort of age a can be written as

$$E(N_a|N_1) = \prod_{i=1}^{a-1} E(S_i) N_1.$$

We have dropped the year subscripts here because we are dealing with a single cohort.

In many fisheries models, mortality rate is assumed to be a random variable (e.g., in the stochastic catch model in chapter 1 and in the stochastic Ricker model in chapter 3). Approximate normality of the probability distribution of annual mortality rate can be reasoned. When the stochastic elements, which make up annual mortality, are a large sum of independent and identically distributed random variables (such as sum of daily mortality rates), then a corollary of the Central Limit Theorem in statistics is that their sum (the annual mortality rate) is approximately normally distributed.

Let us assume annual mortality rate is a normally distributed random variable whose mean and variance can change both with age and year. Annual survival is then lognormally distributed, and so it is better to work with the logarithm of abundance because $\ln(N_a)$ is normally distributed with mean and variance, respectively,

$$\begin{aligned} E[\ln(N_a)|N_1] &= \sum_{i=1}^{a-1} E[\ln(S_i)] + \ln(N_1), \\ V[\ln(N_a)|N_1] &= \sum_{i=1}^{a-1} V[\ln(S_i)]. \end{aligned} \quad (7.35)$$

This normal distribution is the unconditional distribution of cohort abundance $\ln(N_a)$, given initial abundance N_1 ; that is, it does not depend on N_2, \dots, N_{a-1} . The joint distribution of log-abundance of the cohort at all ages ($\ln N_2, \dots, \ln N_a | N_1$) is a multivariate normal with means and variances, as given above, and with covariances

$$\text{cov}[\ln(N_j), \ln(N_k)] = \sum_{i=1}^{\min(j,k)-1} V[\ln(S_i)].$$

We can construct a stochastic treatment of survival of a cohort using Markov chains (cf. Chiang 1968, Gani 1973). Let us assume that the probability any given individual of age a survives to become age $a+1$ is S_a ; that is, we treat the annual survival fraction as an annual probability of survival. Also assume statistical independence of the fate of individuals in a cohort. Starting with N_a individuals of age a , the probability of the number N_{a+1} of survivors is given by a binomial distribution

$$P(N_{a+1}|N_a) = \binom{N_a}{N_{a+1}} S_a^{N_{a+1}} (1 - S_a)^{N_a - N_{a+1}}. \quad (7.36)$$

Therefore, given only initial abundance N_1 , the mean and variance of abundance of the cohort at age a are, respectively,

$$E(N_a|N_1) = N_1 \mathcal{L}_a \quad (7.37)$$

$$V(N_a|N_1) = N_1 \mathcal{L}_a (1 - \mathcal{L}_a). \quad (7.38)$$

The joint distribution of abundance of the cohort at all ages ($N_2, \dots, N_A | N_1$) is simply a chain of the binomials in (7.36).

A better understanding of the joint distribution of abundance is provided by deriving the joint distribution of deaths, which occur throughout the life span of a cohort. Let $d_a = N_a - N_{a+1}$ be a random variable representing the number of deaths that occur for the cohort between ages a and $a + 1$; for the last age category, let $d_A = N_A$. The probability an individual, who is alive in the initial cohort, dies in the a th category equals $\mathcal{L}_a(1 - S_a)$. Because the vector (d_1, \dots, d_A) equals the initial cohort abundance N_1 , we see that their joint distribution is a multinomial:

$$P(d_1, \dots, d_A | N_1) = \frac{N_1!}{d_1! \cdots d_A!} \prod_{a=1}^A [\mathcal{L}_a(1 - S_a)]^{d_a}. \quad (7.39)$$

Abundance of the cohort at age a can be written as

$$N_a = N_1 - \sum_{i=1}^{a-1} d_i,$$

and thus abundance depends on a sum of multinomial random variables. Means, covariances, and variances of the N_a can be found with standard formulas for a sum of random variables; in particular, the mean and variance of N_a are given by (7.37) and (7.38). The mean, variance, and covariance of the d_a random variables are as follows:

$$\begin{aligned} E(d_a) &= N_1 \mathcal{L}_a(1 - S_a), \\ V(d_a) &= N_1 \mathcal{L}_a(1 - S_a)[1 - \mathcal{L}_a(1 - S_a)], \\ \text{cov}(d_i, d_j) &= -N_1 \mathcal{L}_i(1 - S_i) \mathcal{L}_j(1 - S_j) \quad \text{for } i \neq j. \end{aligned}$$

The stochastic model (7.39) forms the basis for Dupont's (1983) method of catch-age analysis, discussed in chapters 1 and 8.

7.4. NONLINEAR DISCRETE LESLIE-TYPE MODELS

Several studies have been made of a generalized Leslie matrix model, which includes density-dependent survival of the young (Allen and Basasibwaki 1974, DeAngelis et al. 1980, Reed 1980, Bergh and Getz 1988). We will modify the Leslie matrix to include a suitable spawner-progeny function. It is convenient to introduce a notation for total egg production at the beginning of a year. Let

$$\mathcal{E}_t = \sum_{a=1}^A f_a N_{a,t}$$

be total egg production for year t . Abundance of one-year-olds is assumed to be a (nonlinear) function of egg production:

$$N_{1,t+1} = \mathcal{F}(\mathcal{E}_t), \quad (7.40)$$

in which the function \mathcal{F} could be any of the spawner-progeny functions discussed in chapter 3. Survival of the young is now a function of egg production,

$$S_0(\mathcal{E}_t) = \mathcal{F}(\mathcal{E}_t)/\mathcal{E}_t. \quad (7.41)$$

In (7.40), it is assumed that first-year survival depends only on the number of individuals of that age and not on the density of older age groups. Even if density dependence occurs after age one, we can still use the function in (7.40), with some modification, as long as the density dependence occurs before the earliest age of sexual maturity. Set $S_a = 1$ for all sexually immature ages above age zero and then modify (7.40) to be the spawner-progeny function that quantifies abundance at the age of first sexual maturity; with this modification to the Leslie matrix, the $N_{a,t}$ for the immature age categories represents a type of transfer function to lag recruitment by the appropriate number of years.

For simple spawner-progeny functions, a unique positive vector of equilibrium abundances exist, which we denote N_a^* for $a = 1, \dots, A$. As shown by Reed (1980), equilibrium conditions imply the following relationships:

$$N_a^* = N_1^* \mathcal{L}_a \quad \text{for } a > 1, \quad (7.42)$$

$$\mathcal{E}^* = N_1^* \sum_{a=1}^A f_a \mathcal{L}_a, \quad (7.43)$$

$$N_1^* = \mathcal{F}(\mathcal{E}^*). \quad (7.44)$$

The summation term $\sum_{a=1}^A f_a \mathcal{L}_a$ equals R_1 , the lifetime reproduction of a one year old, as defined earlier in this chapter. Therefore, we can write (7.43) as

$$\mathcal{E}^* = R_1 N_1^*,$$

which states that, at equilibrium, the total egg production of the population equals the lifetime egg production of an individual one-year-old times the equilibrium abundance of one-year-olds. Equilibrium abundance of the one-year-olds can be calculated by combining (7.43) and (7.44) to get

$$\begin{aligned} N_1^* &= \mathcal{F}(R_1 N_1^*), \\ &= (R_1 N_1^*) S_0(R_1 N_1^*). \end{aligned} \quad (7.45)$$

Solve for N_1^* in (7.45) to get

$$N_1^* = \frac{1}{R_1} S_0^{-1} \left(\frac{1}{R_1} \right) \quad (7.46)$$

for the positive equilibrium solution. The inverse function is merely equilibrium egg production, or $\mathcal{E}^* = S_0^{-1}(1/R_1)$.

Example 7.9. Ricker spawner-recruit model

For the Ricker spawner-recruit model, we have

$$S_0(x) = e^{a - \beta x},$$

where $\alpha = \exp(a)$, and hence, the inverse function of $y = \exp(a - \beta x)$ is

$$\begin{aligned}x &= S_0^{-1}(y), \\&= \frac{a - \ln(y)}{\beta}.\end{aligned}$$

Therefore, equilibrium abundance of one year olds from (7.46) is given in this case by

$$N_1^* = \frac{a + \ln(R_1)}{\beta R_1},$$

and, thus, total equilibrium egg production is given by

$$\mathcal{E}^* = \frac{a + \ln(R_1)}{\beta}.$$

■

In table 7.4, we list equilibrium abundance equations for several different spawner-progeny functions. These are obtained analogously to the Ricker example above.

Equilibrium total yield is the product of yield per recruit times the equilibrium number of recruits. From (6.33), we can write yield per recruit as

$$Y^*/N_1^* = \sum_{a=1}^A \mu_a W_a \mathcal{L}_a \quad (7.47)$$

where μ_a = annual exploitation fraction for age a individuals, and W_a = average weight for an age a individual.

In (7.46) equilibrium abundance of one year olds is given (see also table 7.3). By multiplying abundance in (7.46) and yield per recruit in (7.47), we get the following equation for equilibrium yield:

$$Y^* = \left[\sum_{a=1}^A \mu_a W_a \mathcal{L}_a \right] \left[\frac{1}{R_1} S_0^{-1} \left(\frac{1}{R_1} \right) \right]. \quad (7.48)$$

Table 7.4. Equilibrium abundance of one year olds and equilibrium egg production in a Leslie matrix model with various spawner-progeny functions.

Spawner-progeny model name	Spawner-progeny equation, N_1	Equilibrium abundance, N_1^*	Equilibrium eggs, \mathcal{E}^*
Beverton-Holt	$\alpha\mathcal{E}/(1 + \beta\mathcal{E})$	$(\alpha R_1 - 1)/(\beta R_1)$	$(\alpha R_1 - 1)/\beta$
Cushing	$\alpha\mathcal{E}^\gamma$	$\frac{1}{R_1} (\frac{1}{\alpha R_1})^{1/(\gamma-1)}$	$(\frac{1}{\alpha R_1})^{1/(\gamma-1)}$
Deriso-Schnute	$\alpha\mathcal{E}(1 - \gamma\beta\mathcal{E})^{1/\gamma}$	$\frac{1}{\gamma\beta R_1} [1 - (\frac{1}{\alpha R_1})^\gamma]$	$\frac{1}{\gamma\beta} [1 - (\frac{1}{\alpha R_1})^\gamma]$
Ricker	$\mathcal{E}e^{a-\beta\mathcal{E}}$	$[a + \ln(R_1)]/(\beta R_1)$	$[a + \ln(R_1)]/\beta$
Shepherd	$\alpha\mathcal{E}/[1 + (\beta\mathcal{E})^\psi]$	$\frac{1}{\beta R_1} (\alpha R_1 - 1)^{1/\psi}$	$\frac{1}{\beta} (\alpha R_1 - 1)^{1/\psi}$

$R_1 = \sum_{a=1}^A f_a L_a$ is the equilibrium lifetime egg production of a one year old. In the Ricker model, $a = \ln \alpha$.

An important feature of the equilibrium yield equation, as given above, is that abundance has been removed from the right-hand side of the equation. Thus, yield is expressed as a function of parameters, albeit in a rather complicated equation.

Some simplification is possible when egg production of the population is proportional to exploitable biomass. In particular, suppose that net fecundity, f_a , is proportional to $S_a W_a$, age-specific selectivity of fishing mortality times average weight; we assume also that $\mu_a = \mu S_a$, where μ is the full-recruitment exploitation fraction. Let $f_a = p S_a W_a$, where p is the proportionality constant. We can write

$$\mu R_1 = p \left(\sum_{a=1}^A \mu_a W_a \mathcal{L}_a \right),$$

and thus (7.48) simplifies to

$$Y^* = \frac{\mu}{p} S_0^{-1} \left(\frac{1}{R_1} \right).$$

We see in this equation that changes in exploitation affect the formula for equilibrium yield in two locations: μ and R_1 . The second term, R_1 , is generally more sensitive to changes in fishing mortality rate, F , due to the compounding of F in \mathcal{L}_a . However, this increased sensitivity of R_1 may not translate into decreases in yield because equilibrium egg production (the S_0^{-1} term) is not proportional to R_1 for commonly used spawner-progeny functions. For example, with the Ricker spawner-progeny function substituted into the yield equation above, we get

$$Y^* = \frac{\mu}{p} \left[\frac{a + \ln(R_1)}{\beta} \right].$$

The logarithm function will sufficiently dampen changes in R_1 so that the net effect of increasing F is to increase yield over a range of fishing mortality rates. Further aspects of equilibrium yield are discussed in chapter 11.

Example 7.10. Hypothetical environmental impact assessment

Environmental impact assessment of the loss of yield due to induced mortality on young fish is difficult to estimate (Fletcher and Deriso 1979). Let us consider a hypothetical situation where the parameters of importance are clearly identified.

Part of a hypothetical environmental impact assessment is shown. We assume that the Ricker spawner-recruit model is appropriate and that an additional density-independent mortality, M_0 , is added onto the existing density-independent mortality, a , in the Ricker model. That is, the impacted population now has a Ricker a value of, say, $a' = a - M_0$. Assume further that fishery exploitation fractions are constant for each age and will not be changed as a consequence of the impact. The fractional reduction in equilibrium yield, from a preimpact yield of Y to an impacted yield of Y' , is given by

$$\frac{Y - Y'}{Y} = \frac{\frac{a-a'}{a}}{1 + \frac{\ln(R_1)}{a}}$$

because yield per recruit and the β parameter cancel from numerator and denominator. As seen above, the fractional change in equilibrium yield is proportional to the fractional

change in density-independent mortality rate for the young. The a parameter is negative in value (it is a mortality rate), whereas $\ln(R_1)$ is positive (a one year old produces at least one egg in its lifetime for a meaningful biological model). Furthermore,

$$R_1 e^a > 1 \quad (7.49)$$

is a necessary condition for a positive equilibrium solution to exist. By putting these previous constraints together, we see that the denominator in the equation above must be a number between 0 and 1. Therefore, the fractional reduction in equilibrium yield is larger than the fractional increase in the mortality rate of the young. The extent to which it is larger depends on the ratio $\ln(R_1)/a$. ■

Local stability of the equilibrium of a nonlinear Leslie matrix model can be determined by linearizing the matrix around equilibrium values and then evaluating eigenvalues. Local stability of the equilibrium is assured if all the eigenvalues lie within the unit circle. Reed (1980) shows that a sufficient condition for stability is

$$\left| R_1 \frac{\partial \mathcal{F}(\mathcal{E}^*)}{\partial \mathcal{E}} \right| < 1, \quad (7.50)$$

where the notation $\mathcal{F}(\mathcal{E}^*)$ means that the partial derivative, the slope of the spawner-progeny function, is evaluated at equilibrium, \mathcal{E}^* . Bergh and Getz (1988) provided details of this result, which we present in a slightly different way; stability considerations of nonlinear Leslie models are addressed in a number of essays, including Allen and Basasibwaki (1974), Beddington (1974), DeAngelis et al. (1980), and Levin and Goodyear (1980). Write the dynamics of $N_{1,t}$ from (7.40) as a function of past abundance of one year olds:

$$N_{1,t+1} = \mathcal{F}(\mathcal{E}_t) = \mathcal{F} \left(\sum_{a=1}^A f_a \mathcal{L}_a N_{1,t-a+1} \right); \quad (7.51)$$

then, taking the first-order Taylor expansion of $N_{1,t+1}$ around equilibrium values of past abundance of one year olds, we find that

$$\begin{aligned} x_{t+1} &= \sum_{a=1}^A \frac{\partial \mathcal{F}}{\partial \mathcal{E}_t} \left(\frac{\partial \mathcal{E}_t}{\partial N_{1,t-a+1}} \right) x_{t-a+1} \\ &= \sum_{a=1}^A \frac{\partial \mathcal{F}(\mathcal{E}^*)}{\partial \mathcal{E}} f_a \mathcal{L}_a x_{t-a+1}, \end{aligned}$$

where

$$x_t = N_{1,t} - N_1^*$$

and where all partial derivatives are evaluated at equilibrium. The characteristic equation for this linear equation is found by replacing x_j by λ^j for all the abundance deviations. The resultant equation can be divided by λ^{i+1} to get

$$1 = \frac{\partial \mathcal{F}(\mathcal{E}^*)}{\partial \mathcal{E}} \sum_{a=1}^A f_a \mathcal{L}_a \lambda^{-a}. \quad (7.52)$$

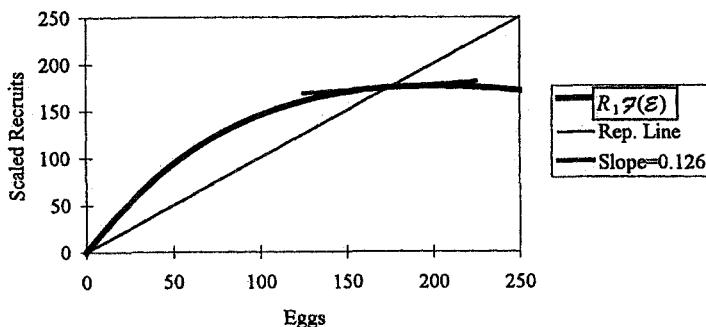


Figure 7.4. Illustration of a scaled spawner–progeny function, $y = R_1\mathcal{F}(E)$, and the replacement (rep.) line, $y = \mathcal{E}$, using parameters described in example 7.11. Equilibrium is given by the intersection, and the slope at that point is shown. Because the slope is between -1 and 1 , the equilibrium point is stable.

If the slope of the spawner–progeny function is positive, then we can write down the same upper bound for the dominant eigenvalue as given by Hearon (1976) for linear Leslie models [see the paragraph below (7.10)]. A symmetrical lower bound exists for negative slopes, which gives us the result (7.50).

The sufficient condition for stability (7.50) is analogous to the necessary and sufficient condition for stability of semelparous (one-age spawning) population models, as presented in chapter 3. Equilibrium egg production is characterized by the condition

$$\mathcal{E}^* = R_1\mathcal{F}(\mathcal{E}^*),$$

which is derived from (7.43) and (7.44). Thus, equilibrium is given by the intersection of the line $y = \mathcal{E}$ and $y = R_1\mathcal{F}(E)$, as shown in figure 7.4 (see example 7.11). The slope of the scaled spawner–progeny function, shown there, is the same slope given in (7.50). Stability is assured if that slope is between -1 and $+1$. Values for several spawner–progeny functions are given in table 7.5.

As shown by Deriso (1978), age-structured models for iteroparous populations (multiple-age spawners) are in general more stable than semelparous population models, where the additional stability depends in a complicated fashion on the maturity and

Table 7.5. Slope of various spawner–progeny models evaluated at equilibrium.

Spawner–progeny model name	Spawner–progeny equation, $\mathcal{F}(\mathcal{E})$	Equilibrium slope, $\partial\mathcal{F}/\partial\mathcal{E}$	Stability if inside $(-1, +1)$
Beverton–Holt	$\alpha\mathcal{E}/(1 + \beta\mathcal{E})$	$1/(\alpha R_1^2)$	$1/(\alpha R_1)$
Cushing	$\alpha\mathcal{E}^\gamma$	γ/R_1	γ
Deriso–Schnute	$\alpha\mathcal{E}(1 - \gamma\beta\mathcal{E})^{1/\gamma}$	$\frac{1}{R_1}(1 - \frac{[\alpha R_1]^\gamma - 1}{\gamma})$	$1 - \frac{[\alpha R_1]^\gamma - 1}{\gamma}$
Ricker	$\mathcal{E}e^{a-\beta\mathcal{E}}$	$\frac{1-a-\ln(R_1)}{R_1}$	$1 - a - \ln(R_1)$
Shepherd	$\alpha\mathcal{E}/[1 + (\beta\mathcal{E})^\psi]$	$\frac{1}{R_1} - \frac{\psi}{R_1} + \frac{\psi}{\alpha[R_1]^2}$	$1 - \psi + \frac{\psi}{\alpha R_1}$

Bergh and Getz (1988) derived the equilibrium slope for both the Deriso–Schnute and Shepherd spawner–progeny models, which are listed below, along with results for other models. Also given is the scaled slope in (7.50), which indicates a locally stable equilibrium if it is < 1 in absolute value. In the Ricker model, $a = \ln \alpha$.

survival parameters in the model. One general conclusion we can reach with (7.50) is that concave spawner-progeny models that do not contain a descending right-hand limb are always stable, as long as a positive equilibrium solution exists (such as the Beverton-Holt model). This follows directly from the fact that these concave functions lie above the replacement line in figure 7.4 for values of $\mathcal{E} < \mathcal{E}^*$. Indeed, as Bergh and Getz (1988) argued, (7.50) is always satisfied for the positive slopes of common spawner-recruit functions, as long as a positive equilibrium solution exists. It is the negative slopes associated with steeply domed spawner-progeny functions where instability is likely to occur; but even here, common functions, such as the Ricker model along with a reasonably smooth fecundity schedule, produce stable oscillations unless the slope is very negative indeed.

Example 7.11. Nonlinear Leslie matrix

Consider a population with dynamics described by a nonlinear Leslie matrix with a Ricker spawner-progeny function. Population parameters given in table 7.6 are the same as for example 7.1, but the Ricker α parameter is twice the S_0 value and the density-dependence parameter β is chosen to be 0.005 to exhibit moderate density dependence. The projection matrix \mathbf{M} corresponding to time 0 is shown, which is a synthesis of fecundity, survival, and Ricker parameters and the initial population vector \mathbf{N}_0 .

Equilibrium abundance N_a^* , the stable age distribution, and lifetime egg production, R_1 , of a one year old given in table 7.6 are calculated from (7.42)–(7.46) (as shown in the previous example for the Ricker model). Equilibrium egg production is abundance at age 0 ($\mathcal{E}^* = N_0^*$). The necessary condition $R_1 e^\alpha > 1$ for a positive equilibrium solution is satisfied, as the left-hand side is equal to 2.396. The slope of the spawner-progeny curve at equilibrium is obtained from table 7.5 and equal to 0.126. As this value is between -1 and 1 , the solution is stable. This example was used to create the spawner-progeny graph in figure 7.4.

A projection of the population is given in table 7.6, which requires annual updating of the projection matrix \mathbf{M} . Convergence to equilibrium occurs rapidly in 8 years. ■

7.5. FORECASTING

Forecasting or projecting age-structured populations into the future is often necessary for a variety of reasons. One might be interested in the future trends occurring in a population. The effect of various management strategies on the population may need to be evaluated. Commercial or recreational industries may require forecasts for planning. Monte Carlo experiments of future population trends might be undertaken to incorporate uncertainties.

The Leslie matrix and its variants are particularly well-suited to population projection. Given a starting population vector, \mathbf{N}_t , future populations can be projected from (7.1) by repeated application of the projection matrix \mathbf{M} .

The variant chosen for projection most often depends on how one characterizes the spawner-progeny relationship. A per-recruit approach, as in chapter 6, is used when the spawner-progeny relationship cannot be determined or is so variable as to preclude other approaches. This approach can be undertaken as a special case of the linear Leslie matrix. One sets abundance at age 1 at time t to some reference level, say 1000, sets the first row of the projection matrix \mathbf{M} to $(1, 0, \dots, 0)$ and then projects the population

Table 7.6. Example of a population following a nonlinear Leslie matrix model.

		Age, a				
		1	2	3		
f_a		0	1	2		
S_a		0.8	0.8			
$\alpha = \exp(a)$		1.152				
a		0.141				
β		0.005				
M		$\begin{pmatrix} 0 & 0.601 & 1.203 \\ 0.8 & 0 & 0 \\ 0 & 0.8 & 0 \end{pmatrix}$			N_0	
					100	
					30	
					50	
					Stable N^*	
					age distribution	
R_1 :		2.080	Age 0	175		
Slope:		0.126	Age 1	84	1.000	
			Age 2	67	0.800	
			Age 3	54	0.640	
			Total	205		
					Time, t	
					0	1
Age, a		0	1	2	3	4
$N_{a,t}$		100	78	78	85	83
		30	80	63	62	68
		50	24	64	50	50
		Total	180	182	204	197
					5	6
					83	84
					84	84
					67	67
					67	67
					53	53
					54	54
					Total	205
						205

Model parameters are fecundity, f_a , survival S_a , and Ricker spawner-recruit parameters α and β . The projection matrix M is shown for time 0, given initial population vector N_0 . Also shown are lifetime egg production, R_1 , of a one-year-old, the slope of the spawner-recruit curve at equilibrium, equilibrium abundance, N^* , the stable age distribution, and projection of the population for eight years.

until the effects of starting abundance disappear. The population is guaranteed to reach equilibrium because N_1 is constant over time.

The second approach is a straightforward application of the linear Leslie matrix approach. An estimate of early life survival, S_0 , is obtained, and the population is projected with (7.1). It is rare with this approach to obtain equilibrium because only for a single value of S_0 is there an equilibrium population. Nevertheless, this approach can be useful for short-term projections. When estimates of abundance by age are available (see catch-age analysis in chapter 8), then early life survival can be estimated as $S_{0,t} = N_{1,t+1}/N_{0,t}$ (Quinn and Szarzi 1993). The average, median, or some trend associated with these estimates can then be used for projection.

The third approach is the nonlinear Leslie matrix method. Here one must determine the spawner-progeny function from several years of data. Quite often, this function is subject to great uncertainty and potential confounding with environmental variables, as was seen in chapter 3. Hence, this approach frequently requires Monte Carlo work or evaluation of several alternative hypotheses about density-dependence to be successful.

Frequently, data are not available before a starting age r . This poses no particular

problem for forecasting with Leslie matrix methods. One simply redefines S_0 to be survival up to age r and other S_a 's prior to age r to be 1. Alternatively, one can simply write the Leslie equations starting at age r , as in Quinn and Szarzi (1993).

7.6. CONTINUOUS LINEAR MODELS

The mathematical theory of linear continuous models for the dynamics of age-structured populations first presented by Sharpe and Lotka in 1911 is well established in the field of population dynamics. However, few of the publications on fishes deal with this type of model; the Leslie discrete model is far more popular. We provide only a brief overview of the theory and refer the reader to Keyfitz (1968), Pollard (1973), Bartlett (1970), and Caswell (1989) for a more complete treatment.

Analogous to our presentation of the Leslie matrix model, we consider only the females of the population. Notation in this section is also similar. Let $N(a, t)$ be the density function of number of age a females at time t ; $f(a, t)$ be the net fecundity rate of age a females at time t ; $L(a, t)$ be the fraction of fish who survive from birth to age a at time t ; and $B(t)$ be the density function of number of births at time t . Notice that the definition of cumulative survival, $L(a, t)$, includes survival from age 0, rather than from age 1, as defined for \mathcal{L}_a in the previous section. Cumulative survival is a function of total mortality rate, $Z(a, t)$, as follows:

$$L(a, t) = \exp \left[- \int_0^a Z(x, t - a + x) dx \right].$$

Density functions are needed to describe continuous populations, but they can be related simply to actual abundance. For example, the number of females of age a to $a + \delta a$ in the time interval t to $t + \delta t$ is given by $N(a, t)\delta a\delta t$ for small δ increments; for larger increments just integrate the density across the increments. Density of females in a given cohort of individuals born in the same small time interval decreases according to the mortality function $Z(a, t)$. We can write the governing partial differential equations for this process of mortality as

$$\frac{\partial N}{\partial a} + \frac{\partial N}{\partial t} = -Z(a, t)N(a, t), \quad (7.53)$$

since, by the chain rule of differentiation,

$$\frac{dN}{dt} = \left(\frac{\partial N}{\partial a} \right) \frac{\partial a}{\partial t} + \frac{\partial N}{\partial t},$$

and $\partial a / \partial t = 1$ for a given cohort. Births in the population are a sum of births by all individuals in the population, which can be written as

$$B(t) = \int_0^A f(x, t)N(x, t)dx, \quad (7.54)$$

where A is the maximum age of reproduction; that is, $f(x, t) = 0$ for $x > A$.

The governing equations for birth and death can be combined into a single integral equation, the Sharpe-Lotka model, by substituting the solution of (7.53) into equation

(7.54). It is readily evident that the solution of (7.53) is $N(a, t) = N(0, t - a)L(a, t)$. By definition, $N(0, t - a) = \mathcal{B}(t - a)$ and, thus, we can write (7.54) as

$$\mathcal{B}(t) = \int_0^A f(x, t)L(x, t)\mathcal{B}(t - x)dx.$$

The solution of this equation is known when age-specific survival and fecundity rates are independent of time; that is, $L(x)$ and $f(x)$ do not depend on time. It is convenient to partition the integral into two parts: the first integration runs from 0 to t while the second integral runs from t to A . When enough time has passed so that $t > A$, then the second integral is zero. We can write this special case of the Sharpe-Lotka model, where $t > A$ and age-specific fecundity and survival are independent of time, as

$$\mathcal{B}(t) = \int_0^t f(x)L(x)\mathcal{B}(t - x)dx, \quad (7.55)$$

which is a homogeneous linear integral equation that can be solved by the method of Laplace transforms. The solution in general is a sum of exponential functions, much like the solution of the Leslie matrix model, except that now the solution can be a sum of an infinite number of exponential functions.

To find an exponential function, e^{rt} , that is an additive component of the solution to (7.55), we substitute the exponential function for $\mathcal{B}(t)$ into (7.55) and then solve for the characteristic root r . The term e^{rt} can be cancelled from both sides of (7.55) and the integral limits shortened to $[0, A]$ to get the characteristic equation:

$$\psi(r) = \int_0^A f(x)L(x)e^{-rx}dx = 1. \quad (7.56)$$

The characteristic roots of (7.56) have the following properties, as shown in Keyfitz (1968):

1. There is exactly one real characteristic root, say, r_1 , which is defined as the *intrinsic rate of growth*, and it is larger than the modulus of any other characteristic root.
2. All remaining characteristic roots are complex numbers, which come in conjugate pairs.
3. The *net reproduction rate*, $R(0) = \int_0^A f(x)L(x)dx$, which is the expected lifetime egg production of a female, can be used to determine the sign of r_1 : if $R(0) < 1$ then $r_1 < 0$; if $R(0) = 1$ then $r_1 = 0$; and if $R(0) > 1$ then $r_1 > 0$.
4. The function $\psi(r)$ is a monotonically decreasing function of r , which implies that the real root r_1 can be found by iteratively increasing trial values of r until $\psi(r)$ crosses below the number 1.

The first property assures that the asymptotic solution, as $t \rightarrow \infty$, is a stable population, whose birth rate is of the form

$$\mathcal{B}(t) = Ce^{r_1 t},$$

where C is a constant that depends on initial conditions. The stable age distribution, $k(a)$, is a continuous analogue to the discrete age vector given previously for Leslie matrix models:

$$k(a) = L(a)e^{-r_1 a},$$

which has been arbitrarily scaled so that $k(0) = 1$. The *mean generation length*, or mean age of reproduction in the stable population, can be written as a function of the derivative of $\psi(r)$:

$$\begin{aligned} T_0 &= \frac{\int_0^A xf(x)k(x)dx}{\int_0^A f(x)k(x)dx}, \\ &= \int_0^A xf(x)L(x)e^{-r_1 x}dx, \\ &= -\frac{d\psi(r_1)}{dr}. \end{aligned}$$

Example 7.12. Hypothetical population

This hypothetical problem illustrates how stable age structure theory can be used to estimate population parameters. Suppose that research is being conducted on an “un-exploited” fish population. Age-specific weight is given by the exponential equation $W(a) = \exp(0.1a)$, and fertility is proportional to weight:

$$f(a) = \alpha e^{0.1a} \quad \text{for } 0 \leq a$$

where the constant α is unknown. We also know that the mean age of reproduction is $T_0 = 4$ years and that the population abundance has doubled in the last 8 years. Assume that their natural mortality rate M is constant with both age and time and that the age distribution has been stable.

From the limited information given above, we can estimate the intrinsic rate of increase, r_1 , the fertility-weight constant, α , the natural mortality rate, M , and equilibrium fishing mortality rate, F , for this population:

1. The doubling of the population means that $B(t+8) = 2B(t)$. Since $B(t+8) = B(t) \exp(r_1 8)$, we can solve for r_1 : $2 = \exp(r_1 8)$ implies $r_1 = 0.0866$.
2. Mean age of reproduction, T_0 , can be written as a function of the derivative of $\psi(r)$. First we write down the characteristic function,

$$\psi(r) = \int_0^\infty \alpha e^{(0.1-r-M)x} dx = \frac{\alpha}{-0.1 + r + M}$$

and, thus,

$$T_0 = -\frac{d\psi(r_1)}{dr} = \frac{\alpha}{(-0.1 + r_1 + M)^2}.$$

Since $\psi(r_1) = 1$ and $T_0 = 4$, we can solve for α and M in the equations above to get $\alpha = 0.25$ and $M = 0.263$.

3. The equilibrium fishing mortality rate is the value of F that will cause the population to become stationary; that is, it will change the intrinsic rate of growth to $r_1 = 0.0$. Since $r_1 = 0.0866$ in the unexploited population, it follows that the equilibrium fishing mortality rate is also $F = 0.0866$ if all individuals are harvested at the same rate. ■

Catch-age and Age-structured Assessment Methods

8.1. ESTIMATION OF AGE COMPOSITION

Age composition is an increasingly important source of information for understanding fish population dynamics. By obtaining length, weight, and age information, it is possible to follow year-classes through time to understand growth (see chapter 4), to monitor population changes over time, and, most importantly, to obtain age- and sex-specific estimates of population parameters. Age information can be used from commercial and sport fisheries and from surveys. Methodology for aging is described by Chilton and Beamish (1982) and by Summerfelt and Hall (1987); the latter includes a review of common methods (Beamish and McFarlane 1987). Richards et al. (1992) derived statistical models for aging error, which can be used to quantify the precision and accuracy of aging, as well as to estimate ages from a sample of fish. Practical aspects of sampling design, including logistics, port sampling, and randomness of sampling, beyond that covered in this chapter, are discussed in the volume edited by Doubleday and Rivard (1983) and for Pacific halibut by Quinn et al. (1983a).

8.1.1. *Length Frequency Analysis*

The most common information collected in fisheries research is length, perhaps due to its ease of collection. A histogram of frequencies of length often shows distinct modes that hypothetically represent distinct age classes. Length frequency analysis (LFA) has been used since at least 1892 to decompose a length frequency histogram into component age classes (Ricker 1975a, pp. 203–204). The oldest method, simple inspection of the histogram, is the least reliable. Other graphical methods and curve fitting techniques (Harding 1949, Tanaka 1956, Doubleday 1976a) are also subjective.

Procedures for LFA have evolved principally from the theory of mixtures of distributions (Hasselblad 1966). The method uses maximum likelihood theory to decompose components from an overall distribution. Applications to fisheries data include those by McNew and Summerfelt (1978), MacDonald and Pitcher (1979), Schnute and Fournier (1980), Foucher and Fournier (1982), Fournier and Breen (1983), and Johnson and Quinn (1987). These applications have extended Hasselblad's original method

by consideration of parameter constraints and auxiliary information about growth and mortality, as shown below. MacDonald (1987) provided a critical review of the various approaches. More advanced length-based methods are covered in chapter 9.

We use the following notation, in which a bold font denotes a column vector:

- L = the number of individuals measured for length,
- l = an index for length interval,
- J = the number of length intervals,
- a = an index for age,
- r = the first age group,
- A = the last age group,
- $A' =$ the number of age groups = $A - r + 1$,
- $\mathbf{L}' = \{L'_l\}$ = the observed length frequencies,
- $\mathbf{L} = \{L_l\}$ = the true length frequencies,
- $\boldsymbol{\theta} = \{\theta_a\}$ = the true proportions of fish by age, and
- $\mathbf{p} = \{L_l/L\}$ = the true proportions of fish by length interval.

The term *age group* connotes that more than one age class may be represented in an age group.

The derivation of the maximum likelihood method has the following assumptions:

1. The length frequency distribution is multinomial:

$$f(\mathbf{L}') = \binom{L}{L'_1 \cdots L'_J} \prod_{l=1}^J p_l^{L'_l}.$$

The log-likelihood is then

$$\ln f(\mathbf{L}') = C + \sum_{l=1}^J L'_l \ln p_l, \quad (8.1)$$

where C is a constant.

2. The probability density function (PDF) of length $f_a(L)$ for each age group a is described by unknown parameter vector $\boldsymbol{\nu}$. Usually, the normal PDF is used with mean μ_a and standard deviation (SD) σ_a , given by

$$f_a(L) = \frac{1}{\sqrt{2\pi} \sigma_a} \exp \left[-\frac{1}{2\sigma_a^2} (L - \mu_a)^2 \right]. \quad (8.2)$$

The unknown parameter vector $\boldsymbol{\nu}$ for the normal PDF is made up of the component vectors $\boldsymbol{\mu}$ and $\boldsymbol{\sigma}$. Alternatively, the lognormal distribution can be used if the component distribution is thought to be positively skewed.

3. The number of age groups A' is known.
4. Each length measurement falls into one and only one interval l .

From assumption 1 and (8.1), the necessary part of the likelihood function for maximization for a multinomial distribution is

$$T(\nu, \theta) = \sum_{l=1}^J L'_l \ln p_l = \sum_{l=1}^J L'_l \ln(L_l/L), \quad (8.3)$$

where L_l is a function of the unknown parameters. From assumptions 2 and 4, the probability that a length measurement falls into interval l for age group a is

$$\psi_{la} = \int_l f_a(L) dL, \quad (8.4)$$

which is the area under the PDF that interval l covers. For a normal PDF, (8.2) is substituted into (8.4). The expected number of individuals of age a is simply $L\theta_a$. The expected number of individuals of age a and length l is $L\theta_a\psi_{la}$. Finally, the expected number of individuals of length l is then

$$L_l = L \sum_{a=r}^A \psi_{la}\theta_a. \quad (8.5)$$

The objective function T is then computed by substituting (8.5) into (8.3) and is to be maximized as a function of unknown parameters ν and θ . Closed-form solutions do not exist, even for the normal PDF, so iterative computer optimization techniques are required.

McNew and Summerfelt (1978) found several problems with length frequency analysis. If year-classes have different growth rates, it is hard to get consistent estimates from year to year. The number of age groups is often unknown, and estimates vary when different values of A' are used. To get reliable estimates, they found that the differences in mean length should be at least twice the minimum SD. Because both means and SDs in the model differ among age groups, several parameters are estimated, and different final solutions may be obtained depending on starting values. In practice, SDs of age groups are relatively large, making it difficult to perform the decomposition. Also, the underlying PDF's for age groups are frequently skewed or non-normal. Finally, sample size required for mixture decomposition is quite large. At least 400 lengths are needed for decomposition into two age groups, and larger sample sizes would be necessary for more age groups. Erzini (1990) investigated sample size and grouping of data for length-frequency analysis and concluded that considerations of sample size and biological parameters are important for determining the best interval size and that sample sizes in excess of 1000 are necessary to identify more than half the modes in the length frequency distribution.

MacDonald and Pitcher (1979) modified the approach to obtain more reasonable estimates by imposing constraints on the parameter estimates. They also gave an algorithm for computer solutions and developed a computer program. Some of the same problems occurred nonetheless.

Further enhancements to LFA were developed by Schnute and Fournier (1980), Foucher and Fournier (1982), and Fournier and Breen (1983). By imposing additional model structure, it is possible to obtain more reliable and less arbitrary estimates. The

Fournier and Breen procedure involves assumptions regarding growth, mortality, and the standard deviations. They used the normal PDF (8.2) in their development, but any other could be implemented. They make 3 assumptions, in addition to the four just described. The first is that growth is a random variable with an underlying LVB growth curve (see section 4.1.2). Specifically, the underlying mean length μ_a^* for age group a is

$$\mu_a^* = l_1 + (l_2 - l_1) \left[1 - e^{-\kappa(a-r)} \right] / \left[1 - e^{-\kappa(A-r)} \right],$$

where $l_1 = \mu_r^*$ is the mean length for age r , $l_2 = \mu_A^*$ is the mean length for age A , and κ is the Brody growth parameter, as in (4.31) with $\gamma = 1$. If some age groups represent multiple ages, then mean age should be used for μ_a^* . Other growth models from section 4.3 can also be used.

The actual mean length, μ_a , is assumed to be normally distributed about μ_a^* . This assumption is implemented into LFA by adding to the objective function T in (8.3) a penalty function for growth

$$G(\nu, l_1, l_2, \kappa) = -U \sum_{a=r}^A (\mu_a - \mu_a^*)^2, \quad (8.6)$$

where U is a specified penalty weight governing the amount of influence of the growth function. There is not enough information in length frequency data to estimate U , so the amount of influence must be specified. Increasing U forces the actual mean lengths to lie closer to the underlying LVB curve. Thus, the mean lengths do not have to follow an LVB curve precisely, allowing for flexibility of parameter estimation while constraining the parameter estimates sufficiently. The LVB curve could also be replaced by any other appropriate growth curve.

The second assumption is that the proportion of individuals of age a is a random variable with an underlying survival curve described by an exponential decline past the age of full recruitment, r' [see equation (6.1)]. Specifically, the underlying survival curve θ_a^* for age group $a > r'$ is

$$\begin{aligned} \theta_a^* &= c \exp(-Za) \\ \text{or } \ln \theta_a^* &= \ln c - Za, \end{aligned}$$

where c is a constant and Z is total mortality. This assumption is satisfied when recruitment and mortality are constant over time for all age groups. Other conditions may occur to make this assumption reasonable. It is unlikely to be useful for fish with highly variable recruitment.

The logarithm of the true proportion, $\ln \theta_a$, is assumed to be normally distributed about $\ln \theta_a^*$. This assumption is implemented into LFA by adding to the objective function T in (8.3) a penalty function for mortality

$$M(\theta, c, Z) = -V \sum_{a=r'}^A (\ln \theta_a - \ln \theta_a^*)^2, \quad (8.7)$$

where V is a specified penalty weight governing the amount of influence of the mortality function. Implementation is identical to the growth function.

Third, it is assumed that SDs are constant or are a function of age. Two functions used in practice are linear functions of \sqrt{a} (Fournier and Breen 1983) or of a (Johnson and Quinn 1987). This strict assumption reduces the number of standard deviations to be estimated from A' to one or two.

A final penalty term can be added to constrain the proportions to add to one (Johnson and Quinn 1987), given by

$$S(\boldsymbol{\theta}) = -W \left(1 - \sum_{a=r}^A \theta_a \right)^2, \quad (8.8)$$

where the penalty term W is chosen large enough to guarantee that the constraint is satisfied. This approach is often easier to implement than rewriting the last proportion in terms of the others.

The final objective function from (8.3), (8.6), (8.7), and (8.8) is

$$T_f(\boldsymbol{\nu}, \boldsymbol{\theta}, l_1, l_2, \kappa, c, Z) = T(\boldsymbol{\nu}, \boldsymbol{\theta}) + G(\boldsymbol{\nu}, l_1, l_2, \kappa) + M(\boldsymbol{\theta}, c, Z) + S(\boldsymbol{\theta}), \quad (8.9)$$

which is to be maximized as a function of all unknown parameters. Other penalty terms could also be envisioned, such as to constrain age composition parameters less than the age of full recruitment to follow an increasing age selectivity curve.

After the solution is obtained, the PDF of each age group is computed by substituting estimates for parameters in $f_a(L)$ [e.g., (8.3) for a normal PDF]. Expected frequencies as a function of l and a are readily obtained from (8.4) and (8.5). Then a straightforward goodness-of-fit test is made. A graphical assessment is made by weighting each PDF by its estimated proportion, $\hat{\theta}_a$, multiplying by the length interval width, and superimposing over the histogram of length frequencies.

In practice, the addition of model structure enhances the performance of LFA (Fournier and Breen 1983, Johnson and Quinn 1987). Reducing the number of standard deviation parameters speeds convergence of the iterative procedure and helps to prevent different solutions. By restricting growth to a specified growth curve such as the LVB, the number of age groups specified is less critical because older fish are spread out among the different groups according to growth. However, growth parameters are not well estimated simultaneously with length frequency parameters and hence should be obtained from independent growth studies (see chapter 4). The mortality function was useful for abalone populations (Fournier and Breen 1983) but not for sablefish populations with low growth rates and variable recruitment (Johnson and Quinn 1987). Parameter Z can be estimated from length frequency data along with other parameters only if an exponential decline in age group proportions is reasonable. Finally, reasonable estimates from LFA are likely only if good auxiliary information on growth and mortality is available.

Example 8.1. Kenai River rainbow trout

Length measurements ($L = 761$) from rainbow trout in the Kenai River, Alaska were collected in 1986 (Lafferty and Quinn 1987); the length frequency data $\{L'_l\}$ are given in table 8.1. Length frequency analysis was performed assuming that growth followed an LVB curve with a penalty weight of $U = 1$, using a penalty weight $W = 1,000,000$, using the true number of ages (2-8), and not assuming that recruitment was constant [omitting (8.7)]. The SDs were assumed to be a proportional to the square root of age.

Table 8.1. Length frequency data $\{L'_l\}$ for rainbow trout in the Kenai River, Alaska, 1986 ("start" indicates start of the 5-mm length interval).

l	Start	L'_l	l	Start	L'_l	l	Start	L'_l
1	182.5	2	38	367.5	22	74	547.5	3
2	187.5	0	39	372.5	13	75	552.5	1
3	192.5	1	40	377.5	17	76	557.5	1
4	197.5	0	41	382.5	18	77	562.5	4
5	202.5	5	42	387.5	17	78	567.5	2
6	207.5	0	43	392.5	13	79	572.5	3
7	212.5	1	44	397.5	10	80	577.5	3
8	217.5	3	45	402.5	10	81	582.5	4
9	222.5	3	46	407.5	14	82	587.5	4
10	227.5	4	47	412.5	8	83	592.5	4
11	232.5	8	48	417.5	16	84	597.5	4
12	237.5	8	49	422.5	12	85	602.5	2
13	242.5	13	50	427.5	5	86	607.5	0
14	247.5	13	51	432.5	10	87	612.5	1
15	252.5	10	52	437.5	9	88	617.5	0
16	257.5	13	53	442.5	8	89	622.5	0
17	262.5	11	54	447.5	8	90	627.5	0
18	267.5	11	55	452.5	12	91	632.5	3
19	272.5	16	56	457.5	5	92	637.5	2
20	277.5	14	57	462.5	2	93	642.5	1
21	282.5	9	58	467.5	3	94	647.5	0
22	287.5	13	59	472.5	3	95	652.5	1
23	292.5	17	60	477.5	4	96	657.5	0
24	297.5	19	61	482.5	1	97	662.5	0
25	302.5	17	62	487.5	5	98	667.5	1
26	307.5	12	63	492.5	3	99	672.5	1
27	312.5	15	64	497.5	2	100	677.5	0
28	317.5	16	65	502.5	4	101	682.5	0
29	322.5	9	66	507.5	7	102	687.5	0
30	327.5	15	67	512.5	4	103	692.5	0
31	332.5	19	68	517.5	4	104	697.5	0
32	337.5	16	69	522.5	2	105	702.5	0
33	342.5	24	70	527.5	3	106	707.5	0
34	347.5	29	71	532.5	2	107	712.5	0
35	352.5	19	72	537.5	4	108	717.5	0
36	357.5	26	73	542.5	3	109	722.5	1
37	362.5	21						

The resultant length-age distributions are shown in figure 8.1; the method produces an excellent fit to the total length frequency data ($\chi^2_{68} = 76$, $P = .24$). The proportionate age composition results are given in table 8.2 and do not agree well with estimates obtained from aging fish (see example 8.2). Had actual LVB estimates been used, the age composition estimates from LFA would have been closer. Hence, it is possible to get an excellent fit to length frequency data while obtaining incorrect age composition estimates, and it may be necessary to have actual growth information (not just the functional form) to obtain reliable estimates. ■

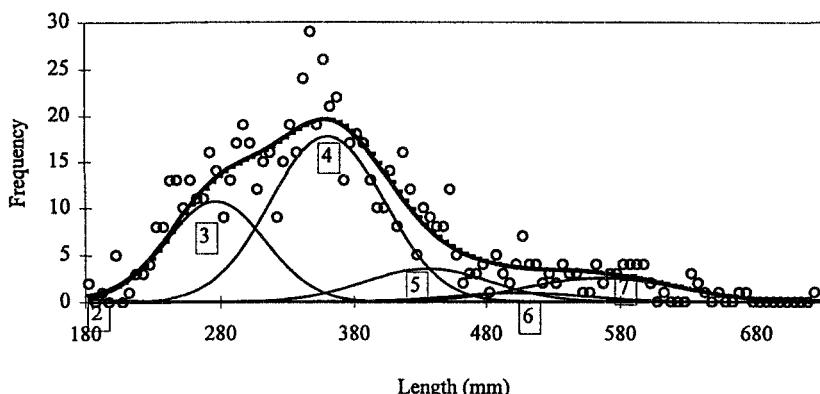


Figure 8.1. Length-age distributions inferred from length frequency analysis of Kenai River rainbow trout data, 1986, along with observed and predicted total length frequency across ages. Ages range from 2 to 8, but the proportions for ages 2 and 8 are so small that the length-age distributions can not be seen.

One further development of LFA is the estimation of parameters from multiple years of data. By following year-classes through several years and tying growth to a growth curve, it is possible to obtain reasonable estimates. The procedure is described by Pauly and David (1981), who provided a BASIC program, ELEFAN I, to extract growth parameters. Other length-based procedures are described in several papers in the volume edited by Pauly and Morgan [eds.] (1987) and in a review article by Rosenberg and Beddington (1988). Basson et al. (1988) compared the accuracy and reliability of Shepherd's length composition analysis (Shepherd 1987a) and a projection matrix approach (Shepherd 1987b), both of which are designed to take advantage of information on changes in length frequency during the growing season. They concluded that both methods are reasonably robust to variations in length at age, as long as the order of magnitude of the parameters is known.

If some age sampling has been undertaken, the length frequency approach of Fournier and Breen (1983) can be modified to incorporate the limited age samples (Fournier 1983). A term is added to the objective function T in (8.3), which invokes a penalty when the estimated age composition strays too far from the observed age-length data.

8.1.2. Simple Random Sampling

Subsequent methods presume that aging is possible for the species considered. The simplest sampling method for age is simple random sampling. Under a simple random sampling protocol, a simple random sample of A fish is taken from a population of C individuals (Cochran 1977). The population may be a commercial catch of fish, a survey catch of fish, or an entire fish population. Suppose that the true but unknown number of age a fish is C_a . Define

$$\theta_a = C_a/C$$

as the true but unknown proportion of age a fish. It is assumed that fish are sampled independently and have the same probability of being sampled. Each fish in the sample is aged, and the resultant frequency of age a fish in the sample is denoted A_a .

If it is assumed that the size of the population, C , is large compared to the sample size, A , then the data $\{A_a\}$ are distributed according to a multinomial distribution. The estimate of the proportion of age a fish is

$$\hat{\theta}_a = A_a/A, \quad (8.10a)$$

with estimated variance

$$SE^2(\hat{\theta}_a) = \hat{\theta}_a(1 - \hat{\theta}_a)/A. \quad (8.10b)$$

If A is large, then the normal approximation can be applied to obtain a confidence interval for $\hat{\theta}_a$. If the size of the population or sample cannot be considered large, then finite population corrections can be applied (Cochran 1977).

The estimate of the number of age a fish is

$$\hat{C}_a = C\hat{\theta}_a \quad (8.11a)$$

with estimated variance

$$SE^2(\hat{C}_a) = C^2 SE^2(\hat{\theta}_a), \quad (8.11b)$$

or, in terms of coefficient of variation (CV),

$$CV(\hat{C}_a) = CV(\hat{\theta}_a). \quad (8.11c)$$

A confidence interval for C_a can be constructed analogously to $\hat{\theta}_a$.

Simple random sampling may be difficult to carry out in practice. Unintentional selection of certain components of the population may occur. For example, sampling of Pacific halibut catch is not representative when samplers attempt to grab fish at random, because there is a tendency to select fish of smaller size (Southward 1976). Other sampling protocols may be preferable in practice to ensure that a representative sample of the population of interest is taken. A two-stage procedure, given in section 8.1.4, is one alternative.

8.1.3. Estimating the Catch

In many situations, the catch, C , is unknown and must be estimated. Common methods of estimating sports catch include creel censuses (e.g., Robson 1960, 1961) and mail and phone surveys (e.g., Mills 1985). Texts on sampling theory should be consulted for appropriate methodology (e.g., Cochran 1977, Thompson 1992).

In commercial fisheries, a procedure described fully in Quinn et al. (1983) may be used. Yield, Y (catch in biomass units), is frequently known from records of fish tickets. Yield is the product of C and the average weight of fish in the catch, \bar{W} , or $Y = C\bar{W}$. If a simple random sample of fish from the catch is taken and the weight of each fish is measured, estimates of \bar{W} and its variance $SE^2(\bar{W})$ can be obtained from the sample. The estimate of the catch is

$$\hat{C} = Y/\bar{W}, \quad (8.12a)$$

with estimated variance from the delta method (Seber 1982, pp. 7–9)

$$\text{SE}^2(\widehat{C}) = \widehat{C}^2 \text{SE}^2(\overline{W}) / \overline{W}^2. \quad (8.12b)$$

In this situation, the estimate of catch-age from (8.11a) is

$$\widehat{C}_a = \widehat{C}\widehat{\theta}_a. \quad (8.13a)$$

The modification of (8.11b) from the delta method (Seber 1982, pp. 7–9) is approximately

$$\text{SE}^2(\widehat{C}_a) = \widehat{C}^2 \text{SE}^2(\widehat{\theta}_a) + \widehat{\theta}_a^2 \text{SE}^2(\widehat{C}), \quad (8.13b)$$

ignoring a usually small covariance term. In terms of CVs,

$$\text{CV}^2(\widehat{C}_a) = \text{CV}^2(\widehat{\theta}_a) + \text{CV}^2(\widehat{C}). \quad (8.13c)$$

The estimator (8.12a) is biased because random variable \overline{W} is in the denominator. The amount of bias depends on the sample size and on the amount of variability in average weight. If a large enough sample size is collected, the bias is small. Sampson (1994) developed two less-biased estimators by taking a Taylor series expansion of (8.12a) for use with small sample sizes.

Example 8.2. Kenai River rainbow trout

Scales from rainbow trout in the Kenai River, Alaska, were collected in 1986 for aging purposes (Lafferty and Quinn 1987). A total of $C = L = 761$ trout were caught, of which $A = 278$ were randomly sampled for age; the age frequency data $\{A_a\}$ are given in table 8.2. Estimates of proportionate age composition and corresponding SE based on simple random sampling are made using (8.10a) and (8.10b) (table 8.2). Projections to the catch are made using (8.11a) and (8.11b). Standard errors representing absolute error are highest for ages with the highest age composition, whereas coefficients of variation representing relative error are lowest.

The age-specific abundance of the exploitable population was of interest, so a mark-recapture study was carried out, which produced a pilot estimate, \widehat{N} , of 3608 with a $\text{CV}(\widehat{N})$ of 0.116. Projections to the exploitable population are made using (8.13a) and (8.13b) by replacing C with N (table 8.2). Only when $\text{CV}(\widehat{N})$ is large compared to $\text{CV}(\widehat{\theta}_a)$ is there much effect on the $\text{CV}(\widehat{N}_a)$ (e.g. age 4). ■

8.1.4. Two-Stage Random Sampling

The two-stage stratified sampling (or double sampling) protocol has been studied by several authors (Ketchen 1950, Kutkuhn 1963, Southward 1976, Quinn et al. 1983a, b, Gavaris and Gavaris 1983). Under two-stage sampling, two assumptions are necessary.

1. A simple random sample of size L from the catch C is taken in the first stage. The sample is classified into length intervals with frequencies $\{L_l\}$, $l = 1, \dots, J$. The stratification variable could also be some other measurement related to age, such as otolith weight.
2. A subsample of size A is taken for aging in the second stage, with A_l taken randomly from L_l . The first well-known allocation for the A_l is *fixed* allocation, where a constant number of fish are aged from each length class. The

Table 8.2. Age composition estimates, $\hat{\theta}_a$, from length frequency analysis and from a simple random sample of ages for rainbow trout in the Kenai River, Alaska, 1986.

	a							
	2	3	4	5	6	7	8	
Length frequency analysis								
$\hat{\theta}_a$	0.006	0.260	0.497	0.110	0.033	0.094	0.0002	
Simple random sampling								
A_a	17	72	110	46	13	14	6	A: 278
$\hat{\theta}_a$	0.061	0.259	0.396	0.165	0.047	0.050	0.022	
SE($\hat{\theta}_a$)	0.014	0.026	0.029	0.022	0.013	0.013	0.009	
CV($\hat{\theta}_a$)	24%	10%	7%	13%	27%	26%	40%	
\hat{C}_a	47	197	301	126	36	38	16	$\hat{C}: 761$
SE(\hat{C}_a)	11	20	22	17	10	10	7	
CV(\hat{C}_a)	24%	10%	7%	13%	27%	26%	40%	\hat{N}
\hat{N}_a	221	934	1428	597	169	182	78	3608
SE(\hat{N}_a)	58	144	197	106	50	52	33	419
CV(\hat{N}_a)	26%	15%	14%	18%	29%	29%	42%	12%

For simple random sampling, projections, \hat{C}_a and \hat{N}_a , to the total length sample and to exploitable abundance, respectively, are also given.

second is *proportional* allocation, where the number of fish aged is selected proportional to the length frequencies. As proportional allocation results in self-weighting of data across strata, it is usually the best default allocation. However, any other allocation for the $\{A_l\}$ can also be used. After ages are obtained, age frequencies are classified by length l and age a into an age-length key, denoted $\{A_{la}\}$, $l = 1, \dots, J$, $a = r, \dots, A$ where r is the youngest age and A is the oldest age.

Let C_{la} be the true number of length l and age a fish in the catch. Omission of a subscript implies summation over the subscript for C , C_l , and C_a . Define the proportion of fish of length l as

$$\alpha_l = C_l/C$$

and the proportion of fish of length l and age a as

$$\theta_{la} = C_{la}/C_l.$$

By multiplying the previous two quantities and summing, it is easily shown that the proportion of age a fish can be obtained as

$$\theta_a = C_a/C = \sum_l \alpha_l \theta_{la}$$

An unbiased estimator of α_l is

$$\hat{\alpha}_l = L_l/L$$

from the first assumption, and an unbiased estimator of θ_{la} is

$$\widehat{\theta}_{la} = A_{la}/A_l$$

from the second assumption. An unbiased estimator of θ_a is then

$$\widehat{\theta}_a = \sum_l \widehat{\alpha}_l \widehat{\theta}_{la} \equiv \sum_l r_{la}, \quad (8.14a)$$

where r_{la} is the estimated proportion of fish of length l and age a . Its estimated variance comes from the theory of two-stage sampling and consists of a within-length component and a between-length component, given by

$$\text{SE}^2(\widehat{\theta}_a) = \sum_l \frac{\widehat{\alpha}_l^2 \widehat{\theta}_{la}(1 - \widehat{\theta}_{la})}{A_l - 1} + \sum_l \frac{\widehat{\alpha}_l (\widehat{\theta}_{la} - \widehat{\theta}_a)^2}{L} \quad (8.14b)$$

$$\equiv \sum_l \text{SE}^2(r_{la}) \quad (8.14c)$$

Catch-age estimates are obtained by projection to the total catch using (8.11a) and (8.11b) in section 8.1.2 when the catch is known and (8.12a) and (8.12b) in section 8.1.3 when the catch is estimated.

Another important set of data necessary for age-structured analyses is average weight at age. Suppose that a sample of weights is obtained for each l and a , with the average denoted \overline{W}_{la} and its estimated variance denoted $\text{SE}^2(\overline{W}_{la})$. For most fish, weight is simply a function of length l , and the subscript a can be omitted. An unbiased estimator of average weight at age uses r_{la} , the estimated proportion of fish of length l and age a from (8.14a), as a weighting variable, or

$$\overline{W}_a = \sum_l r_{la} \overline{W}_{la} / \sum_l r_{la}. \quad (8.15a)$$

Its variance estimator from the delta method from Quinn et al. (1983a) using (8.14c) is

$$\text{SE}^2(\overline{W}_a) = \widehat{\theta}_a^{-2} \left[\sum_l r_{la}^2 \text{SE}^2(\overline{W}_{la}) + \sum_l (\overline{W}_{la} - \overline{W}_a)^2 \text{SE}^2(r_{la}) \right]. \quad (8.15b)$$

All previous formulae in this section apply to a single stratum, wherein the distribution of length and the distributions of age within a length interval for all length intervals can be considered homogeneous. If differences among strata occur due to different stocks, fish growth, migration, gear, or other factors, then formulae for combining data across strata are needed; such formulae are given in Quinn et al. (1983a). There it is shown that data can be pooled only if the length and age length distributions are identical among strata. Otherwise, stratum estimates should be weighted by the appropriate quantities related to the amount of stratum catch. Statistical methods for evaluating differences among age-length distributions are given in Kimura (1980), Quinn et al. (1983a), and Hayes (1993).

A different situation is when the variation in landings between vessels is large. Formulae derived in Davies et al. (1993) use the theory of cluster sampling. Between

landing variation is frequently much more important than within landing variation (Baird and Stevenson 1983, Gavaris and Gavaris 1983, Davies et al. 1993, Crone 1995), but sometimes the opposite occurs (e.g., Pacific halibut, Southward 1976).

Two-stage protocols also occur in sampling species composition in multispecies fisheries (Crone 1995). Here the categories are species rather than ages, but the theory applies equally well.

Example 8.3. Hauraki Gulf snapper, New Zealand

A marine species known as snapper *Pagrus auratus* is commercially important in Australia and New Zealand. Port sampling in 1992–93 was conducted according to a two-stage design with fixed allocation in the Hauraki Gulf, New Zealand, and other areas; details of the methodology and logistics are found in Davies et al. (1993). Table 8.3 gives the age-length frequencies $\{A_{la}\}$ and the estimated length frequencies $\{L_l\}$ from longline vessels; a total of $L = 6724$ fish were collected and measured, of which $A = 808$ were subsampled for aging. (The estimation of length frequency took into account within-vessel variation, which made up a negligible component of the total variation.)

Estimates of proportionate age composition and corresponding SE based on two-stage sampling are made using (8.14a) and (8.14b) (table 8.4). The total estimated catch is $\hat{C} = 444,790$ with an almost negligible CV of 0.00011783. Estimates of catch at age in table 8.4 are made using (8.13a) and (8.13b). The results show that ages that are more dominant in the catch have the higher absolute errors (SEs) but smaller relative errors (CVs). Also, because the relative error in estimating total catch numbers is so small, the CV for projected catch is almost identical to that for its proportionate value.

■

8.1.5. Sample Size Considerations

Methods for determining sample size necessary to achieve some sampling goal have long been investigated in the theory of survey sampling (e.g., Cochran 1977). In the situation of two-stage sampling, the sample sizes L and $\{A_l\}$ are chosen to achieve a specified level of precision. If a pilot study has been conducted, so that preliminary estimates $\{\hat{\alpha}_l\}$ and $\{\hat{\theta}_{la}\}$ are available, variance formula (8.14b) can be used to examine of effects of alternative sampling strategies as a function of L and $\{A_l\}$. In the two special cases of fixed and proportional allocation, the sample size problem can be simplified to choosing total sample sizes for length L and age A .

Three different approaches for determining sample size are described. The first method requires fixed or proportional allocation and involves sampling criteria measured by CV. Formulae below can equivalently be formulated in terms of SE, because $SE = \hat{\theta}_a CV$. The second method determines optimal allocations based on cost and precision for fixed and proportional two-stage sampling. The third uses Bayesian methods to obtain optimal allocation for two-stage sampling in general.

Define

$$V_a = \sum_l \hat{\alpha}_l \hat{\theta}_{la} (1 - \hat{\theta}_{la}) \quad (8.16a)$$

$$B_a = \sum_l \hat{\alpha}_l (\hat{\theta}_{la} - \hat{\theta}_a)^2 \quad (8.16b)$$

Table 8.3. Length frequencies and age frequencies within each length interval of snapper from longline vessels in the Gulf of Hauraki, 1992–93.

<i>l</i>	(cm)	<i>L_l</i>	<i>A_l</i>	<i>A_{la}</i>													
				3	4	5	6	7	8	9	10	11	12	13	14	15	16+
1	23	5	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0
2	24	41	20	1	14	4	1	0	0	0	0	0	0	0	0	0	0
3	25	94	21	0	7	10	2	2	0	0	0	0	0	0	0	0	0
4	26	259	21	0	2	13	5	1	0	0	0	0	0	0	0	0	0
5	27	314	20	0	2	11	3	3	1	0	0	0	0	0	0	0	0
6	28	443	20	0	1	13	5	1	0	0	0	0	0	0	0	0	0
7	29	525	19	0	0	11	4	0	4	0	0	0	0	0	0	0	0
8	30	538	21	0	0	3	6	8	3	1	0	0	0	0	0	0	0
9	31	484	21	0	0	1	0	7	10	2	0	0	1	0	0	0	0
10	32	482	20	0	0	0	4	6	3	5	0	2	0	0	0	0	0
11	33	450	20	0	0	0	0	8	7	3	1	1	0	0	0	0	0
12	34	352	21	0	0	0	1	6	6	8	0	0	0	0	0	0	0
13	35	290	20	0	0	1	1	4	5	8	0	1	0	0	0	0	0
14	36	260	20	0	0	0	0	5	3	5	2	1	3	1	0	0	0
15	37	184	20	0	0	0	0	1	1	6	1	1	8	0	1	0	1
16	38	211	21	0	0	0	0	1	5	3	1	0	3	1	4	1	2
17	39	155	22	0	0	0	0	0	2	6	0	3	6	2	2	0	1
18	40	157	25	0	0	0	0	1	2	5	1	3	8	1	0	0	4
19	41	127	21	0	0	0	0	0	1	4	0	0	8	3	2	0	3
20	42	128	25	0	0	0	0	0	0	5	1	2	6	2	2	2	5
21	43	106	19	0	0	0	0	0	1	1	1	1	3	2	4	1	5
22	44	111	19	0	0	0	0	0	1	4	0	1	4	4	2	0	3
23	45	88	25	0	0	0	0	0	0	2	0	1	6	1	3	3	9
24	46	88	20	0	0	0	0	0	0	1	1	0	6	3	3	1	5
25	47	91	29	0	0	0	0	0	1	2	0	1	9	5	1	2	8
26	48	84	20	0	0	0	0	0	0	2	0	1	5	1	4	2	5
27	49	70	22	0	0	0	0	0	0	1	0	1	2	4	2	3	9
28	50	72	20	0	0	0	0	0	0	0	0	0	4	2	3	2	9
29	51	54	19	0	0	0	0	0	0	1	0	1	2	0	1	2	12
30	52	47	17	0	0	0	0	0	0	1	0	0	1	2	3	0	10
31	53	59	21	0	0	0	0	0	0	0	0	0	2	3	3	1	12
32	54	46	18	0	0	0	0	0	0	0	0	0	0	5	0	3	10
33	55	42	22	0	0	0	0	0	0	0	0	0	1	1	4	2	14
34	56	40	21	0	0	0	0	0	0	0	0	0	0	0	5	3	13
35	57	36	18	0	0	0	0	0	0	0	0	0	1	0	0	2	15
36	58	29	17	0	0	0	0	0	0	0	0	0	0	0	2	0	15
37	59	31	22	0	0	0	0	0	0	0	0	0	0	2	1	2	17
38	60–64	113	39	0	0	0	0	0	0	0	0	0	0	2	0	1	36
39	65+	18	17	0	0	0	0	0	0	0	0	0	0	1	1	1	15

Sum *L*: 6724 *A*: 808

Data are pooled for the last two length intervals and for fish aged 16 or older. The subsampling goal was to obtain about 20 otoliths from each cm category (fixed allocation).

$$\text{and } F_a = J \sum_l \widehat{\alpha}_l^2 \widehat{\theta}_{la} (1 - \widehat{\theta}_{la}). \quad (8.16c)$$

The terms V_a and F_a are components of variance within length intervals for proportional and fixed allocation, respectively. The term B_a is a variance component between length intervals. If proportional allocation is assumed, then $A_l = A\alpha_l$, and an approximate variance expression from (8.14b) is

$$\text{SE}^2 = \frac{V_a}{A} + \frac{B_a}{L} \quad (8.17a)$$

Table 8.4. Estimates of proportionate age composition and catch at age, SEs, and CVs from longline vessels for Hauraki Gulf snapper, 1992–93.

Age, a	$\hat{\theta}_a$	SE($\hat{\theta}_a$)	CV($\hat{\theta}_a$)	\hat{C}_a	SE(\hat{C}_a)	CV(\hat{C}_a)
3	0.0003	0.0003	1.012	136	137	1.012
4	0.0213	0.0056	0.261	9476	2477	0.261
5	0.1624	0.0157	0.097	72255	7004	0.097
6	0.0926	0.0158	0.171	41173	7024	0.171
7	0.1533	0.0185	0.121	68169	8237	0.121
8	0.1461	0.0182	0.124	64967	8081	0.124
9	0.1260	0.0150	0.119	56060	6666	0.119
10	0.0133	0.0050	0.378	5896	2226	0.378
11	0.0277	0.0074	0.269	12299	3306	0.269
12	0.0763	0.0083	0.109	33936	3699	0.109
13	0.0298	0.0047	0.159	13238	2106	0.159
14	0.0332	0.0050	0.151	14770	2224	0.151
15	0.0162	0.0031	0.190	7192	1367	0.190
16+	0.1017	0.0063	0.062	45226	2815	0.062
$V: 0.0017$		$\hat{C}: 444790$		52	0.0001178	
$D: 0.0409$						

or in terms of CV,

$$\text{CV}^2 = \left(\frac{V_a}{A} + \frac{B_a}{L} \right) / \hat{\theta}_a^2. \quad (8.17b)$$

For fixed allocation, $A_l = A/J$, and the previous formulae apply with V_a replaced with F_a .

Solving for A in (8.17b),

$$A = \frac{V_a}{\hat{\theta}_a^2 \text{CV}^2 - B_a/L}. \quad (8.18a)$$

This equation can be used to find a value of A given L that permits the particular age composition estimate, $\hat{\theta}_a$, to have a specified level of precision. In the case where the smallest number of fish is to be collected, one sets $A = L$ in (8.17b) to obtain

$$A = L = (V_a + B_a) / (\hat{\theta}_a^2 \text{CV}^2). \quad (8.18b)$$

Frequently the term B_a is much smaller than V_a and can be ignored for the purpose of sample size determination, making a choice for L unnecessary. Otherwise, several values for L can be examined for their effect on reducing the age sample size.

A possible summary statistic is the accumulated variance among ages, V , defined as

$$V = \sum_a \text{SE}^2(\hat{\theta}_a) \quad (8.19a)$$

or its transform, $D = \sqrt{V}$ (Lai 1987). For specified A and L , V for proportional allocation is about equal to

$$V = \frac{\sum_a V_a}{A} + \frac{\sum_a B_a}{L}, \quad (8.19b)$$

which follows directly from (8.17a). A weighted sum across ages could also be considered (Jinn et al. 1987).

The determination of sample size rests on the goals to be achieved. Considering estimation precision, one possibility is to achieve a specified CV or SE for a range of important ages (Quinn et al. 1983a). One might want to achieve a CV of at least a specified level for at least one age (Quinn et al. 1983a), or one might want to obtain V or D to within a specified level (Lai 1987).

When cost is an important consideration, optimal sample sizes A and L can be determined to maximize precision for a fixed cost or to minimize cost for a specified level of precision (Lai 1987). Let

$$p_1 = \sum_a V_a \quad (8.20a)$$

$$f_1 = \sum_a F_a \quad (8.20b)$$

$$\text{and } p_2 = f_2 = \sum_a B_a. \quad (8.20c)$$

Define total cost as

$$C = c_1 L + c_2 A, \quad (8.21a)$$

where c_1 and c_2 are per unit costs of measuring length and age, respectively.

For proportional allocation, the optimal solution to the maximal precision problem for fixed cost, C , is a function of the optimal subsampling fraction

$$r^* = \frac{A^*}{L^*} = \sqrt{\frac{p_1 c_1}{p_2 c_2}}. \quad (8.21b)$$

Solutions A^* and L^* are

$$A^* = r^* L^* \text{ and } L^* = \frac{C}{c_1 + c_2 r^*} \quad (8.21c)$$

with the minimum V of

$$V_{\min} = p_1/A^* + p_2/L^*. \quad (8.21d)$$

The fixed allocation answer is the same as above with p 's replaced with f 's.

The solution to the problem of minimizing cost for a specified level of precision D is identical, with a slightly different sequence of calculations. The value L^* for proportional allocation is calculated as

$$L^* = (\frac{p_1}{r^*} + p_2)/D^2. \quad (8.21e)$$

Using this value, the optimal subsampling fraction from (8.21b), the optimal number to age from (8.21c), and the minimum cost from (8.21a) are calculated. Application of this approach to three fish stocks determined sample size requirements and led to a recommendation that proportional allocation was better than fixed allocation for these stocks (Lai 1987).

Sample size determination to optimize survey design with cost information was also considered by Schweigert and Sibert (1983, 1984) with a comment by Smith (1984). In their situation, the focus is on combining estimates of age composition among multiple loads and samples.

A Bayesian approach can be used to determine optimal sample size (Jinn et al. 1987). The goal is to select values for the A_l and for L to minimize V for a fixed cost C . The Bayesian method leads to the appropriate allocation rather than being restricted to fixed and proportional allocation. The algorithm is a complicated search algorithm, but a computer program is available.

Deciding whether two-stage sampling is preferred over simple random sampling has been considered by Cochran (1977) in general and by Smith (1989) for estimating age composition. Smith compared the performance of the two sampling strategies for different criteria and showed that the preferred approach depends on the ultimate use of the data. Kimura (1989a) determined the effect of sample size on estimates of abundance from cohort analysis (section 8.2).

Example 8.4. Hauraki Gulf snapper, New Zealand

The sampling for example 8.3 was conducted according to a two-stage design with fixed allocation (Davies et al. 1993). Sample size recommendations are now obtained for fixed and proportional allocation schemes. The within- and between- variance components using (8.16a-c) are given in table 8.5. These are used to calculate total age sample sizes A needed to achieve two levels of CV (0.1, 0.25) for particular ages for three different length sample sizes L (1000, 2500, 5000) for the two allocations, as shown in table 8.6, using (8.18a). For example, to achieve a CV of no more than 0.25 for age 6 under fixed allocation, at least 348 ages are needed for a length sample of 2500 fish. Because there are 39 length intervals, approximately 9 otoliths per length interval would be needed. There is not much difference in age sample size as the length sample size increases. To achieve a CV of 0.1 for at least one age, at least 367 ages would be needed under proportional allocation, 873 under fixed. To achieve a CV of 0.25 for important ages of the catch (arbitrarily defined as having age composition greater than 2.5%), at least 549 ages would be needed under proportional allocation, 902 under fixed. Under these criteria, proportional allocation is clearly superior to fixed.

The minimum number of fish to collect where all would be aged ($A = L$), derived from (8.18b), is given in table 8.7 for the two levels of CV under proportional allocation. To achieve a CV of 0.1 for at least one age, a minimum of 516 fish should be collected; to achieve a CV of 0.25 for important ages of the catch, at least 563 should be collected.

As an alternative criterion, D is calculated using (8.19b) for proportional allocation for different age and length sample sizes (table 8.8). Similar calculations for fixed allocation (not shown) produce higher values of D , which again suggests the superiority of proportional allocation. To achieve a D of no more than 0.05, about 300 ages would be needed; for a D of 0.04, about 500 ages would be needed. The actual sample collected in 1992–93 had a subsample of $A = 808$ under fixed allocation and achieved a value of D of 0.0409 (table 8.4). Thus, the same precision could be obtained under proportional allocation with a subsample of 300 fewer otoliths. A plot of D versus age for the three values of length shows very small gain in increasing length sample size beyond 1000 (figure 8.2). The values of D are approximately proportional to $1/\sqrt{A}$.

One possible criterion using D is the slope of the D -age curve in figure 8.2. For

Table 8.5. Variance components for estimating sample size, Hauraki Gulf snapper, 1992–93.

Age, a	V_a	F_a	B_a
3	0.00029	0.00007	0.00002
4	0.01504	0.02268	0.00581
5	0.07424	0.17648	0.06182
6	0.07199	0.18463	0.01201
7	0.10647	0.25826	0.02330
8	0.10454	0.24618	0.02018
9	0.09395	0.16936	0.01620
10	0.01242	0.01883	0.00066
11	0.02541	0.04177	0.00148
12	0.05642	0.05304	0.01405
13	0.02585	0.01751	0.00302
14	0.02827	0.01893	0.00384
15	0.01462	0.00759	0.00128
16+	0.04816	0.02730	0.04319
Sum	0.67766 (p_1)	1.24260 (f_1)	0.20687 ($p_2 = f_2$)

example, one could find where on the curve the slope decreases to say, 2.5%, of the slope at the beginning. This could be measured empirically by taking the tangent between $A = 25$ and $A = 50$ as the beginning and using increments of 25 to calculate successive slopes. These empirical slope calculations for proportional allocation are shown in table 8.8 for $L = 1000$. Using the upper end of the interval for the recommendation, the recommended age sample size A using the slope criterion is 425 with a corresponding D of 0.042. Considering the overall results, proportional allocation is superior to fixed, length sample sizes in excess of 1000 do not improve precision much at all, and an age sample size in the range of 400 to 600 is needed to meet various sampling criteria.

Net cost data permit the determination of optimal length and age sample sizes using (8.20a–c) and (8.21a–e) and previously calculated summed variance components from table 8.5. The net cost c_1 of collecting and measuring snapper is about NZ\$2700/6725 fish and the net cost c_2 of aging is about NZ\$7000/800 otoliths (N. Davies, personal communication, 1993). To minimize cost for selected values of D , the appropriate calculations are shown in table 8.9. For example, to obtain a D of 0.04, $L = 1222$ and $A = 474$ for proportional allocation, and $L = 1609$ and $A = 845$ for fixed allocation. For any value of D , proportional allocation is superior to fixed. ■

8.1.6. Separate Length and Age Samples and Other Approaches

Subsampling data for age are frequently not available, but there is often the need to apply age-length keys to length frequency data to obtain age composition estimates. Using the two-stage formulae in section 8.1.4 with separate length and age samples results in biased estimates (Kimura 1977, Westheim and Ricker 1978, Clark 1981).

To see this, consider the two-stage sampling design of section 8.1.4, wherein a random sample of length frequencies $\{L_l\}$ and a random subsample of age frequencies within each length category $\{A_{la}\}$ are obtained. The parameters estimated from this sampling design are age composition proportions $\{\theta_a = C_a/C\}$, length composition

Table 8.6. Age sample sizes, A , needed to achieve particular values of the CV for a particular age, and summary age sample sizes achieving a CV of 0.1 for at least one age and a CV of 0.25 for important ages ($> 2.5\%$ of the catch).

Age	Objective: CV = 0.1			Objective: CV = 0.25		
	<i>L</i>			<i>L</i>		
	1000	2500	5000	1000	2500	5000
Proportional allocation						
3	-20367	-56456	-137922	-31020	-1175745	104039
4	-11810	6793	4454	667	577	553
5	367	310	295	47	46	45
6	977	890	864	138	136	135
7	503	472	462	74	73	73
8	541	509	499	80	79	79
9	659	617	604	96	95	95
10	11341	8322	7643	1203	1159	1145
11	4121	3602	3457	549	538	535
12	1278	1073	1018	161	158	156
13	4431	3380	3133	494	477	472
14	3931	2978	2755	434	420	415
15	10985	6961	6203	971	924	909
16+	800	559	508	80	77	76
To achieve CV of 0.1 for at least one age						
	367	310	295			
To achieve CV of 0.25 for ages with at least 2.5% of catch						
				549	538	535
Fixed allocation						
3	-4843	-13426	-32799	-7377	-279600	24741
4	-17812	10245	6718	1006	871	834
5	873	738	702	111	109	108
6	2506	2283	2217	353	348	346
7	1221	1145	1122	179	177	176
8	1274	1199	1176	187	186	185
9	1187	1111	1088	173	172	171
10	17202	12622	11593	1825	1758	1736
11	6775	5922	5683	902	885	880
12	1201	1009	957	152	148	147
13	3001	2290	2122	335	323	320
14	2633	1995	1845	291	281	278
15	5698	3611	3218	504	479	472
16+	453	317	288	45	43	43
To achieve CV of 0.1 for at least one age						
	873	738	702			
To achieve CV of 0.25 for ages with at least 2.5% of catch						
				902	885	880

Negative numbers indicate that sample size is too large to be determined.

Table 8.7. Minimum number of fish to collect ($A = L$) to achieve a CV value at a particular age for Hauraki Gulf snapper using proportional allocation.

Age	CV	
	0.25	0.1
3	52421	327633
4	735	4594
5	82	516
6	157	980
7	88	552
8	94	585
9	111	693
10	1191	7444
11	563	3517
12	194	1211
13	522	3260
14	466	2911
15	974	6085
16+	141	883

To achieve CV of 0.1 for at least one age	516
To achieve CV of 0.25 for ages > 2.5% of catch	563

proportions $\{\alpha_l = C_l/C\}$, and age composition proportions within length category $\{\theta_{la} = C_{la}/C_a\}$. It then follows that the age proportions can be obtained from the relationship $\theta_a = \sum_l \alpha_l \theta_{la}$.

Alternatively, the proportions $\{\psi_{la} = C_{la}/C_a\}$ in the length categories l for each age class a can be examined. Note that ψ_{la} can be written as

$$\psi_{la} = \frac{\frac{C_l}{C} \frac{C_{la}}{C_l}}{\frac{C_a}{C}} = \frac{\alpha_l \theta_{la}}{\theta_a}.$$

Thus, the relationship between θ_{la} and ψ_{la} is

$$\theta_{la} = \frac{\psi_{la}}{\alpha_l} \theta_a,$$

which shows that θ_{la} is a function of age composition θ_a . It is estimated from the information in the age-length key ($\widehat{\theta}_{la} = A_{la}/A_l$). Therefore, one cannot blithely apply the age-length key to any other sample; such an approach would tend to reproduce the age composition from the sample from which it was collected.

For later use below, the length proportions can be written as

$$\alpha_l = \sum_a \frac{C_{la}}{C_a} \frac{C_a}{C} = \sum_a \psi_{la} \theta_a.$$

Table 8.8. Values of D as a function of age and length sample sizes (A and L) and calculations of the slope for $L = 1000$, Hauraki Gulf snapper.

A	L			Slope ($L = 1000$) ($\times 10^6$)
	500	1000	2500	
25	0.166	0.165	0.165	1919 ^a
50	0.118	0.117	0.117	847
75	0.097	0.096	0.095	503
100	0.085	0.084	0.083	342
125	0.076	0.075	0.074	251
150	0.070	0.069	0.068	195
175	0.065	0.064	0.063	156
200	0.062	0.060	0.059	129
225	0.059	0.057	0.056	109
250	0.056	0.054	0.053	93
275	0.054	0.052	0.050	81
300	0.052	0.050	0.048	71
325	0.050	0.048	0.047	63
350	0.048	0.046	0.045	57
375	0.047	0.045	0.043	51
400	0.046	0.044	0.042	46
425	0.045	0.042	0.041	42
450	0.044	0.041	0.040	39
475	0.043	0.040	0.039	36
500	0.042	0.040	0.038	33
525	0.039	0.037	0.037	31
550	0.038	0.036	0.036	29
575	0.037	0.036	0.036	27
600	0.037	0.035	0.035	25
625	0.036	0.034	0.034	23
650	0.035	0.034	0.034	22
675	0.035	0.033	0.033	21
700	0.034	0.032	0.032	20
725	0.034	0.032	0.032	19
750	0.033	0.031	0.031	18
775	0.033	0.031	0.031	17
800	0.032	0.030	0.030	16
825	0.032	0.030	0.030	15
850	0.032	0.030	0.030	14
875	0.031	0.029	0.029	14
900	0.031	0.029	0.029	13
925	0.031	0.029	0.029	13
950	0.030	0.028	0.028	12
975	0.030	0.028	0.028	12
1000	0.030	0.028	0.028	

^aThe 2.5% criterion is $1919 \times 2.5\% = 48$.

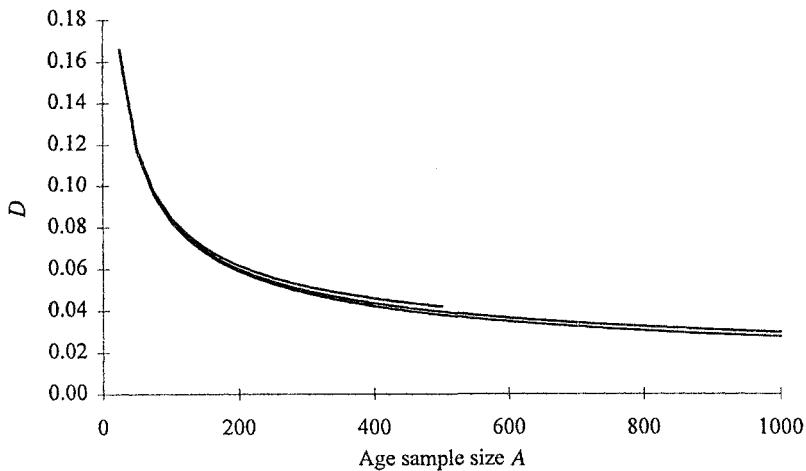


Figure 8.2. Level of imprecision measured by variable D for snapper in the Hauraki Gulf as a function of age sample size A for three values of L (1000, 2500, 5000). The three curves are virtually indistinguishable.

Table 8.9. Optimal allocation calculations using net cost data and variance components under fixed and proportional allocations, Hauraki Gulf snapper.

	c_1	\$0.40
	c_2	\$8.75
	c_1/c_2	0.0459
<hr/>		
	Proportional	
p_1	0.6777	f_1 1.2426
p_2	0.2069	f_2 0.2069
p_1/p_2	3.2758	f_1/f_2 6.0067
r^*	0.3877	r^* 0.5250

D	L	A	$\min C$	L	A	$\min C$
0.050	782	303	\$2,966	1030	540	\$5,143
0.049	814	316	\$3,089	1072	563	\$5,355
0.048	848	329	\$3,219	1117	586	\$5,580
0.047	885	343	\$3,357	1165	612	\$5,820
0.046	924	358	\$3,505	1216	639	\$6,076
0.045	965	374	\$3,662	1271	667	\$6,349
0.044	1010	391	\$3,831	1329	698	\$6,641
0.043	1057	410	\$4,011	1392	731	\$6,953
0.042	1108	430	\$4,204	1459	766	\$7,288
0.041	1163	451	\$4,412	1531	804	\$7,648
0.040	1222	474	\$4,635	1609	845	\$8,035

For various values of D , the values of L and A are found that minimize net cost, C .

Thus, the length distribution is a mixture of length-at-age distributions weighted by age composition, as shown previously in section 8.1.1.

Suppose now that a second random sample has been collected from a possibly new population with a different length frequency distribution $\{L_l^*\}$. The question to be addressed is whether the age composition $\{\theta_a^*\}$ can be estimated. The answer is yes if it can be assumed that ψ_{la} is constant for the two populations. Four procedures for doing so are given by Clark (1981) and Bartoo and Parker (1983) using least squares methods, and by Kimura and Chikuni (1987) and Hoenig and Heisey (1987) using an iterative method further described below.

In the method by Bartoo and Parker (1983), the first step is to estimate ψ_{la} as

$$\widehat{\psi}_{la} = \widehat{\alpha}_l \widehat{\theta}_{la} / \widehat{\theta}_a$$

by using the estimates from section 8.1.4. Then the true length frequency proportions for the second sample can be written as

$$\alpha_l^* = \sum_a \psi_{la} \theta_a^*,$$

or in vector/matrix notation as

$$\boldsymbol{\alpha}_{(J \times 1)}^* = \boldsymbol{\psi}_{(J \times A')} \boldsymbol{\theta}_{(A' \times 1)}^*,$$

where J is the number of length categories, $A' = A - r + 1$ is the number of age classes, and the subscript denotes the size of the vector or matrix. This latter system of J equations in A' unknowns can be solved by linear least squares if $J > A'$, which results in the age composition estimates

$$\boldsymbol{\theta}^* = (\boldsymbol{\psi}' \boldsymbol{\psi})^{-1} (\boldsymbol{\psi}' \boldsymbol{\alpha}^*),$$

with variance estimates from the standard general linear theory. A further refinement by Bartoo and Parker is to assume that mean lengths at age follow an LVB curve (chapter 4 and section 8.1.1). They showed that unbiased parameter estimates are obtained by allowing growth to be stochastic.

As pointed out by Clark (1981), the principal problems with this procedure are that estimates may not be between 0 and 1, and their sum may not add to 1. Clark recommended restricted least squares with the constraints $0 \leq \theta_a^* \leq 1$ and $\sum_a \theta_a^* = 1$.

In the method of Kimura and Chikuni (1987), which they called the iterated age-length key (IALK) approach, similar equations are solved using maximum likelihood estimates with the E-M (expectation-maximization) algorithm of Dempster et al. (1977); a detailed algorithm for calculating estimates is found therein. This approach assumes no sampling errors in the first sample, which is approximately true as long as a large sample is taken. Hoenig and Heisey (1987) also applied the iterative E-M algorithm and allowed for error in the first sample. They showed that the same procedure is applicable to stock composition problems and to adjusting for aging errors. Both algorithms are easy to apply and can be done within a spreadsheet. With the use of a hybrid age- and length-structured model, Mesnil and Shepherd (1990) found that the iterative method was preferable to the least squares method.

Among other approaches for analyzing age composition, Martin and Cook (1990) developed a likelihood procedure for combined analysis of length frequency data and age-length data. This procedure combines the multinomial likelihood (8.3) and normality assumption (8.2) from LFA (section 8.1.1) with multinomial likelihoods for the age-length distributions. A maximum likelihood procedure for estimating age composition from length-age data and scale or otolith measurements was developed by Smith (1987). An approach by Boehlert (1985) established predictive relationships for aging fish based on otolith measurements (section 4.6), which can be undertaken without considering the sampling design.

8.2. ESTIMATION OF ABUNDANCE AND POPULATION PARAMETERS

One of the most important approaches for estimating abundance and other population parameters is the analysis of catch-age data. As documented in Ricker (1975a), early approaches date back to the 1910s in Russia with some variants appearing into the 1960s. At that point, virtual population analysis and cohort analysis became widely used until the 1980s, when statistical methods and tuning methods to auxiliary data became prominent. The value of having age-structured data is that year-classes can be traced throughout their lives in the data, as long as methods can separate the confounding factors of fishing, natural death, migration and movement, and catchability. Megrey (1989) provided a comprehensive review of catch-age methods for estimating abundance and their underlying assumptions. These methods are also referred to as age-structured analysis, sequential population analysis, integrated analysis, and synthetic analysis. We agree with Kimura (1990) that these methods come from a common family of approaches linked by consideration of statistical principles and a flexible model-building technology.

8.2.1. General Catch-Age Relationship

The approach used here is to present a general catch-age relationship for a single year-class that will be used to derive catch curve analysis, virtual population analysis, and cohort analysis. As before, let r be the first age for which data are available; A be the last age for which data are available; and $A' = A - r + 1$, the number of ages for which data are available. Age r provides a reference age for year-class strength; if the year-class were age r in year t , then the year-class is labeled $t - r$. Furthermore, let

$$\begin{aligned}
 N_a &= \text{abundance at the start of age } a, \\
 W_a &= \text{average weight at age } a, \\
 B_a &= N_a W_a = \text{biomass at age } a, \\
 M_a &= \text{natural mortality at age } a, \\
 F_a &= \text{fishing mortality at age } a, \\
 C_a &= \text{catch at age } a, \\
 Z_a &= M_a + F_a = \text{total mortality at age } a, \\
 S_a &= \exp(-Z_a) = \text{survival at age } a, \text{ and} \\
 \mu_a &= C_a / N_a = \text{exploitation fraction at age } a.
 \end{aligned} \tag{8.22}$$

As shown in section 1.2, population abundances for successive ages are calculated according to the recursive relationship

$$N_a = N_{a-1} e^{-Z_{a-1}} = N_{a-1} S_{a-1}, \quad a = r + 1, \dots, A, \quad (8.23)$$

which can be written as a function of N_r as

$$N_a = N_r \exp\left(-\sum_{x=r}^{a-1} Z_x\right). \quad (8.24)$$

Substituting the Baranov catch equation (1.22) with age subscripts into (8.24), the general catch-age relationship is then

$$C_a = \frac{F_a}{Z_a} (1 - e^{-Z_a}) N_a = \mu_a N_a \quad (8.25)$$

$$= \frac{F_a}{Z_a} (1 - e^{-Z_a}) N_r \exp\left(-\sum_{x=r}^{a-1} Z_x\right). \quad (8.26)$$

The ratio of successive catches of the same year-class from (8.26) is

$$\frac{C_{a+1}}{C_a} = \frac{(F_{a+1}/Z_{a+1})(1 - e^{-Z_{a+1}})}{(F_a/Z_a)(1 - e^{-Z_a})} e^{-Z_a} = \frac{\mu_{a+1}}{\mu_a} S_a, \quad (8.27)$$

showing that the catch ratio is a function of four parameters for fishing and natural mortality in the two years. Even if natural mortality is assumed known, it is not possible to estimate the two fishing mortality parameters from the one observation of the catch ratio.

If $F_{a+1} = F_a$ and $M_{a+1} = M_a$, then $\mu_a = \mu_{a+1}$ from (8.25). Then, (8.27) reduces to

$$\frac{C_{a+1}}{C_a} = e^{-Z_a} = S_a \quad (8.28)$$

showing that if conditions are constant, then C_{a+1}/C_a estimates survival S_a , and from (8.22), $-\ln(C_{a+1}/C_a)$ estimates total mortality Z_a .

The approximation (8.28) is not very accurate when F and M are not constant. Table 8.10 shows the effect on the catch ratio calculated from (8.27) of varying F_{a+1} and M_{a+1} for default values $F_a = 0.2$ and $M_a = 0.2$. For these default values, S_a is 0.670 from (8.22) and would be the approximation for the catch ratio, as in (8.28). The actual catch ratio varies from 0.335 to 1.005, as F_{a+1} and M_{a+1} vary from 0.1 to 0.3. Fishing mortality, F_{a+1} , has a much greater effect than natural mortality, M_{a+1} .

Table 8.10. The ratio of catches of successive years of the same year-class from (8.27) for various combinations of F and M in the second year ($a+1$), compared to survival for default values of F and M in the first year (a) of 0.2.^a

F_{a+1}	C_{a+1} / C_a from (8.27)				
	M_{a+1}				
	0.10	0.15	0.20	0.25	0.30
0.10	0.369	0.360	0.351	0.343	0.335
0.15	0.540	0.527	0.515	0.503	0.491
0.20	0.703	0.686	0.670	0.655	0.640
0.25	0.858	0.838	0.819	0.800	0.782
0.30	1.005	0.982	0.960	0.938	0.917

^a $M_a = 0.2$; $F_a = 0.2$; S_a from (8.22) = 0.670; μ_a from (8.25) = 0.165.

Example 8.5. Pacific halibut in the northeast Pacific

In practice, conditions do vary substantially between years, and, as a result, estimates of survival and mortality from (8.28) can be extremely variable and inconsistent. Table 8.11 presents commercial catch-age data from longline vessels for the 1960 year-class of Pacific halibut (*Hippoglossus stenolepis*) aged 8–20. Natural mortality, $M_a = M$, is assumed constant at 0.2 (Quinn et al. 1985). Using the approximation (8.28), estimates of survival, S_a , total mortality, $Z_a = -\ln S_a$, and fishing mortality, $F_a = Z_a - M$ can be calculated for ages 8–19. The wide ranges of the estimates for survival and mortality suggest that the estimates are too variable to be of much use, and unrealistic estimates of survival > 1 and mortality < 0 are produced. Pacific halibut gear is thought to be fully selective for ages 15 and older (Quinn et al. 1985), so one might expect that estimates for older ages might be less variable. However, this does not occur, as the breakdowns by ages 8–14 and 15–19 have about the same ranges of variability. In fact, older ages are less well represented in the catch, and CVs for catch at older ages are substantially higher (Quinn et al. 1985).

In contrast, fishing mortality estimates from catch-age analysis, described in section 8.2.5, are far less variable (table 8.11), and for purposes of this comparison, will be treated as close to the unknown, true values. The average fishing mortality by the two age groups is lower using approximation (8.28) than using catch-age analysis, suggesting that the approximation produces biased estimates in this example. This result is in accord with the example in table 8.10, which shows that biased estimates can occur if fishing mortality between the two successive ages is not constant. For example, the CAGEAN estimate of fishing mortality drops from 0.20 at age 13 to 0.15 at age 14. Table 8.10 suggests that survival at age 13 would be underestimated for $F_{a+1} = 0.15$ and $M = 0.2$. Consequently, fishing mortality at age 13 would be overestimated, which is what is observed in this case (0.58 versus 0.2). Overall, these results indicate that approximation (8.28) should be avoided. ■

8.2.2. Catch Curve Analysis

Suppose that beyond age f survival is constant, or $S_a = S$. Then from (8.23), abundance can be written

$$N_{f+x} = N_f S^x. \quad (8.29)$$

If μ is the probability of catching a fish, or equivalently the expected exploitation fraction, assume that catch C_{f+x} is lognormally distributed with median catch, μN_{f+x} , or

$$\text{med}(C_{f+x}) = \mu N_{f+x} = \mu N_f S^x.$$

The logarithm of catch is then normally distributed with mean

$$E(\ln C_{f+x}) = \ln(\mu N_{f+x}) = \ln(\mu N_f) + x \ln S.$$

Making the substitutions $Z = -\ln S$ and $x = a - f$,

$$E(\ln C_a) = [\ln(\mu N_f) + fZ] - Za, \quad (8.30)$$

which is of the form of a linear regression of $\ln C_a$ versus a . The estimate \widehat{Z} is the negative of the slope estimated from the linear regression, and its standard error, SE_z , is

Table 8.11. Catch data from the 1960 year-class of Pacific halibut, estimates of S_a , Z_a , and F_a using approximation (8.28), and estimates of F_a using catch-age analysis (CAGEAN) ($M = 0.2$).

a	C_a	S_a	Z_a	F_a	F_a
				from (8.28)	from CAGEAN
8	169887	1.18	-0.17	-0.37	0.09
9	201074	0.89	0.12	-0.08	0.16
10	179187	0.69	0.38	0.18	0.21
11	122785	0.73	0.32	0.12	0.21
12	89241	0.65	0.43	0.23	0.21
13	58111	0.46	0.78	0.58	0.20
14	26682	0.87	0.13	-0.07	0.15
15	23339	0.63	0.46	0.26	0.21
16	14668	0.69	0.38	0.18	0.20
17	10050	0.58	0.54	0.34	0.15
18	5866	0.53	0.63	0.43	0.12
19	3121	1.55	-0.44	-0.64	0.12
20	4837				0.13
Ages 8–19					
Min		0.46	-0.44	-0.64	0.09
Max		1.55	0.78	0.58	0.21
Average		0.79	0.30	0.10	0.17
Ages 8–14					
Min		0.46	-0.17	-0.37	0.09
Max		1.18	0.78	0.58	0.21
Average		0.78	0.28	0.08	0.18
Ages 15–19					
Min		0.53	-0.44	-0.64	0.12
Max		1.55	0.63	0.43	0.21
Average		0.80	0.31	0.11	0.16

equal to the SE of the slope. The corresponding estimates of S and its SE are $\hat{S} = \exp(\hat{Z})$ and $SE_S = \hat{S}(SE_z)$ (from the delta method), respectively (Seber 1982, section 10.3.2).

A plot of $\ln C_a$ versus a is called a catch curve. Typical plots of catch curves show an increasing section of the curve for younger ages, which is usually a consequence of increasing selectivity of the gear and/or availability of fish. A decreasing section of the curve for older ages follows, which is usually due to mortality.

One important consideration of catch curve analysis is which ages to use in the regression. Frequently this decision is made in an ad hoc way by plotting the catch curve and choosing the ages which appear to show a linear decrease. A statistical method for choosing the age range is given by Seber (1982, section 10.3).

Example 8.6. Pacific halibut in the northeast Pacific

The catch curve for the Pacific halibut data from example 8.5 (table 8.11) has a short left section and a broad right section (figure 8.3). Using data for ages 10–20, linear

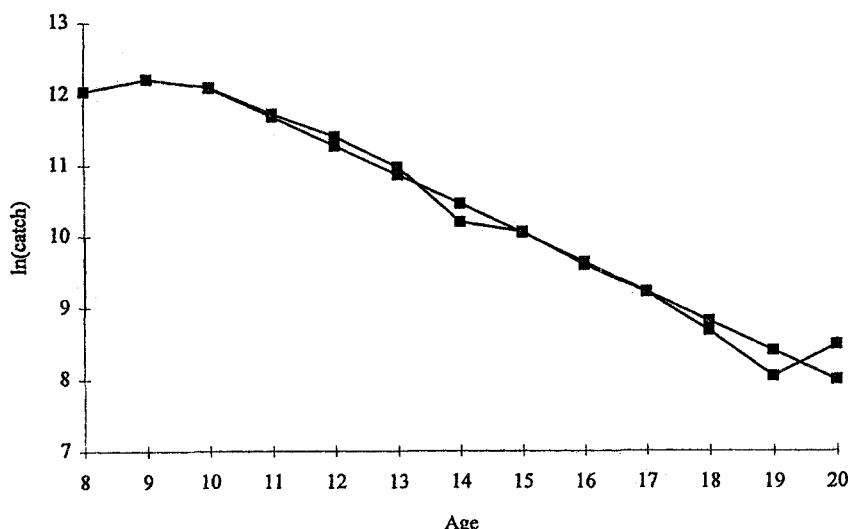


Figure 8.3. Observed and predicted catch curves for the 1960 year class of Pacific halibut in the northeastern Pacific Ocean.

regression of $\ln C_a$ versus a results in an estimated slope of $-\widehat{Z} = -0.409$ with SE 0.022 and a 95% confidence interval for Z of (0.359, 0.459). Hence, estimated survival is $\widehat{S} = 0.664$ with SE of 0.147 and a 95% confidence interval for S of (0.632, 0.698). The regression has an R^2 of 97% and a residual root mean square of 0.235, indicating a good fit to the data. The predicted straight line appears to fit the data well (figure 8.3).

The average fishing mortality, \bar{F} , for ages 10–20 from catch-age analysis from table 8.11 is 0.174, so that average total mortality is $\bar{Z} = \bar{F} + M = 0.374$. That this value is contained in the 95% confidence interval from catch curve analysis is an indication that catch curve analysis provides reasonable estimates of survival and mortality for this example. ■

Quite often, catch curve analysis is applied to a single year of data rather than to data from a single year-class; the resulting data set is sometimes said to be from a “synthetic” cohort. To obtain an unbiased estimate of total mortality, the two assumptions of constant recruitment and constant survival at age over time must be satisfied.

Seber (1982, section 10.3) summarized the estimation methods when a simple random sample is taken. Among the estimators are a maximum likelihood estimator (MLE) and one from a “simple” method by Ssentongo and Larkin (1973). One simulation study suggests that the regression method is the most precise of the three in most cases, but the MLE is better if variation is high (Jensen 1985). On first principles, the MLE should be used only if a simple random sample is taken and is sensitive to departures from that assumption. Generally, samples from fisheries are not simple random samples (Doubleday and Rivard 1983, Quinn et al. 1983a). The regression estimator is robust to the sampling procedure used, but its variance is inversely related to the number of ages used. If the gear is not fully selective for many ages, this method may perform poorly.

When using data from a single year, nonconstant survival frequently shows up in

the catch curve as variation about the straight line or as curvilinearity. Fluctuations in recruitment about a constant value also produce variation in the catch curve (Ricker 1975a). Curvilinearity can also occur when subpopulations have different mortalities (Jensen 1984b).

However, the appearance of a straight line with low variation past some age should not be construed as support for the assumptions of constant recruitment and survival (Ricker 1975a). Indeed, an exponential time trend in abundance, either negative or positive, will affect the slope of the catch curve directly. If recruitment over time decreases exponentially such that

$$N_{rt} = N_r^* e^{\nu t}, \quad \nu < 0,$$

then the slope of the catch curve becomes $Z + \nu$, which is $< Z$. Hence, decreasing recruitment leads to underestimation of mortality and the perception that mortality is not as great as it really is. Conversely, exponentially increasing recruitment ($\nu > 0$) causes overestimation of Z . Thus, catch curve analysis applied to data from a single year can be a dangerous procedure that should be used only if one knows that no trend in recruitment has been present.

Example 8.7. Hypothetical population with decreasing recruitment

Suppose that a population has constant survival over time, $S_4 = 0.5$ at age 4 and $S_x = 0.67$ ($Z = 0.4$) at ages 5–8. The lower survival at age 4 is used to show that partial recruitment at early ages has no effect on the catch curve results, as long as it is constant over time. Recruitment decreases exponentially with instantaneous parameter $\nu = -0.1$. Table 8.12 shows the abundance and log abundance over time at each age, with each cohort represented as one diagonal of the abundance (or log abundance) table.

With the use of fully recruited ages 5 and older and data from any one year, the negative of the slope is always 0.3 ($Z + \nu$), which can be seen by taking the differences in log abundance between any two successive ages in a given year. In contrast, the negative of the slope for two successive fully recruited ages of a particular cohort is 0.4 (Z),

Table 8.12. Hypothetical population with $S_4 = 0.5$ and $S_x = 0.67$ ($Z_x = 0.4$) for ages $x = 5–8$.

Age, a	Year, t					
	1	2	3	4	5	6
$N_{a,t}$	4	2000	1810	1637	1482	1341
	5		1000	905	819	741
	6			670	607	549
	7				449	407
	8					301
	9					202
$\ln N_{a,t}$	4	7.60	7.50	7.40	7.30	7.20
	5		6.91	6.81	6.71	6.61
	6			6.51	6.41	6.31
	7				6.11	6.01
	8					5.71
	9					5.31

Recruitment decreases exponentially with instantaneous parameter ν (-0.1). Abundances and corresponding logarithms are shown for a starting recruitment of 2000.

which can be observed as the difference in log abundance of two successive ages on the diagonal. Thus, application of catch-curve analysis would produce an underestimate, \widehat{Z} , of 0.3 rather than the true Z of 0.4 in the face of declining recruitment. Worse yet, the catch curve is a straight line for ages 5 and older, suggesting no violation of the underlying assumptions. These results suggest that catch curve analysis with data from a single year should be avoided if possible. ■

8.2.3. Virtual Population Analysis and Cohort Analysis

A virtual population is a population as it would be if it did not experience natural mortality (Fry 1949). By assuming that catch is measured without error, the virtual population at each age is obtained by subtracting the catch from the virtual population at the previous age, or $V_{a+1} = V_a - C_a$. A back-calculation procedure can be used to obtain the virtual population. Starting at age A , the terminal abundance is the final catch, or $V_A = C_A$. Going backward,

$$V_a = V_{a+1} + C_a, \quad a = A - 1, \dots, r. \quad (8.31)$$

The closed form solution to this recursive equation is

$$V_a = \sum_{x=a}^A C_x. \quad (8.32)$$

The virtual population is the minimum population size possible because losses due to natural causes are ignored. As a result, the ratio of two successive ages of a virtual population would underestimate survival and overestimate mortality.

Gulland (1965), in a much-cited, gray-literature ICES mimeo, developed an approach to correct the virtual population approach for natural mortality. This approach assumes that M and F_A are known and that catches are measured without error. Gulland used a constant natural mortality, M , but the generalization to M_a is straightforward and is presented below. Starting at the oldest age, A , the Baranov equation in (8.25) is inverted to estimate terminal abundance

$$N_A = \frac{C_A}{\frac{F_A}{Z_A} (1 - e^{-Z_A})}, \quad (8.33)$$

where $Z_A = M_A + F_A$. For the other ages, the two equations from (8.25) and (8.23)

$$\begin{aligned} C_a &= N_a \frac{F_a}{Z_a} (1 - e^{-Z_a}) \\ N_{a+1} &= N_a e^{-Z_a} \end{aligned}$$

can be divided to obtain

$$\frac{C_a}{N_{a+1}} = \frac{F_a}{Z_a} (e^{Z_a} - 1). \quad (8.34)$$

For $a = A - 1$, (8.34) is a function of known quantities, N_A , C_{A-1} , and M_{A-1} , and one unknown quantity, F_{A-1} . Hence this equation can be solved numerically for F_{A-1} .

The inverted Baranov catch equation (8.33) with A replaced by $A - 1$ then provides N_{A-1} . This process is repeated back to age r .

Gulland (1965) wrote his paper in the context of virtual population analysis (VPA) and derived the relationship between his method and VPA. To maintain historical consistency, we continue the dubious convention of referring to his method and its variants as VPA methods, although nothing in the approach requires the use of a virtual population. Megrey (1989) suggested calling it Gulland's sequential population analysis, but familiarity with the term VPA may be difficult to overcome. Other VPA-type procedures are described in Megrey (1989). The major limitation to the VPA methods is the need to solve the nonlinear equation (8.34).

Cohort analysis, an approximation to VPA, was developed by Pope (1972), which makes use of the approximation

$$\frac{1 - e^{-x}}{x} \approx e^{-x/2}. \quad (8.35)$$

This presentation is a generalization of Pope's, which used constant natural mortality, M . Equation (8.23) is rewritten

$$\begin{aligned} N_{a+1}e^{M_a} &= N_a e^{-F_a} = N_a - N_a(1 - e^{-F_a}) \\ &= N_a - C_a \frac{Z_a(1 - e^{-F_a})}{F_a(1 - e^{-Z_a})} \quad \text{using (8.25)} \\ &\approx N_a - C_a \frac{e^{-F_a/2}}{e^{-Z_a/2}} \quad \text{using (8.35)} \\ &= N_a - C_a e^{M_a/2}. \end{aligned} \quad (8.36)$$

Pope showed that the error in this approximation was less than 4% if $M_a < 0.3$ and $F_a < 1.2$. Further modification of (8.36) results in the "forward" equation

$$N_{a+1} = N_a e^{-M_a} - C_a e^{-M_a/2} = (N_a e^{-M_a/2} - C_a) e^{-M_a/2}. \quad (8.37)$$

Writing (8.36) or (8.37) in terms of N_a results in the "backward" equation

$$N_a = N_{a+1}e^{M_a} + C_a e^{M_a/2}. \quad (8.38)$$

This equation provides a backward recursive system for obtaining abundance at age. The equations are exact if catch is taken exactly halfway through the year.

The approach starts out the same way as VPA using (8.33) to obtain terminal abundance, but (8.38) is used to obtain all N_a for $a = A - 1, \dots, r$. Fishing mortality is calculated from

$$F_a = -\ln(N_{a+1}/N_a) - M_a. \quad (8.39)$$

[Because N_a refers to abundance at the start of age a , it is possible to obtain N_{A+1} from the basic survival equation (8.23) as $N_{A+1} = N_A \exp(-Z_A)$ if desired.]

Two alternative formulations have been used to calculate terminal abundance in lieu of (8.33). The first treats terminal abundance N_{A+} as a plus group for all ages A and older, denoted $A+$. It is assumed that fishing mortality and natural mortality are

constant for these ages. The pooled catch for the plus group, denoted C_{A+} , is the sum of all catches of a year-class in subsequent years starting at age A . The Baranov catch equation (1.22) applies to this situation and can be written

$$C_{A+} = N_{A+} \frac{F_{A+}}{Z_{A+}} \left(1 - e^{-Z_{A+\tau}}\right),$$

where τ is the number of years represented by the plus group. Terminal abundance can be calculated from

$$N_{A+} = \frac{C_{A+} Z_{A+}}{F_{A+} (1 - e^{-Z_{A+\tau}})}, \quad (8.40a)$$

or if $\tau \rightarrow \infty$, from

$$N_{A+} = \frac{C_{A+} Z_{A+}}{F_{A+}}. \quad (8.40b)$$

Strictly speaking, this alternative has limited use, because it requires precise determination of the oldest ages and a long period of time to track a year-class to its final dissolution. This approach is not valid for catch data pooled over several ages in a single year, because then several year-classes would be represented.

The second alternative is to use one greater than the oldest age in the data, ($A + 1$). Terminal abundance from Ricker (1975a) is

$$N_{A+1} = \frac{C_A e^{M_A/2 - Z_A}}{1 - e^{M_A - Z_A}} = \frac{C_A e^{M_A/2}}{1 - e^{-F_A}} e^{-Z_A}, \quad (8.41)$$

which was obtained by combining (8.23) and (8.38). The first term on the far right-hand side of the equation divides catch by the conditional mortality from fishing and adjusts from the midpoint of the year to the beginning. The second term is survival from the beginning to the next year, corresponding to age $A + 1$. This alternative has the advantage of projecting the year-class one more year, as does (8.34), but it has the disadvantage of errors due to the cohort approximation used in (8.38).

Estimates of variation are not directly obtainable from VPA or cohort analysis because there are A' observations of a year-class but at least $A' + 2$ parameters ($\{F_a\}$, N_r , and at least one M) to be determined. However, if auxiliary estimates of the SEs of catch, terminal fishing mortality, and natural mortality [denoted $SE(C_A)$, $SE(F_A)$, and $SE(M_A)$] and their covariances are available, it is possible to derive estimates of variance and covariance of abundance and fishing mortality estimates [see Sailya et al. (1985) for cohort analysis, Sampson (1987) for VPA]. This presentation shows the appropriate computations for cohort analysis when only variation in catch, such as obtained in section 8.1, is available. From the terminal abundance equation (8.33), the squared SE of terminal abundance is

$$SE^2(N_A) = \frac{SE^2(C_A)}{\left[\frac{F_A}{Z_A} \left(1 - e^{-Z_A}\right) \right]^2}. \quad (8.42)$$

From the recursive equation (8.38), the squared SE of the other abundance estimates is

$$\begin{aligned} \text{SE}^2(N_a) &= \text{SE}^2(N_{a+1})e^{2M_a} + \text{SE}^2(C_a)e^{M_a} + 2e^{3M_a/2}\text{cov}(N_{a+1}, C_a) \\ &= \text{SE}^2(N_{a+1})e^{2M_a} + \text{SE}^2(C_a)e^{M_a} \end{aligned} \quad (8.43)$$

where the covariance term is 0, because N_{a+1} does not depend on C_a . The squared SE for F_a from (8.39) requires use of the delta method, resulting in

$$\begin{aligned} \text{SE}^2(F_a) &= \text{SE}^2(\ln N_{a+1}) + \text{SE}^2(\ln N_a) - 2 \text{cov}(\ln N_a, \ln N_{a+1}) \\ &\approx \text{CV}^2(N_{a+1}) + \text{CV}^2(N_a) \\ &\quad - \frac{2}{N_a N_{a+1}} \left[e^{M_a} \text{SE}^2(N_{a+1}) + e^{M_a/2} \text{cov}(C_a, N_{a+1}) \right] \\ &= \text{CV}^2(N_{a+1}) + \text{CV}^2(N_a) - \frac{2N_{a+1}}{N_a} e^{M_a} \text{CV}^2(N_{a+1}). \end{aligned} \quad (8.44)$$

First, (8.42) is calculated, which then allows (8.43) to be computed in sequence for all other ages down to age r . From (8.42) and (8.43), equation (8.44) can be computed.

The popularity of cohort analysis stems from certain properties of the back-calculation algorithm. Estimates of abundance and fishing mortality become progressively less sensitive to the choice of terminal fishing mortality as the back-calculation proceeds (Pope 1972). Thus, cohort analysis is a fairly robust procedure for examining historical trends in abundance and fishing mortality. A rough rule of thumb is that errors are small once the true cumulative fishing mortality exceeds 1 in the back-calculation. The principal disadvantage to cohort analysis is that it is quite sensitive to natural mortality, errors in catch at age, and migration (Ulltang 1977, Hoag and MacNaughton 1978, Sims 1982b, 1984, Rivard 1989). It is possible to apply cohort analysis to several year-classes up to the most recent time; see section 8.2.7. Zhang and Sullivan (1988) developed a modification of cohort analysis in terms of biomass calculations.

Rather than backward calculation of abundance and fishing mortality, it is also possible to start at the youngest or germinal age (or even an intermediate age) and project forward through a year-class using (8.37) (Sims 1982a). The robust properties of backward projection do not apply to forward projection. For some choices of germinal fishing mortality, negative estimates of abundance can occur because catches are subtracted from successive abundances.

Example 8.8. Walleye pollock in the eastern Bering Sea

One of the largest fisheries in the world is the trawl fishery for walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea off the coast of Alaska with an annual catch of about 1 million metric tons (Wespestad 1993, Quinn and Collie 1990). To illustrate backward cohort analysis, catch data from the 1975 year-class (ages 2–9) and natural mortality values and cohort analysis calculations are given in table 8.13. For a terminal fishing mortality $F_9 = 0.12$, terminal abundance, N_9 , is calculated from (8.33). Abundances, N_a , at successively younger ages are back-calculated from N_9 using (8.38). Then fishing mortalities, F_a , at younger ages are calculated using (8.39).

Results of perturbing input quantities are also shown in table 8.13. Increasing terminal F by 50% leads to an increase in fishing mortality and a decrease in abundance at younger ages. In both cases, the percentage change compared to the initial analysis (base case) decreases as the back-calculation proceeds to younger ages, showing that the effect of terminal fishing mortality lessens. Increasing M_a by 50% leads to a decrease

Table 8.13. Backward cohort analyses for the 1975 year class of walleye pollock in the eastern Bering Sea.

Age, <i>a</i>	C_a	M_a	F_a	Z_a	N_a	% change <i>F</i>	% change <i>N</i>
Base case							
2	1073816	0.45	0.17	0.62	8797193		
3	1097360	0.30	0.31	0.61	4751878		
4	682467	0.30	0.37	0.67	2575772		
5	228463	0.30	0.22	0.52	1320774		
6	74749	0.30	0.12	0.42	781813		
7	21178	0.30	0.05	0.35	514845		
8	13306	0.30	0.04	0.34	363178		
9	25241	0.30	0.12	0.42	257596		
10					169253		
Increase F_9 by 50%							
2	1073816	0.45	0.18	0.63	8028384	11	-9
3	1097360	0.30	0.36	0.66	4261664	14	-10
4	682467	0.30	0.44	0.74	2212612	21	-14
5	228463	0.30	0.29	0.59	1051739	30	-20
6	74749	0.30	0.16	0.46	582507	37	-25
7	21178	0.30	0.07	0.37	367195	42	-29
8	13306	0.30	0.06	0.36	253797	44	-30
9	25241	0.30	0.18	0.48	176565	50	-31
10					109255		-35
Increase M_a by 50%							
2	1073816	0.68	0.09	0.76	17618018	-46	100
3	1097360	0.45	0.18	0.63	8204103	-41	73
4	682467	0.45	0.22	0.67	4354907	-41	69
5	228463	0.45	0.14	0.59	2231851	-39	69
6	74749	0.45	0.08	0.53	1240659	-33	59
7	21178	0.45	0.04	0.49	731391	-25	42
8	13306	0.45	0.04	0.49	449445	-13	24
9	25241	0.45	0.12	0.57	275953	0	7
10					156059		-8
Increase C_a by 50%							
2	1610724	0.45	0.17	0.62	13195790	0	50
3	1646040	0.30	0.31	0.61	7127818	0	50
4	1023701	0.30	0.37	0.67	3863657	0	50
5	342695	0.30	0.22	0.52	1981161	0	50
6	112124	0.30	0.12	0.42	1172720	0	50
7	31767	0.30	0.05	0.35	772267	0	50
8	19959	0.30	0.04	0.34	544767	0	50
9	37862	0.30	0.12	0.42	386395	0	50
10					253879		50

Different analyses show the effect (in percentage change) of terminal fishing mortality, natural mortality, and directional bias in catch estimation. Catch and abundance are in thousands of fish.

in fishing mortality and an increase in abundance at younger ages. In both cases, the percentage change increases as the back-calculation proceeds to younger ages, showing that the effect of natural mortality intensifies. Increasing C_a by 50% has no effect on F but leads to a constant increase in abundance. Thus, if there is a positive bias in estimating catch, the same percentage bias also occurs in estimating abundance.

To illustrate forward cohort analysis, the same input values are used as for backward cohort analysis; calculations are given in table 8.14. In forward analysis, abundance calculations continue to age 10, so fishing mortality at age 9 can be determined. A germinal fishing mortality of $F_2 = 0.16$ is used to reproduce the same base case as was used in backward analysis. Germinal abundance, N_2 , is calculated from (8.33), and abundances, N_a , at successively older ages are calculated forward from N_2 using (8.37). Then fishing mortalities, F_a , at younger ages are calculated using (8.39).

Results of perturbing input quantities are also shown in table 8.14. Increasing germinal F by 50% leads to an increase in fishing mortality and decrease in abundance at older ages, until, at age 7 and beyond, abundance becomes negative and fishing mortality values are either undefined or negative. In both cases, the percentage change increases as the fore-calculation proceeds to older ages, showing that forward analysis is not robust to the choice of germinal fishing mortality. Increasing M_a by 50% leads to an increase in fishing mortality and a decrease in abundance at older ages, until, at age 10, abundance becomes negative. In both cases, the percentage change increases as the forward-calculation proceeds to older ages, showing that the effect of natural mortality intensifies. This is the same result as for backward analysis, except that the direction of change is opposite. Increasing C_a by 50% has no effect on F but leads to a constant increase in abundance, the same result as for backward analysis. ■

Despite the lack of robustness of forward cohort analysis to input values, a forward projection model is frequently useful for population modeling. The forward cohort analysis approach can be generalized for catches occurring at different times during the year. The general equations in section 8.2.1 are based on natural and fishing mortality occurring at constant rates throughout the year, which may be unrealistic when fisheries are constrained by seasonal restrictions. The equivalent relationship to (8.24) of abundance N_a as a function of N_r , constant natural mortality M , and catches $\{C_a\}$ can be derived for forward cohort analysis by repeated use of (8.24), as follows:

$$\begin{aligned}
 N_a &= N_{a-1}e^{-M} - C_{a-1}e^{-M/2} \\
 &= N_{a-2}e^{-2M} - C_{a-2}e^{-3M/2} - C_{a-1}e^{-M/2} \\
 &= N_{a-r}e^{-rM} - \sum_{i=1}^r C_{a-i}e^{-(i-1/2)M} \\
 &= N_r e^{-(a-r)M} - \sum_{x=r}^{a-1} C_x e^{-[a-(x+1/2)]M}
 \end{aligned} \tag{8.45}$$

Essentially, (8.45) replaces the fishing mortality component of (8.24) with subtraction of a weighted sum of catches adjusted for natural mortality. If the cohort analysis is treated as exact, then the term $(x + 1/2)$ in (8.45) represents the time halfway through the year when the catches are taken.

This approach can be generalized for catches at arbitrary times of the year by letting a_i be the combined age and fraction of the year when caught for the i th fish

Table 8.14. Forward cohort analyses for the 1975 year class of walleye pollock in the eastern Bering Sea.

	Age, <i>a</i>	<i>C_a</i>	<i>M_a</i>	<i>F_a</i>	<i>Z_a</i>	<i>N_a</i>	% change <i>F</i>	% change <i>N</i>
Base case								
	2	1073816	0.45	0.16	0.61	8797193		
	3	1097360	0.30	0.31	0.61	4751878		
	4	682467	0.30	0.37	0.67	2575772		
	5	228463	0.30	0.22	0.52	1320774		
	6	74749	0.30	0.12	0.42	781813		
	7	21178	0.30	0.05	0.35	514845		
	8	13306	0.30	0.04	0.34	363178		
	9	25241	0.30	0.12	0.42	257596		
	10					169107		
Increase <i>F₂</i> by 50%								
	2	1073816	0.45	0.24	0.69	6082237	50	-31
	3	1097360	0.30	0.55	0.85	3020746	76	-36
	4	682467	0.30	0.95	1.25	1293317	158	-50
	5	228463	0.30	1.26	1.56	370708	461	-72
	6	74749	0.30	NA	NA	77987	NA	-90
	7	21178	0.30	-1.56	-1.26	-6563	NA	NA
	8	13306	0.30	-0.51	-0.21	-23090	NA	NA
	9	25241	0.30	-0.71	-0.41	-28558	NA	NA
	10					-42881	NA	NA
Increase <i>M_a</i> by 50%								
	2	1073816	0.68	0.16	0.84	9712802	0	10
	3	1097360	0.45	0.40	0.85	4179112	28	-12
	4	682467	0.45	0.65	1.10	1788460	77	-31
	5	228463	0.45	0.65	1.10	595411	192	-55
	6	74749	0.45	0.64	1.09	197220	447	-75
	7	21178	0.45	0.51	0.96	66064	948	-87
	8	13306	0.45	1.08	1.53	25214	2386	-93
	9	25241	0.45	NA	NA	5452	NA	-98
	10					-16679	NA	NA
Increase <i>C_a</i> by 50%								
	2	1610724	0.45	0.16	0.61	13195790	0	50
	3	1646040	0.30	0.31	0.61	7127818	0	50
	4	1023701	0.30	0.37	0.67	3863657	0	50
	5	342695	0.30	0.22	0.52	1981161	0	50
	6	112124	0.30	0.12	0.42	1172720	0	50
	7	31767	0.30	0.05	0.35	772267	0	50
	8	19959	0.30	0.04	0.34	544767	0	50
	9	37862	0.30	0.12	0.42	386395	0	50
	10					253660	50	50

Different analyses show the effect of starting fishing mortality, natural mortality, and directional bias in catch estimation. Catch and abundance are in thousands of fish.

(Hearn et al. 1987, W.S. Hearn, personal communication, 1993). From (B1) in Hearn et al. (1987), the appropriate abundance relationship is analogous to (8.45) with capture ages ($x + 1/2$) replaced with a_i , which results in

$$N_a = N_r e^{-(a-r)M} - \sum_{i=1}^{C_a^-} e^{-(a-a_i)M}, \quad (8.46)$$

where the summation is done for all fish caught up to the start of age a , say C_a^- .

As an example of the use of (8.46), suppose that $C_{x,1}$ fish at age x are caught one-third of the way through the year, that $C_{x,2}$ fish at age x are caught two-thirds of the way through the year, and that fish are not caught at any other time. Then the equivalent representation of (8.46) is

$$N_a = N_r e^{-(a-r)M} - \sum_{x=1}^{a-1} \sum_{y=1}^2 C_{x,y} e^{-[a-(x+y/3)]M},$$

because the age of a fish when caught is $(x + y/3)$.

Analogously, backward cohort analysis can be generalized for catches at different times. By using the same approach, the backward equation (8.38) can be rewritten in terms of terminal abundance, N_A , natural mortality, M , and catches $\{C_a\}$ as

$$N_a = N_A e^{(A-a)M} + \sum_{x=a}^{A-1} C_x e^{[(x+1/2)-a]M}. \quad (8.47)$$

By noticing the similarity between (8.45) and (8.47), the generalization of (8.46) for different times a_i is then

$$N_a = N_A e^{(A-a)M} + \sum_{i=1}^{C_a^+} e^{(a_i-a)M}, \quad (8.48)$$

where the summation is done for all fish caught after the start of age a , say C_a^+ .

8.2.4. Relative Abundance Analysis

An intermediate approach between catch curve analysis with its stringent assumptions and analyses of catch-age data with their greater complexities was developed by Deriso et al. (1985, 1989) and extended by Johnson and Quinn (1988). The basis of the approach is to use age composition proportions rather than absolute catch-age data to determine relative abundances over time. Let

r = first age for which data are available,

A = last age for which data are available,

t = year index for years in which data are available, $t = 1, \dots, T$,

$C_{a,t}$ = survey catch at age a in year t from the model,

$p_{a,t} = C_{a,t} / \sum C_{a,t}$ = predicted survey proportion at age a in year t ,

- $C'_{a,t}$ = observed survey catch at age a in year t ,
- $p'_{a,t}$ = observed survey proportion at age a in year t ,
- $\mu_{a,t}$ = survey exploitation fraction for age a in year t ,
- μ_t = survey exploitation fraction in year t for fully recruited ages,
- s_a = gear selectivity for age a , and
- Z = total instantaneous mortality from all causes in a year.

This model assumes that total mortality from all causes, Z , is constant for all years and across all ages, which results in the forward projection equation

$$N_{a,t} = N_{r,t-a+r} e^{-Z(a-r)}. \quad (8.49)$$

Each year a survey is undertaken from which a sample from the population is aged; the numbers at each age are denoted the “catches” whether they are harvested or not. Presumably the survey would have a small effect on abundance, if any. The exploitation fraction is written

$$\mu_{a,t} = C_{a,t} / N_{a,t}, \quad (8.50)$$

but this alone produces $A'T$ parameters, which is too many to allow parameter estimation. A *separability* assumption is made to reduce the number of parameters; exploitation fraction is separable into a time-dependent exploitation fraction for fully recruited fish and an age-dependent gear selectivity coefficient, or

$$\mu_{a,t} = s_a \mu_t, \quad (8.51)$$

where $s_a = 1$ for fully recruited ages. Let P be the number of selectivity parameters to be estimated. By combining (8.49), (8.50), and (8.51), the predicted survey catch from this model is

$$C_{a,t} = \mu_t s_a N_{r,t-a+r} e^{-Z(a-r)}, \quad (8.52)$$

which shows that abundance cannot be estimated from survey catch data alone because exploitation fraction and abundance are confounded. By expressing (8.52) as the proportion at age a in the survey catch

$$p_{a,t} = \frac{s_a N_{r,t-a+r} e^{-Z(a-r)}}{\sum_{x=r}^A s_x N_{r,t-x+r} e^{-Z(x-r)}}, \quad (8.53)$$

the exploitation fraction is eliminated, reducing further the number of parameters to be estimated. From $A'T$ total observations, the parameters now to be estimated are P selectivities, one Z , and $A' + T - 1$ year-class parameters.

If an underlying multinomial distribution is assumed as in section 8.1.1, one appropriate goal is to minimize the goodness-of-fit objective function

$$\chi^2 = \sum_t \sum_a \frac{(C'_{a,t} - C_{a,t})^2}{C_{a,t}}.$$

This objective function can also be derived under the weaker assumption that the variance in the catch-age data is proportional to catch at age. An alternative objective function for the multinomial is to maximize the nonconstant portion of the log likelihood

$$\ln L_1 = \sum_t \sum_a C'_{a,t} \ln p_{a,t}.$$

This equation is strictly correct only if all fish caught are aged. If this is not the case, let $n_{a,t}$ be the number of fish in year t aged a and rewrite the log likelihood as

$$\ln L_1 = \sum_t \sum_a n_{a,t} \ln p_{a,t}.$$

Because this equation does not involve catch, it may be wise to add an auxiliary sum of squares (RSS) term to keep total catch close to that observed, which is written

$$\text{RSS}(T) = \lambda_T \sum_t (C'_t - C_t)^2,$$

where $C_t = \Sigma C_{a,t}$ and λ_T is a penalty weight chosen to be large enough so that the observed and predicted total catches are close. An alternative to $\ln L_1$ is not strictly correct, but allows optimization in terms of only proportions:

$$\ln L_2 = \sum_t \sum_a p'_{a,t} \ln p_{a,t}.$$

The observed proportions of catch at age are often thought to have higher variances than one would expect for a multinomial distribution. A logistic type structure proposed by Schnute and Richards (1995) allows parameter control over the variance. An additional advantage of the logistic structure is that it provides a simple transformation method which ensures that the model proportions sum to one. Proportions $p_{a,t}$ are parameterized with a logistic transformation:

$$p_{a,t} = \frac{\exp(x_{a,t})}{\sum_{a=1}^A \exp(x_{a,t})},$$

where the transformation allows one to estimate the $x_{a,t}$ parameters as unconstrained, except for $x_{1,t}$, which is defined by the constraint

$$\sum_{a=1}^A x_{a,t} = 0.$$

The residuals for the logistic structure are defined by the equation

$$\eta_{a,t} = [\ln(p'_{a,t}) - \ln(p_{a,t})] - \frac{1}{A} \sum_{j=1}^A [\ln(p'_{j,t}) - \ln(p_{j,t})].$$

Following Schnute and Richards, assume the probability density for $\{\eta_{2,t}, \dots, \eta_{A,t}\}$ is an $A - 1$ dimensional multivariate normal distribution with zero mean and a variance-covariance matrix, \mathbf{V} , given by

$$\mathbf{V} = \tau^2 (\mathbf{I}_{A-1} - A^{-1} \mathbf{U}_{A-1}),$$

in which \mathbf{I}_k denotes a $k \times k$ identity matrix and \mathbf{U}_k is a $k \times k$ unit matrix. The remaining residual, $\eta_{1,t}$, is defined by the constraint, namely,

$$\sum_{a=1}^A \eta_{a,t} = 0.$$

It follows that the probability density for the vector $\boldsymbol{\eta}_t$ of residuals for a given year t of data is given by

$$P(\boldsymbol{\eta}_t | \mathbf{p}_a, \tau) = (\sqrt{2\pi}\tau)^{-(A-1)} \sqrt{A} \exp \left[-\frac{1}{2\tau^2} \sum_{a=1}^A \eta_{a,t}^2 \right].$$

Further reductions in the number of parameters can be made. If it is assumed that year-class strength is constant for all year-classes occurring in the first year, say, $N_{r,x} = N_r^*$ for $x = -A' + 1, \dots, 1$, then abundances in the first year can be calculated as

$$N_{a,1} = N_r^* e^{-Z(a-r)}.$$

If it is assumed that selectivity can be parameterized as a normalized gamma density function

$$s_a = \frac{a^\alpha e^{-\beta a}}{\max_j j^\alpha e^{-\beta j}}, \quad (8.54)$$

then selectivity increases as a function of age if $\alpha > 0$ and $\beta = 0$, follows a dome-shaped curve if $\alpha \neq 0$ and $\beta \neq 0$, and is constant if $\alpha = \beta = 0$. Then (8.53) can be simplified as

$$p_{a,t} = \frac{a^\alpha e^{-\beta^* a} N_{r,t-a+r}}{\sum_{x=r}^A x^\alpha e^{-\beta^* x} N_{r,t-x+r}}, \quad (8.55)$$

where $\beta^* = \beta + Z$. For the solution to be well defined, at least two parameters must be set to known values, such as setting $N_{r,T} = 1$ and $N_{r,T-1} = 1.1$, or setting β^* for one of the parameters (Deriso et al. 1989).

Johnson and Quinn (1987) extended this approach to include auxiliary information on survey catch-per-unit-effort, along the lines of section 8.2.5. They found that this auxiliary information was necessary to stabilize relative estimates of abundance even when two parameters were set to known values.

8.2.5. Catch-Age Analysis with Auxiliary Information

VPA and cohort analysis can be viewed as providing exact solutions to A' Baranov catch equations for a year-class. If the number of parameters can be reduced, then least squares and likelihood objective functions can be used to obtain parameter estimates. We use the same notation as in the previous section, which is based on a set of data from T years and A' ages, resulting in a total of $A'T$ observations. However, in this case, the catch is not necessarily from a survey with minimal impact on the population but rather can be from any source (commercial, sport, survey, subsistence) and can be of any magnitude of removal from the population. To allow fishing mortality to be a variable and important source of mortality, let Z be a function of age and time, where

$$Z_{a,t} = F_{a,t} + M_{a,t}. \quad (8.56)$$

From the general theory of catch-age relationships, the following dynamics are evident:

$$C_{a,t} = \mu_{a,t} N_{a,t} \quad (8.57)$$

$$\mu_{a,t} = \frac{F_{a,t}}{Z_{a,t}} (1 - e^{-Z_{a,t}}) \quad (8.58)$$

$$N_{a+1,t+1} = N_{a,t} e^{-Z_{a,t}}. \quad (8.59)$$

Combining (8.56) – (8.59) and writing in terms of year-class strength, $N_{r,t}$, results in the basic catch equation

$$C_{a,t} = \mu_{a,t} N_{r,t-a+r} \exp \left(- \sum_{j=1}^{a-r} Z_{a-j,t-j} \right), \quad (8.60)$$

because an age a fish in year t was age r in year $t - a + r$.

One simple model by Pope and Shepherd (1982) uses the logarithm of the ratio of catches of a year-class in two successive years as a dependent variable. This eliminates year-class strengths as parameters in (8.60) but doubles the variance of the dependent variable (Doubleday 1976b), so it is not used much.

There are $A' + T - 1$ year-classes in a rectangular catch-age data set, each of which must have a year-class parameter estimated. There are $A'T$ fishing mortality parameters, $F_{a,t}$, which is too many to be estimated. To reduce the number of parameters, fishing mortality is assumed to be separable into a time-dependent fishing mortality term, F_t , for fully recruited fish and an age-dependent gear selectivity term, s_a , or

$$F_{a,t} = s_a F_t, \quad (8.61)$$

where $s_a = 1$ for fully recruited ages. Suppose that there are P ages for which selectivity is to be estimated, where $P < A'$. It is also possible to model age selectivity using one of the growth models in chapter 4 or the normalized gamma model in (8.54); P would then be the number of model parameters. The separability assumption (8.61) reduces the number of fishing mortality parameters from $A'T$ to $P + T$. Thus the total number of parameters to be estimated is $A' + 2T + P - 1$ from $A'T$ observations.

One might also attempt to estimate natural mortality parameters. However, it is usually difficult, if not impossible, to estimate natural mortality from catch data because the residual sum of squares surface is often flat over a wide range of natural mortality values. In a comprehensive examination of catch-age models, Schnute and Richards (1995) found that natural mortality is difficult to estimate. Methot (1989) modeled natural mortality as a linear function of a predator population but concluded that estimating natural mortality was not successful. Thus, natural mortalities are usually treated as fixed constants and obtained from other information or approaches. See section 8.3 for methods of estimating natural mortality.

Measurement error model

To complete the model specifications, observed catch is assumed to differ from model catch due to measurement error. Lognormal deviations are commonly used, which leads to

$$\ln C'_{a,t} = \ln C_{a,t} + \epsilon_{a,t}, \quad \text{where } \epsilon_{a,t} \sim N(0, \sigma_C^2). \quad (8.62)$$

Parameter estimates are found by minimizing the residual sum of squares

$$\text{RSS}(C) = \sum_t \sum_a (\ln C'_{a,t} - \ln C_{a,t})^2. \quad (8.63a)$$

The measurement error model was first developed by Doubleday (1976b), who showed that the logarithmic transformation of catch tended to linearize the parameter space. Principal components analysis was used to show that many parameter estimates were linear combinations of others, leading to the conclusion that catch-age data alone cannot be used to estimate absolute abundance. Only relative trends over a short time period can be obtained.

Several alternative objective functions for catch-age data can also be contemplated. A general formalism can be written

$$O(C) = \sum_x \lambda_x \sum_t \sum_a w_{a,t,x} \mathcal{G}(C'_{a,t,x}, C_{a,t,x}), \quad (8.63b)$$

where \mathcal{G} is a generic function used to subsume such objectives as sum of squares, chi-square, and multinomial, and catch is stratified into various categories x , such as gear type (section 8.2.6), area, or season. The term λ_x is a weighting term for each category, where one category would be standardized to $\lambda = 1$. The terms $w_{a,t,x}$ are weighting terms for each datum within category. The weights might be proportional to sample size or the inverse of variance, for example. This same formalism can be used for other types of information described below. The issue of how data should be weighted is a critical one in age-structured analyses, and much additional research effort is needed.

Multinomial model

If measurement errors are due to aging errors and variation due to simple random sampling for catch, then a multinomial distribution is reasonable. Either the chi-square or log-likelihood objective functions in section 8.2.4 may be used.

Process error model

Suppose that catch is measured without error, but that error in the population dynamics process occurs. Specifically suppose that the true exploitation fraction differs from that in the model by a lognormal variable, which might occur because of error in the separability of selectivity and mortality. Then

$$\mu_{a,t} = \frac{s_a F_t}{s_a F_t + M_{a,t}} \left[1 - e^{-(s_a F_t + M_{a,t})} \right] e^{\epsilon_{a,t}}, \quad \text{where } \epsilon_{a,t} \sim N(0, \sigma_\mu^2). \quad (8.64)$$

This structure leads to a slight difference in estimation procedure. Because the catch is assumed known without error, cohort analysis is used to solve for abundance conditional on year-class parameters. Nonlinear least squares is used to estimate year-class parameters.

Auxiliary information

For catch-age analysis to produce accurate estimates, some type of auxiliary information must be collected. Paloheimo (1980) and Dupont (1983) developed catch-age models with auxiliary fishing effort information that assumed that catchability is constant. Paloheimo's approach led to a linearized model for catch-age per unit of effort reminiscent of the DeLury method of estimating abundance. Dupont's approach was a stochastic model wherein the fishing hazard was proportional to fishing effort.

The first attempt to include auxiliary information without the strict assumption of constant catchability was Fournier and Archibald (1982) in a likelihood setting. Their work motivated a similar approach in Deriso et al. (1985) in a least squares setting. Full-recruitment fishing mortality is assumed to differ from the constant catchability relationship by a lognormal variable, or

$$F_t = q E_t e^{\epsilon_t}, \quad \text{where } \epsilon_t \sim N(0, \sigma_E^2). \quad (8.65)$$

Inclusion of fishing effort adds T observations and one parameter (q) to the estimation framework, leading to the inclusion of the sum of squares term

$$\text{RSS}(E) = \lambda_E \sum_t [\ln F_t - (\ln q + \ln E_t)]^2, \quad (8.66)$$

where λ_E is a prespecified weighting term to govern how strongly the catchability relationship should influence the overall fit of the model. If $\lambda_E \rightarrow 0$, then fishing effort has little effect on fishing mortality. As $\lambda_E \rightarrow \infty$, then the constant catchability assumption is strictly satisfied. The term λ_E may also be thought of as the ratio of the variances of log-catch observations to log-effort observations σ_C^2/σ_E^2 (Deriso et al. 1985). If the relationship between catch-per-unit-effort (CPUE) and abundance is nonlinear, then (8.65) can be modified as in section 1.3.4.

The choice of λ_E and other such weighting terms for auxiliary information (given below) is one of the most critical aspects of catch-age analysis. From the theory of maximum penalized likelihood, it is not possible to estimate λ_E , so it must be prespecified before undertaking the analysis. The null situation corresponds to $\lambda_E = 1$; that is, there is no compelling evidence to weight an effort observation more or less strongly than a catch observation. In some cases, there is a range of λ_E values that provide roughly the same estimates of population parameters (e.g., Deriso et al. 1985). If such robustness occurs, then the smallest value of λ_E that does not have a trend in the effort residuals can be used.

In other cases, population estimates vary monotonically as a function of λ_E , so that some method of determining λ_E must be sought. It is not valid to use the total residual sum of squares in (8.69) below as a criterion for choosing λ_E , as this would be tantamount to estimating λ_E . Kimura (1989b) determined an empirical estimate of λ_E by examining measurement errors in the catch-age and effort data using sampling theory. Such sampling estimates of variance are given in section 1.3 for effort data and in section 8.1 for catch-age data. Although this accounts for sampling error, it does not measure process error due to changes in catchability, which could be investigated using the methods in section 1.3. Other approaches include choosing the lowest $\text{RSS}(C)$ value or lowest SEs of population estimates of interest as a function of λ_E .

Auxiliary information in the form of a spawner-recruit curve can be used to add structure to the catch-age model, as shown originally in Fournier and Archibald (1982). Recent year-classes have few observations of catch and deviations of catch due to sampling errors or changes in catchability can produce inaccurate estimates of abundance. However, as spawner-recruit curves are notoriously variable, it would not be wise to impose a spawner-recruit curve without variation. The number of spawners, as defined in chapter 4, is

$$\mathcal{S}_t = \sum_a f_a N_{a,t},$$

where f_a is net fecundity—that is, the product of maturity and proportion of females and number of eggs per mature female, or a proportional quantity, depending on available information. It is assumed that year-class strength differs from a spawner-recruit curve by a lognormal error. For the example of a Ricker spawner-recruit curve from chapter 3, the relationship is

$$N_{r,t+r} = \alpha \mathcal{S}_t e^{-\beta \mathcal{S}_t} e^{\epsilon_r} \quad \text{where } \epsilon_r \sim N(0, \sigma_R^2), \quad (8.67)$$

where r is the lag between spawning and recruitment. Inclusion of the Ricker spawner-recruit curve adds two parameters (α and β) to the estimation framework, leading to the inclusion of the sum of squares term

$$\text{RSS}(R) = \lambda_R \sum_{t=1}^{T-r} [\ln N_{r,t+r} - (\ln \alpha + \ln \mathcal{S}_t - \beta \mathcal{S}_t)]^2, \quad (8.68)$$

where λ_R is a prespecified weighting term to govern how strongly the spawner-recruit relationship should influence the overall fit of the model. With all three sources of information, the total sum of squares is

$$\text{RSS} = \text{RSS}(C) + \text{RSS}(E) + \text{RSS}(R). \quad (8.69)$$

Abundance indices or estimates from a standardized survey or other sampling approach [such as mark-recapture, line transect, or other direct methods of estimating abundance in Seber (1982)] can also be used to provide auxiliary information to stabilize estimates. Suppose that annual indices or estimates of total abundance, N'_x , have been made from some survey of the population, where x indexes the years in which a survey is made. It is assumed that the survey abundance differs proportionally from true total abundance by a lognormal variable, or

$$N'_x = \left(q_S \sum_a N_{a,x} \right) e^{\epsilon_x} \quad \text{where } \epsilon_x \sim N(0, \sigma_S^2), \quad (8.70)$$

and q_S is a calibration coefficient for the survey. If the survey provides an estimate of total abundance rather than an index, the parameter q_S is set to 1. Only one parameter is added to the estimation framework (or none if q_S is set to 1), but the survey estimates increase the number of observations. The sum of squares term

$$\text{RSS}(S) = \lambda_S \sum_x \left[\ln N'_x - \ln \left(q_S \sum_a N_{a,x} \right) \right]^2 \quad (8.71)$$

can be added to the others in (8.69), where λ_S is a prespecified weighting term to govern how strongly the survey should influence the overall fit of the model. If the survey measures biomass rather than abundance in numbers, then (8.70) and (8.71) can be modified by multiplying by average weight, $W_{a,t}$ (Kimura 1989b). If the survey is selective for particular ages of fish, then (8.70) and (8.71) can be modified by summing only over appropriate ages or by including selectivity parameters, s_a . These parameters could be the same as for the catch or could be different if the survey has different parameters. If survey abundance is available for each age, then (8.70) and (8.71) can be modified by adding a subscript for age and removing the sum for the abundance term. In particular, recruitment indices $\{N'_{r,x}\}$ are often available, so that an alternative or an addition to the spawner-recruit sum of squares is

$$\text{RSS}(S) = \lambda_S \sum_x [\ln N'_{r,x} - \ln(q_S N_{r,x})]^2.$$

An alternative approach from Deriso et al. (1989) to incorporate survey information is to solve for fishing mortality F'_t corresponding to the observed exploitation fraction for fully recruited ages. If $C_t = \sum_a C_{a,t}$, the observed exploitation fraction is $\mu'_t = C'_t/N'_t$. This fraction is then equated to its formulaic representation in the transcendental exploitation equation

$$\mu'_t = \frac{F'_t}{M + F'_t} [1 - e^{-(M+F'_t)}]. \quad (8.72)$$

This approach requires constant natural mortality for fully recruited ages, so that the exploitation equation can be written independently of abundance. Iterative numerical solution of (8.72) for F'_t is required. These fishing mortalities, F'_t , calculated from (8.72) are then used as the observed effort data ($E_t = F'_t$) and modeled as in (8.65), where it is often assumed that $q = 1$. The term λ_E in (8.66) then controls the influence of the survey estimates. This approach has been used successfully for walleye pollock in the Bering Sea, in conjunction with CPUE data in years before surveys occurred (Quinn and Collie 1990). If q is left unfixed, the estimate of q becomes a calibration coefficient for the survey. It is currently not known under what conditions there is sufficient information to estimate such a calibration coefficient without bias, so caution is warranted.

For many populations, aging is difficult for ages beyond some threshold level, say A , and data for these ages are aggregated into a plus group A^+ . If these ages are fully recruited ($s_a = 1$), abundance of the aggregate in a given year is made up of survivors from age $A - 1$ and survivors in the aggregate A^+ the previous year (Fournier and Archibald 1982, Deriso et al. 1989). Thus, abundance in the aggregate can be calculated as

$$N_{A^+,t+1} = N_{A^+-1,t} e^{-Z_{A^+-1,t}} + N_{A^+,t} e^{-Z_{A^+,t}}. \quad (8.73)$$

Equations for all other ages remain the same, which is equivalent to leaving out the second term in (8.73).

In practice, it is useful to estimate parameters on a logarithmic scale rather than on the original scale, because the catch-age relationship is more linear as a function of

the logarithms (Doubleday 1976b). Thus, in carrying out the nonlinear least squares procedure, the actual parameters are $\{\ln N_{a,1}\}$, $\{\ln N_{r,t}\}$, $\{\ln F_t\}$, $\{\ln s_a\}$, $\ln q$, and so on. This convention also assures that the estimates on the original scale after exponentiation are non-negative.

Several diagnostic checks should be undertaken to assure that reasonable estimates are obtained. The results should be insensitive to initial parameter values used to initiate the nonlinear least squares approach. Catch, effort, recruitment, and survey residuals should show no patterns in age or time or as a function of predicted catches. Runs with different values for the weighting terms λ should be made to determine the robustness of the estimates. If natural mortality is uncertain, runs with different values can indicate if different trends over time may emerge. The range of full selectivity should be varied to determine if selectivity parameters are needed for particular ages. Statistical F tests using (4.35) of models with different numbers of parameters can be undertaken as was done for growth models. Richards et al. (1997) described a variety of exploratory data analysis tools useful for validating a catch-age analysis.

After these diagnostic tests are performed, several useful quantities can be calculated. Tables of fishing mortality, $F_{a,t}$, and abundance, $N_{a,t}$, by age a and time t are useful and lead to other useful population statistics. Some of these summary variables predicted from the catch-age model are given in table 8.15. Note that if the values of F and M are not too large, the exploitation fraction in table 8.15 can be approximated by

$$\mu_{a,t} \approx s_a F_t,$$

so that

$$C_t \approx F_t EN_t \text{ and } Y_t \approx F_t EB_t.$$

From the quantities in table 8.15, analyses concerning surplus production (chapter 2), the relationship of spawning and recruitment (chapter 3), delay-difference models (chapter 5), yield and spawning biomass considerations (chapter 6), and age-structured models (chapter 7) can be undertaken.

Nonlinear least squares algorithms are available for estimating SEs associated with parameter estimates (Kennedy and Gentle 1980). However, if the number of parameters

Table 8.15. Some summary variables calculated from catch-age analysis.

Notation	Formula	Description
N_t	$\sum_{a=r}^A N_{a,t}$	Total abundance
\bar{F}_t	$\sum_{a=r}^A F_{a,t} / (A - r + 1)$	Average fishing mortality
B_t	$\sum_{a=r}^A N_{a,t} W_{a,t}$	Total biomass
C_t	$\sum_{a=r}^A \mu_{a,t} N_{a,t}$	Total catch
Y_t	$\sum_{a=r}^A \mu_{a,t} N_{a,t} W_{a,t}$	Total yield
ASP_t	$Y_t + B_{t+1} - B_t$	Annual surplus production
EN_t	$\sum_{a=r}^A s_a N_{a,t}$	Exploitable abundance
EB_t	$\sum_{a=r}^A s_a N_{a,t} W_{a,t}$	Exploitable biomass
$EASP_t$	$Y_t + EB_{t+1} - EB_t$	Exploitable annual surplus production
$S_{N,t}$	$\sum_{a=r}^A f_a N_{a,t}$	Spawning or mature abundance
$S_{B,t}$	$\sum_{a=r}^A f_a N_{a,t} W_{a,t}$	Spawning or mature biomass

Table 8.16. Pacific halibut catch at age, $C_{a,t}$ (numbers of fish), fishing effort, E_t (skates), natural mortality at age, M_a , net fecundity at age, f_a (thousands of eggs), and weight at age, $W_{a,t}$ (pounds).

Year	Age													E_t
	8	9	10	11	12	13	14	15	16	17	18	19	20	
$C_{a,t}$														
1967	211308	375722	341843	211958	259713	140778	94341	71888	55225	25558	18344	11806	10590	547798
1968	169887	180397	283797	216081	138895	160262	87386	63821	49326	29880	14934	8795	5511	470830
1969	344660	201074	186684	281016	221147	147306	140792	69472	55381	44241	23624	13669	7831	607806
1970	187480	373633	179187	159899	211099	148782	101970	88937	47476	30580	23129	17852	10473	589115
1971	237872	204121	301536	122785	108078	119164	83786	66944	42005	25199	16413	11017	6438	521222
1972	206106	197958	165899	236469	89241	91110	67538	50948	32778	22633	10726	8578	6355	530470
1973	91745	118215	127814	106123	134494	58111	47121	45082	28388	14599	14532	6228	6378	489316
1974	50040	63755	72696	72567	57979	72737	26682	25649	26287	15066	8249	6373	3789	341612
1975	70835	92406	97279	91138	89150	53473	68700	23339	23749	19549	11934	5582	5953	435696
1976	87683	106198	99257	84334	78954	55986	43557	44997	14668	14666	11043	6588	4165	510134
1977	59415	79991	89188	60629	58086	49360	36702	26665	26545	10050	7954	4391	3359	363062
1978	71040	75358	79858	67575	56331	37835	32958	23957	17309	10027	5866	3361	3889	326835
1979	61451	88345	85477	74907	67440	41731	35525	22948	18233	10270	6425	3121	3146	318251
1980	70474	77111	97831	83617	71325	49961	39498	26984	20232	13333	10689	6701	4837	243137
1981	75358	109754	95416	105240	79380	58337	41648	26108	19072	14129	10615	4398	5049	222329
1982	63386	114577	117243	95894	92319	63386	44267	25489	16848	14487	7332	6601	3112	236985
M_a	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
f_a	32.5	88.3	174.4	298.1	467.6	691.5	978.8	1171.9	1386.9	1624.6	1885.9	2171.6	2482.6	

$W_{a,t}$

1967	17.07	20.16	23.86	27.68	31.09	35.07	39.18	42.72	45.82	49.48	50.48	56.48	56.96
1968	17.77	21.21	25.90	29.18	32.03	35.46	38.98	42.52	45.73	49.11	49.77	52.59	54.31
1969	18.18	21.88	27.23	30.51	33.93	36.42	39.58	43.32	46.32	50.01	50.69	51.02	53.69
1970	18.30	22.06	27.40	31.31	35.92	38.30	41.72	45.73	47.83	53.30	54.55	53.38	55.44
1971	18.38	22.17	27.13	32.18	37.72	41.27	45.21	49.46	50.74	58.32	60.67	59.68	60.17
1972	18.63	22.58	27.27	33.27	39.41	44.62	48.89	53.28	55.00	62.06	65.12	66.35	65.03
1973	19.26	23.43	28.27	34.54	40.85	47.02	51.93	56.56	59.37	63.97	66.76	70.95	68.06
1974	20.27	24.56	29.39	35.66	42.02	48.40	54.14	59.00	62.51	65.37	67.75	73.38	70.11
1975	21.05	25.40	30.14	36.42	43.06	49.39	55.53	60.42	64.26	66.81	69.09	73.81	71.84
1976	21.29	25.66	30.73	36.98	43.95	50.31	56.76	61.71	65.79	69.22	71.43	74.28	73.93
1977	20.95	25.66	31.08	37.21	44.39	51.10	58.06	63.47	67.66	72.99	75.69	76.28	77.92
1978	19.86	25.21	31.02	37.16	44.44	51.41	58.64	64.63	68.85	75.91	80.72	79.72	83.51
1979	18.55	24.06	30.21	36.58	44.05	51.17	58.53	64.81	69.06	76.58	84.98	83.55	89.04
1980	17.82	23.09	28.90	35.53	43.36	50.59	58.30	64.36	68.73	76.25	88.04	87.74	94.16
1981	17.66	22.78	28.14	34.97	43.01	50.18	58.26	63.66	68.20	75.58	89.85	93.71	97.63
1982	17.65	22.76	28.02	34.93	43.01	50.10	58.32	63.35	67.95	74.59	91.04	100.82	98.62

A standard skate is 1800 feet of groundline with 100 equally spaced hooks.

is large compared to the number of observations and/or the sum of squares surface is irregular, SEs may be biased. Measures of nonlinearity are useful in detecting this problem (Ratkowsky 1986, Bates and Watts 1988, Welch and McFarlane 1990).

As an alternative approach to estimating bias and SE of parameter estimates, the bootstrap technique of Efron (1982) is preferable. In this procedure, residuals are resampled with replacement and added to the predicted values to form new bootstrap data sets. The nonlinear least squares procedure is then replicated for each new data set, producing sets of bootstrap parameter estimates. Any parameter, θ , of interest can then be estimated for each replicate. The difference between the mean of the bootstrap estimates, $\hat{\theta}^*$, and the original estimate, $\hat{\theta}$, is an estimate of bias, although there is no clear indication from the statistical literature that the bias estimate should be subtracted from the original estimate to correct for bias. The standard deviation (SD) of the bootstrap estimates is an estimate of the SE of the original estimate. This approach was first applied to catch-age analysis by Deriso et al. (1985).

The presence of catch-age data and auxiliary information makes analysis possible in situations where non-age-structured methods do not work. The age data increase sample size, so that abundance and other parameters can be estimated, whereas the surplus production and catch-effort approaches only have a single observation each year to work with. Quinn (1986) showed with an age-structured simulation model that catch-age analysis produced unbiased estimates of abundance and outcompeted catch-effort methods.

Example 8.9. Pacific halibut in the northeast Pacific

Data on catch at age, fishing effort, and average weight at age from the Pacific halibut longline fishery for the years 1967–82 are given in table 8.16; see Quinn et al. (1985) and Deriso et al. (1985) for further details about the data. There are $A' = 13$ ages from age 8 to 20 and $T = 16$ years from 1967 to 1982, resulting in 208 catch-age observations and 16 fishing effort observations. Also given in table 8.16 are values for fecundity at age and natural mortality at age. With a lag of 8 years between spawning and recruitment, recruitment from the Ricker spawner-recruit model can be determined for the years 1975 to 1982, resulting in an additional 8 “observations.”

The program CAGEAN (see section 8.2.7) is used to perform catch-age analysis and 100 bootstrap replications are made to estimate bias and SE of parameter estimates. Initial values for the nonlinear least squares procedure are generated by the program using cohort analysis with a terminal F of 0.16. The values $\lambda_E = 0.5$ and $\lambda_R = 0.5$ used in the base case analysis imply that the variabilities in the fishing mortality relationship (8.65) and in the Ricker spawner-recruit relationship (8.67) are twice that in the catch-age relationship (8.62). The age range of full recruitment is 15–20, found by trial and error using different ranges and performing F tests like those in section 4.3.5. The minimum size limit increased from 65 cm to 82 cm in 1973, raising the possibility that gear selectivity and catchability may have changed. Two sets of selectivity and catchability parameters for the years 1967–72 and 1973–82 are used to handle this change.

Parameter estimates and summary statistics from catch-age analysis are shown in table 8.17. There are estimates of $A' + T - 1 = 28$ year-class parameters on a logarithmic scale (denoted $\ln N$ in the table), 16 fishing mortality parameters (denoted $\ln F$), two sets of 7 selectivity parameters for ages 8–14 (denoted $\ln s$), two catchability

Table 8.17. Parameter estimates (Est) and summary statistics from catch-age analysis of Pacific halibut data in table 8.16, bootstrap mean, estimated bias, and standard deviation (SE) from 100 replications, and exponential estimates and corresponding standard errors [$SE_2 = \exp(Est) * SE$].

Parameter	Age	Year	Est	Mean	Est bias	SE	$\exp(Est)$	SE_2
ln N	20	1967	10.780	10.773	-0.007	0.139	48048	6684
ln N	19	1967	10.808	10.799	-0.009	0.093	49396	4613
ln N	18	1967	11.260	11.257	-0.004	0.068	77684	5306
ln N	17	1967	11.810	11.805	-0.005	0.058	134564	7804
ln N	16	1967	12.399	12.402	0.002	0.052	242649	12606
ln N	15	1967	12.826	12.826	0.000	0.059	371874	22021
ln N	14	1967	13.141	13.145	0.005	0.054	509330	27278
ln N	13	1967	13.438	13.445	0.007	0.047	685511	31946
ln N	12	1967	14.072	14.067	-0.004	0.042	1292251	54412
ln N	11	1967	14.141	14.139	-0.001	0.041	1384279	57348
ln N	10	1967	14.580	14.584	0.004	0.041	2147642	87854
ln N	9	1967	14.894	14.891	-0.002	0.041	2938933	121134
ln N	8	1967	14.802	14.795	-0.007	0.036	2681138	97360
ln N	8	1968	14.602	14.602	0.000	0.032	2195918	70173
ln N	8	1969	15.075	15.071	-0.004	0.032	3524127	114397
ln N	8	1970	14.636	14.636	0.001	0.041	2270605	93574
ln N	8	1971	14.686	14.684	-0.003	0.036	2389209	85763
ln N	8	1972	14.561	14.560	-0.001	0.046	2106680	97733
ln N	8	1973	14.488	14.482	-0.006	0.046	1958471	89561
ln N	8	1974	14.470	14.469	-0.001	0.058	1924404	111933
ln N	8	1975	14.620	14.617	-0.003	0.062	2234674	137569
ln N	8	1976	14.738	14.738	0.000	0.071	2516323	178286
ln N	8	1977	14.805	14.797	-0.008	0.080	2690179	215147
ln N	8	1978	15.004	14.991	-0.012	0.092	3280909	300236
ln N	8	1979	14.945	14.960	0.015	0.100	3095154	309227
ln N	8	1980	15.142	15.148	0.006	0.117	3768495	441781
ln N	8	1981	15.228	15.219	-0.009	0.133	4107393	544899
ln N	8	1982	15.110	15.139	0.029	0.147	3648915	534580
ln F		1967	-1.283	-1.286	-0.002	0.040	0.277	0.011
ln F		1968	-1.423	-1.416	0.006	0.042	0.241	0.010
ln F		1969	-1.132	-1.123	0.009	0.043	0.322	0.014

(continued)

parameters (denoted $\ln q$), and two spawner-recruit parameters (denoted $\ln \alpha$ and $\ln \beta$), for a total of 62 parameters estimated from the 232 observations. The residual root mean square of 0.125 can be interpreted as the SE of the log transformed data and the CV of the untransformed data after fitting the model.

Residual plots on a logarithmic scale are shown for catch at age (figure 8.4a), fishing effort (figure 8.4b), and recruitment (figure 8.4c). There is no trend in any of the plots, suggesting that the catch-age model adequately fits the data.

Also shown in table 8.17 for each parameter are the bootstrap mean, estimated bias (the bootstrap mean minus the estimate), SE of the estimate (equal to the bootstrap SD), and the exponentiated estimate and corresponding SE. Estimated bias is negligible for all parameter estimates. The SEs on a logarithmic scale are equivalent to CVs after exponentiation. Thus, the range of CVs for the untransformed parameter estimates is from 0.03 to 0.15 for abundances, 0.03 to 0.08 for fishing mortalities, 0.04 to 0.07

Table 8.17. *Continued.*

Parameter	Age	Year	Est	Mean	Est bias	SE	exp(Est)	SE ₂
ln F		1970	-1.078	-1.073	0.005	0.050	0.340	0.017
ln F		1971	-1.228	-1.226	0.002	0.048	0.293	0.014
ln F		1972	-1.312	-1.307	0.005	0.043	0.269	0.012
ln F		1973	-1.401	-1.405	-0.004	0.038	0.246	0.009
ln F		1974	-1.789	-1.788	0.001	0.037	0.167	0.006
ln F		1975	-1.576	-1.574	0.001	0.038	0.207	0.008
ln F		1976	-1.626	-1.629	-0.003	0.044	0.197	0.009
ln F		1977	-1.916	-1.919	-0.003	0.045	0.147	0.007
ln F		1978	-2.093	-2.089	0.004	0.047	0.123	0.006
ln F		1979	-2.141	-2.135	0.006	0.056	0.118	0.007
ln F		1980	-2.048	-2.048	0.000	0.064	0.129	0.008
ln F		1981	-2.123	-2.123	0.001	0.074	0.120	0.009
ln F		1982	-2.209	-2.215	-0.006	0.081	0.110	0.009
ln s	8	1967–72	-1.032	-1.056	-0.024	0.062	0.356	0.022
ln s	9	1967–72	-0.719	-0.722	-0.003	0.063	0.487	0.031
ln s	10	1967–72	-0.494	-0.493	0.001	0.057	0.610	0.035
ln s	11	1967–72	-0.356	-0.366	-0.010	0.057	0.700	0.040
ln s	12	1967–72	-0.238	-0.250	-0.012	0.061	0.788	0.048
ln s	13	1967–72	-0.087	-0.088	-0.001	0.064	0.917	0.059
ln s	14	1967–72	-0.054	-0.061	-0.007	0.061	0.947	0.057
ln s	8	1973–82	-1.706	-1.705	0.001	0.062	0.182	0.011
ln s	9	1973–82	-1.129	-1.127	0.003	0.067	0.323	0.022
ln s	10	1973–82	-0.749	-0.753	-0.004	0.055	0.473	0.026
ln s	11	1973–82	-0.523	-0.522	0.001	0.056	0.593	0.033
ln s	12	1973–82	-0.265	-0.270	-0.005	0.050	0.767	0.038
ln s	13	1973–82	-0.205	-0.206	-0.001	0.056	0.815	0.046
ln s	14	1973–82	-0.077	-0.077	-0.001	0.047	0.926	0.043
ln q		1967–72	-14.447	-14.439	0.008	0.088	5.32E-07	4.68E-08
ln q		1973–82	-14.615	-14.608	0.007	0.071	4.49E-07	3.17E-08
ln α			-4.905	-4.874	0.032	0.278	7.41E-03	2.06E-03
ln β			-21.178	-21.169	0.009	0.106	6.35E-10	6.71E-11

Number of observations = 232; number of parameters = 62; residual degrees of freedom = 170; residual root mean square = 0.125; residual mean square = 0.0157; residual sum of squares = 2.674.

for selectivities, 0.07 to 0.09 for catchabilities, and 0.10 to 0.28 for spawner-recruit parameters. Except for the spawner-recruit estimates, these levels of CV suggest that high precision has been obtained from catch-age analysis.

Abundance, $N_{a,t}$, and fishing mortality, $F_{a,t}$, can be easily obtained from the parameter estimates in table 8.17. First, $F_{a,t}$ is obtained from (8.61) using the selectivity and fishing mortality estimates appropriate to the age and year, as shown in table 8.18. The year-class parameters are inserted into the appropriate places on the left and upper ends of the abundance matrix in table 8.18. Abundance for other ages and years follows from the recursion relationship (8.59), as shown in table 8.18.

Estimates of selected summary variables from table 8.15, and their bootstrap means and SDs, are shown for each year in table 8.19. For any variable, the estimated bias (the bootstrap mean minus the estimate) is low compared to the SD, and both tend to get larger over time, suggesting that the most recent estimates are the least well determined. All the same, the SDs are fairly small compared to the estimates, suggesting that the precision of the variables is high. As selectivity is < 1 for ages under 15, exploitable

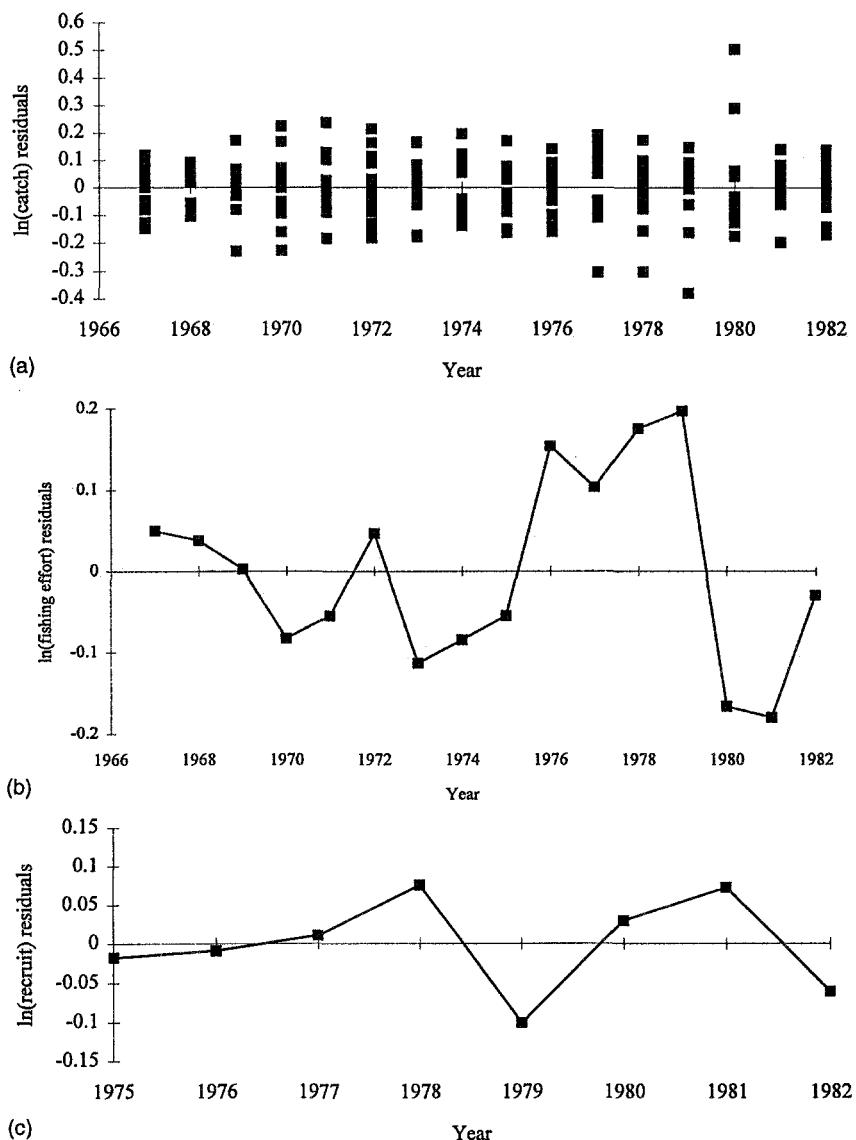


Figure 8.4. Residuals from catch-age analysis of Pacific halibut data from 1967–82 as a function of time: (a) $\ln C_{a,t}$ residuals; (b) $\ln F_t$ residuals; (c) $\ln N_{8,t}$ residuals.

biomass and exploitable annual surplus production are less than total biomass and annual surplus production. These exploitable variables are used in determining catch limits for Pacific halibut (Quinn et al. 1985). Total catch biomass in table 8.19 is always the same for bootstrap replications, so that its SD is 0. This variable uses predicted catch from the catch-age model, so it will differ slightly from observed total catch biomass.

The effects of λ_E and λ_R on the analysis are determined by rerunning the catch-age analysis with several different values. In figure 8.5a, the effect of λ_E on full-recruitment

Table 8.18. Abundance, $N_{a,t}$, and fishing mortality, $F_{a,t}$, for age a and year t from catch-age analysis with $\lambda_E = 0.5$ and $\lambda_R = 0.5$.

Year	Age													
	8	9	10	11	12	13	14	15	16	17	18	19	20	
$N_{a,t}$	1967	2681138	2938933	2147642	1384279	1292251	685511	509330	371874	242649	134564	77684	49396	48048
	1968	2195918	1988804	2102331	1484860	933452	850390	435319	320750	230770	150578	83505	48208	30653
	1969	3524127	1649933	1447876	1485857	1026877	631984	558172	283663	206353	148465	96873	53723	31014
	1970	2270605	2572239	1154479	973743	970641	652033	384987	336736	168228	122378	88048	57451	31860
	1971	2389209	1646763	1784195	767988	628174	607686	390731	228351	196158	97997	71289	51290	33467
	1972	2106680	1762310	1168958	1221741	512173	408264	380346	242407	139484	119819	59860	43545	31330
	1973	1958471	1567073	1265492	812098	828403	339144	261137	241315	151618	87242	74943	37440	27236
	1974	1924404	1533319	1184838	922197	574561	561510	227169	170194	154439	97034	55834	47963	23961
	1975	2234674	1528476	1189378	896372	683824	413838	401197	159325	117901	106987	67220	38679	33226
	1976	2516323	1762130	1170470	883035	649177	477734	286250	271197	106065	78489	71223	44749	25749
	1977	2690179	1987915	1353870	873214	643412	457103	333216	195340	182399	71336	52789	47903	30097
	1978	3280909	2144435	1551952	1033933	655186	470554	331938	238047	138040	128895	50411	37304	33851
	1979	3095154	2626691	1687114	1198660	786833	488018	348420	242436	172284	99905	93287	36485	26999
	1980	3768495	2480588	2070402	1306632	915334	588689	363063	255844	176481	125414	72726	67908	26559
	1981	4107393	3013920	1947975	1594770	990994	678808	433865	263767	184109	126998	90250	52335	48868
	1982	3648915	3290585	2374012	1507167	1216303	740246	504139	317968	191607	133741	92255	65560	38017
$F_{a,t}$	1967	0.099	0.135	0.169	0.194	0.218	0.254	0.262	0.277	0.277	0.277	0.277	0.277	0.277
	1968	0.086	0.117	0.147	0.169	0.190	0.221	0.228	0.241	0.241	0.241	0.241	0.241	0.241
	1969	0.115	0.157	0.197	0.226	0.254	0.296	0.305	0.322	0.322	0.322	0.322	0.322	0.322
	1970	0.121	0.166	0.208	0.238	0.268	0.312	0.322	0.340	0.340	0.340	0.340	0.340	0.340
	1971	0.104	0.143	0.179	0.205	0.231	0.269	0.277	0.293	0.293	0.293	0.293	0.293	0.293
	1972	0.096	0.131	0.164	0.189	0.212	0.247	0.255	0.269	0.269	0.269	0.269	0.269	0.269
	1973	0.045	0.080	0.116	0.146	0.189	0.201	0.228	0.246	0.246	0.246	0.246	0.246	0.246
	1974	0.030	0.054	0.079	0.099	0.128	0.136	0.155	0.167	0.167	0.167	0.167	0.167	0.167
	1975	0.038	0.067	0.098	0.123	0.159	0.169	0.192	0.207	0.207	0.207	0.207	0.207	0.207
	1976	0.036	0.064	0.093	0.117	0.151	0.160	0.182	0.197	0.197	0.197	0.197	0.197	0.197
	1977	0.027	0.048	0.070	0.087	0.113	0.120	0.136	0.147	0.147	0.147	0.147	0.147	0.147
	1978	0.022	0.040	0.058	0.073	0.095	0.101	0.114	0.123	0.123	0.123	0.123	0.123	0.123
	1979	0.021	0.038	0.056	0.070	0.090	0.096	0.109	0.118	0.118	0.118	0.118	0.118	0.118
	1980	0.023	0.042	0.061	0.076	0.099	0.105	0.120	0.129	0.129	0.129	0.129	0.129	0.129
	1981	0.022	0.039	0.057	0.071	0.092	0.097	0.111	0.120	0.120	0.120	0.120	0.120	0.120
	1982	0.020	0.035	0.052	0.065	0.084	0.089	0.102	0.110	0.110	0.110	0.110	0.110	0.110

Table 8.19. Estimates, bootstrap means, and bootstrap standard deviations (SE) from catch-age analysis of Pacific halibut data, calculated using the formulae of Table 8.15.

Year	Total numerical abundance (millions)	Total biomass (10^6 pounds)	Total catch biomass (10^6 pounds)	Total exploitable biomass (10^6 pounds)	Annual surplus production (10^6 pounds)	Exploitable annual surplus production (10^6 pounds)
1967 Estimate	12.6	321.9	51.0	219.0	25.0	37.2
Mean	12.6	321.9	51.0	218.3	25.3	37.4
SE	0.2	5.3	0.0	8.0	2.2	1.7
1968 Estimate	10.9	295.9	42.0	205.2	49.5	41.1
Mean	10.9	296.2	42.0	204.8	49.1	40.5
SE	0.2	4.6	0.0	7.2	2.5	1.6
1969 Estimate	11.1	303.5	52.9	204.3	25.3	36.9
Mean	11.1	303.4	52.9	203.3	25.2	36.9
SE	0.2	4.4	0.0	6.9	2.8	2.2
1970 Estimate	9.8	275.9	49.9	188.3	30.3	36.6
Mean	9.8	275.7	49.9	187.4	30.3	36.7
SE	0.2	4.2	0.0	5.9	2.6	1.6
1971 Estimate	8.9	256.3	42.8	175.0	31.8	36.1
Mean	8.9	256.1	42.8	174.2	32.0	36.0
SE	0.2	4.2	0.0	5.9	2.8	2.0
1972 Estimate	8.2	245.4	39.2	168.3	33.1	12.4
Mean	8.2	245.3	39.2	167.5	33.0	13.0
SE	0.2	4.6	0.0	5.3	2.1	5.9
1973 Estimate	7.7	239.4	29.5	141.5	33.1	30.3
Mean	7.6	239.1	29.5	141.3	33.3	30.4
SE	0.2	4.7	0.0	3.9	2.5	1.2
1974 Estimate	7.5	243.0	20.1	142.3	37.9	29.4
Mean	7.5	242.9	20.1	142.2	37.9	29.3
SE	0.2	6.0	0.0	3.6	2.9	1.2
1975 Estimate	7.9	260.8	26.3	151.5	41.2	31.5
Mean	7.9	260.6	26.3	151.4	41.4	31.5
SE	0.3	8.0	0.0	3.5	4.0	1.6
1976 Estimate	8.3	275.7	25.9	156.7	43.3	33.9
Mean	8.3	275.7	25.9	156.5	43.1	33.8
SE	0.4	10.7	0.0	3.5	4.2	1.7
1977 Estimate	8.9	293.1	21.0	164.7	50.9	35.8
Mean	8.9	292.9	21.0	164.5	50.4	35.6
SE	0.5	13.8	0.0	4.3	5.6	2.1
1978 Estimate	10.1	323.1	19.2	179.4	40.3	35.2
Mean	10.1	322.4	19.2	179.2	41.4	35.2
SE	0.6	18.4	0.0	5.7	5.4	2.3
1979 Estimate	10.9	344.1	20.4	195.4	50.6	38.8
Mean	10.9	344.5	20.4	195.1	51.4	38.9
SE	0.8	22.5	0.0	7.5	7.4	3.1
1980 Estimate	12.2	374.3	22.9	213.8	59.0	44.0
Mean	12.3	375.6	22.9	213.6	59.1	44.1
SE	1.0	28.5	0.0	10.1	9.3	3.9
1981 Estimate	13.5	410.5	24.9	234.9	53.6	48.0
Mean	13.6	411.7	24.9	234.8	56.2	48.5
SE	1.3	36.0	0.0	13.5	9.7	4.9
1982 Estimate	14.1	439.2	25.6	258.0	NA	NA
Mean	14.3	443.1	25.6	258.5	NA	NA
SE	1.5	43.8	0.0	17.9	NA	NA

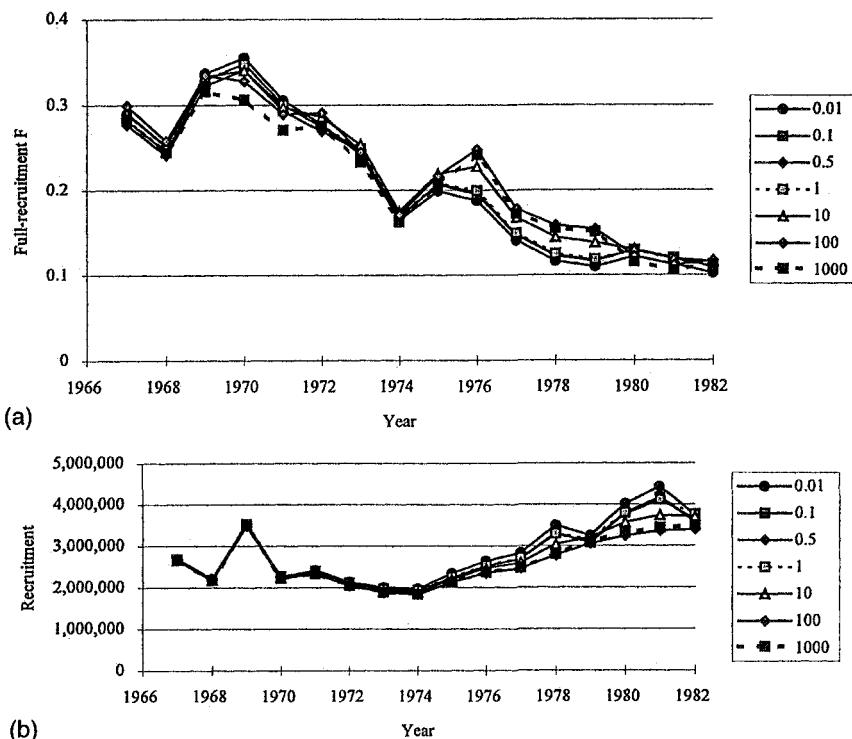


Figure 8.5. Effect of λ on catch-age analysis of Pacific halibut: (a) full-recruitment fishing mortality, F_t , versus time for different values of λ_E ; (b) recruitment, $N_{8,t}$, versus time for different values of λ_R .

fishing mortality across time is shown. As λ_E increases, the model approaches a constant catchability model with no variation. Only high values of λ_E in excess of 10 have much effect on F_t . The value $\lambda_E = 0.5$ used in the base case analysis was selected to provide estimates of F_t that are robust to the choice of λ_E and to avoid a constant catchability model as being too restrictive. In figure 8.5b, the effect of λ_R on recruitment $N_{8,t}$ across time is shown. As λ_R increases, the model approaches a constant Ricker spawner-recruit model with no variation. Only low values of λ_R below 0.1 and high values of λ_R in excess of 10 have much effect on $N_{8,t}$. The value $\lambda_R = 0.5$ used in the base case analysis was selected for the same robustness and flexibility reasons used to select λ_E . ■

Example 8.10. Walleye pollock in the Bering Sea

In addition to catch-age data used in section 8.2.3, CPUE data from the Japanese fishery up to 1985 and age-specific biomass estimates from a combined hydroacoustic and bottom trawl survey in the years 1979, 1982, 1985, and 1988 were used in catch-age analysis by Quinn and Collie (1990). The age range of full selectivity was set to ages 4–5. To use auxiliary information from the survey, commercial catch biomass was divided by survey biomass estimates for ages 4 and 5 to obtain the observed full-recruitment exploitation fraction, μ'_t . The exploitation fractions are 0.427 in 1979, 0.122 in 1982, 0.082 in 1985, and 0.106 in 1988. Using $M = 0.3$ and (8.72), the respective auxiliary

estimates of fishing mortality F_t' are 0.666, 0.152, 0.100, and 0.130. These estimates were used as effort values with catchability, q , set to 1 (Quinn and Collie 1990). As the combined survey takes place only once every three years, the value of λ_E was set to $3^2 = 9$, in order to give the same weight to the fishing mortality values as if an annual survey had occurred. ■

8.2.6. Stratified Catch-Age Analysis

If several gear types exploit a population, separate catch and effort data sets may be available to estimate population parameters. Several different approaches may be contemplated in this situation. First, the catch data could be pooled over gear type, and total effort could be obtained by dividing catch by CPUE of a predominant gear type, as in chapter 1. Overall selectivity for an age would then be a weighted average of the selectivities of the different gear types. This overall value would be expected to change if selectivities of the gear types differed and if the mixes of the gear types in the fishery changed. Such a situation would invalidate the separability assumption of section 8.2.5.

A second approach would be to standardize each gear type using the methods in chapter 1. However, if selectivities differed among gear types, the standardization could be difficult or impossible to perform without substantial experimentation.

The third approach is to generalize the general catch-age analysis approach of section 8.2.5 for multiple gear types, which would obviate the selectivity issue by defining separate selectivities for each gear type (Deriso et al. 1989).

The notation of section 8.2.5 is used, except let

g = index for gear type,

$C_{a,t,g}$ = catch of gear type g at age a in year t from the model,

$C'_{a,t,g}$ = observed catch,

$F_{a,t,g}$ = fishing mortality,

$\mu_{a,t,g}$ = exploitation fraction,

$s_{a,g}$ = gear selectivity, and

$F_{t,g}$ = fishing mortality for fully-recruited ages.

Then total instantaneous mortality, $Z_{a,t}$, is

$$Z_{a,t} = M_{a,t} + \sum_g F_{a,t,g}. \quad (8.74)$$

The following dynamics are then evident:

$$C_{a,t,g} = \mu_{a,t,g} N_{a,t} \quad (8.75)$$

$$\mu_{a,t,g} = \frac{F_{a,t,g}}{Z_{a,t}} (1 - e^{-Z_{a,t}}) \quad (8.76)$$

$$N_{a+1,t+1} = N_{a,t} e^{-Z_{a,t}}. \quad (8.77)$$

As in section 8.2.5, (8.74)–(8.77) can be combined to write catch by age, year, and gear in terms of year-class strength, $N_{r,t}$, fishing mortality, $F_{a,t,g}$, and natural mortality,

$M_{a,t}$. To reduce the number of parameters to be estimated, fishing mortality for each gear type, g , is assumed separable into a time-dependent fishing mortality term, $F_{t,g}$, for fully recruited fish and an age-dependent gear selectivity term, $s_{a,g}$, or

$$F_{a,t,g} = s_{a,g} F_{t,g}. \quad (8.78)$$

The sum of squares term (8.63a) for catch is modified for the several gear types as

$$\text{RSS}(C) = \sum_g \lambda_{Cg} \sum_t \sum_a (\ln C'_{a,t,g} - \ln C_{a,t,g})^2, \quad (8.79)$$

where λ_{Cg} is a weighting term for the catches of each gear type. This formulation allows the variances of the logarithmic catches to be different for each gear type (Deriso et al. 1989). By convention, the weighting term of one gear type is set to 1, in order for (8.77) to be well defined. Similarly, the sum of squares term for effort is modified to be

$$\text{RSS}(E) = \sum_g \lambda_{Eg} \sum_t (\ln F_{t,g} - \ln q_g - \ln E_{t,g})^2, \quad (8.80)$$

where q_g is catchability for fully recruited ages and λ_{Eg} is the prespecified weighting term for gear type g , representing the ratio of the variance of logarithmic catch of the standard gear type to logarithmic effort.

The major advantage to stratified catch-age analysis is that it fully accounts for the different gear types affecting the population. Also, the separability assumption is more likely to be satisfied by gear type than with pooled data. The number of observations is also increased by including different gear types.

The major disadvantage of stratified analysis is its greater complexity compared to regular catch-age analysis. Also, the data are broken into smaller pieces, which exhibit greater variability than pooled data. The inclusion of a gear type with high variability or bias could easily overwhelm the other data and produce biased estimates if not weighted properly. There are more parameters to be estimated, so it takes more time to complete an analysis.

8.2.7. Miscellaneous Alternative Approaches

Linear models

Shepherd and Nicholson (1986, 1991) provide an approximation to the general catch-age relationship (8.60), which results in $\ln C_{a,t}$ being written as a linear model with age, year, and year-class parameters. Constraints must be imposed on the parameters for estimability; however, such constraints may not be appropriate biologically and cannot be tested. This approach has been further generalized with interaction terms by Pope and Stokes (1989).

VPA and cohort analysis across time

Cohort analysis can be applied over several years by specifying terminal fishing mortality for each year-class. In the last year, this is frequently done by using the separability assumption with auxiliary estimates of selectivity. An algorithm for this approach is shown in figure 8.6, showing the sequence of calculations. This approach is amenable to implementation on a spreadsheet. As spreadsheets have the ability to optimize an

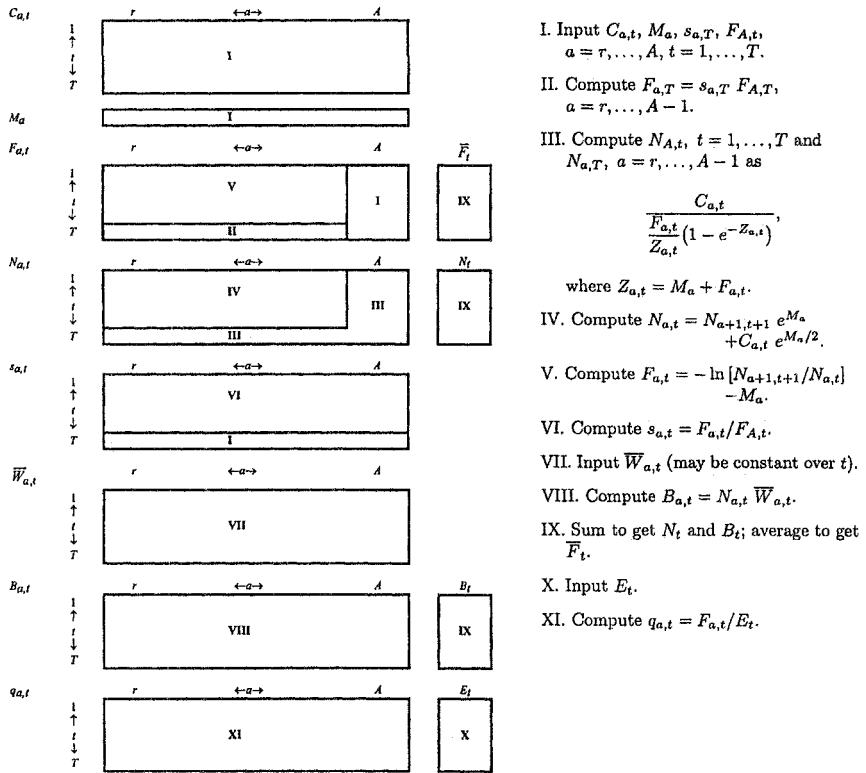


Figure 8.6. One possible algorithm for implementation of cohort analysis for data collected over years and ages.

objective function, auxiliary information can also be included to permit estimation of selectivity in the last year and terminal fishing mortalities. An example of this approach is given by Wespestad (1993).

Incorrect specification of natural mortality leads to incorrect trends in abundance and fishing mortality (Bradford and Peterman 1989). Trends in catchability may lead to inaccurate values of terminal fishing mortality, which in turn lead to errors in trends of abundance and fishing mortality. Furthermore, the relationship, or lack thereof, between recruitment and oceanographic variables can be incorrectly determined when M is mis-specified (Lapointe and Peterman 1991).

In the situation where the oldest age is a plus group (denoted $A+$ as before) and $N_{A+,t}$ represents the abundances of several year-classes in year t , the following modifications are necessary for cohort analysis (J. Collie, personal communication, 1991). If fishing and natural mortalities are assumed constant for all ages in the plus group, then the estimate of terminal abundance, $N_{A+,t}$, can be calculated from (8.33) with A replaced with $A+$. The abundance for the plus group in year $t + 1$ is made up of those in the plus group that survive during year t plus those at age $A - 1$ that survive during year t , which results in

$$N_{A+,t+1} = (N_{A+,t} e^{-M_{A+}} - C_{A+,t} e^{-M_{A+}/2})$$

$$+ \left(N_{A-1,t} e^{-M_{A-1}} - C_{A-1,t} e^{-M_{A-1}/2} \right).$$

Solving for $N_{A-1,t}$ results in

$$N_{A-1,t} = N_{A+,t+1} e^{M_{A-1}} - N_{A+,t} e^{M_{A-1}-M_{A+}} + C_{A+,t} e^{M_{A-1}-M_{A+}/2} + C_{A-1,t} e^{M_{A-1}/2}.$$

For other ages, the standard back-calculation (8.38) applies. The number at age A (without the rest of the plus group) is

$$N_{A,t+1} = \left(N_{A-1,t} e^{-M_{A-1}} - C_{A-1,t} e^{-M_{A-1}/2} \right),$$

from which fishing mortality can be calculated [cf. (8.39)] as

$$F_{A-1,t} = -\ln(N_{A,t+1}/N_{A-1,t}) - M_{A-1}$$

for age $A - 1$. This same equation applies to earlier ages by replacing A with $a + 1$ throughout, which is equivalent to using (8.39).

Tuned VPA

Several VPA- and cohort analysis-like approaches, reviewed by Pope and Shepherd (1985), attempt to use auxiliary information to determine terminal fishing mortalities. Most approaches involve a regression of fishing mortality versus fishing effort to estimate catchability and an iterative solution. These approaches often work with stratified catch-age data and are quick. In particular, the Laurec-Shepherd (1983) and a hybrid method appear to work well with simulated data. However, there is little theoretical work to justify or validate those approaches.

ADAPT

An approach of including auxiliary information into cohort analysis or VPA, called the ADAPT (shorthand for “adaptive framework”) approach, has evolved, with its development found mostly in the gray literature (Perrick 1985, Gavaris 1988, Conser and Powers 1989, Conser 1993). Various least squares algorithms have been used to obtain parameter estimates.

Gavaris (1988) first coined the term ADAPT and presented two scenarios. In scenario A, catch, C' , and a survey index, I' , are available for each age and year. The index is assumed proportional to abundance for each age over years with additive error ($I_{a,t} = q_a N_{a,t}$, $I'_{a,t} = I_{a,t} + \epsilon$). No separability assumption is made, and estimates of terminal abundance for each cohort, fishing mortality by age and year, and the calibration coefficients q_a are obtained by minimizing the weighted sum of squares

$$\text{RSS}_A = \sum_a \sum_t w_{C,a,t} (C'_{a,t} - C_{a,t})^2 + \sum_a \sum_t w_{I,a,t} (I'_{a,t} - I_{a,t})^2,$$

where w refers to weights applied to each datum. According to Gavaris (1988), each weight is the inverse of the estimated variance of the catch or survey index based on the sampling design. As this scenario represents a large number of parameters to be

estimated ($A'T + 2A' + T - 1$) from only $2A'T$ observations, this approach is rarely used.

Scenario B is a VPA-type approach that assumes error only in the auxiliary indices. The indices may be from surveys or from the fisheries (i.e., CPUE data). The basic framework involves the VPA or cohort analysis back-calculation for abundance [(8.34) or (8.38)] and a set of indices of abundance $\{I'_{i,a,x}\}$ for index i , survey years x , and possibly different age ranges for each index. The assumption is made that each index is linearly related to abundance with additive error; that is,

$$\begin{aligned} I'_{i,a,x} &= q_0,i,a + q_1,i,a N_{a,x} + \epsilon \\ &= I_{i,a,x} + \epsilon, \end{aligned}$$

where q_0 and q_1 are calibration coefficients for each index and age. Parameter q_0 is an optional intercept term, which allows an index to be linearly related to abundance without being directly proportional. Once again, no separability assumption is made, but in this case estimates of abundance and fishing mortality by age and year follow from VPA or cohort analysis back-calculations, given initial estimates of terminal abundance. Only the terminal abundances and calibration coefficients, q_a , are estimated by minimizing

$$\text{RSS}_B = \sum_i \sum_a \sum_t w_{i,a,t} (I'_{i,a,t} - I_{i,a,t})^2.$$

In practice, terminal abundances are not directly estimated; some structure is imposed which allows the terminal abundances to be calculated indirectly or by ad hoc approaches.

The weights may once again be chosen through measurement error considerations. Other weighting considerations include weights to stabilize the variance of the survey indices and weights to stabilize the variance across years to counteract the convergence properties of VPA (Conser and Powers 1993). Conser and Powers also suggested the method of iterative reweighting, wherein the weights are estimated iteratively as a part of the estimation procedure. Although this is theoretically possible, a major caveat is that such a procedure depends on the model assumption that each index is proportional to abundance. In practice, indices may have different trends, and the method of iterative reweighting can favor an index that is biased if it has low variability among indices in relationship to estimated abundance.

Other extensions to the ADAPT scenario B approach include equations for a plus group and stratification by gear type (Conser and Powers 1993). The main advantages of this approach are the lack of the separability assumption, parameter parsimony, and use of diagnostics (Conser 1993). The main disadvantages are the assumption of no error in the catches and the ad hoc approaches to setting terminal abundance.

More complicated models

Collie and Sissenwine (1983) developed a combined measurement error and process error model that models survival as a random variable and applied the model to relative abundance data. Mendelsohn (1988) generalized their approach by allowing the underlying population dynamics to be random and by using a combination of the Kalman filter and the E-M algorithm to obtain MLEs. Lassen (1983) developed a model that does not make a separability assumption. At least $A'T$ parameters must be estimated

in these models. Gudmundsson (1987, 1994) also did not make the separability assumption but rather assumed that fishing mortality at age follows a time series process. It appears to produce reliable estimates but takes a substantial amount of time for convergence. Myers and Cadigan (1995) extended the typical catch-age analysis to include correlated errors. Schnute and Richards (1995) gave a state space formulation for catch-age analysis. The extension of catch-age analysis to a migratory population is described in chapter 10.

AD Model Builder

This assessment method is a framework for general model building using an automatic differentiation (AD) algorithm to optimize an objective function (Fournier 1996). While it is a general approach for use in nonlinear modeling and statistics, it has particular applicability for both age- and length-structured population assessment. A variety of robust objective functions can be used to minimize the influence of outliers, and a variety of measurement and process errors can be included. Model parameters can be replaced by random variables with Bayesian prior distributions and/or with time series relationships like those used by Gudmundsson (1994). For example, selectivity can be a random variable related to the previous year's selectivity with an error term, such as $s_{a,t} = s_{a,t-1} \exp(\epsilon_t)$. Posterior distributions for desired quantities (such as exploitable biomass for the most recent time period) can be readily obtained to present the uncertainty present in parameter estimates. The flexibility of its approach means that there can be hundreds of parameters estimated; an unresolved issue is whether there is an optimal number of estimated parameters for stock assessment models. A test of modern stock assessment models by means of computer simulation suggested that this method offers much promise for future stock assessment (NRC 1998a), although no one method emerged as best and large errors in stock assessments did occur. This approach has been applied to walleye pollock (Ianelli 1996, Hollowed et al. 1997), sablefish (Sigler et al. 1997), and Pacific halibut (Parma and Sullivan 1998).

Bayesian estimation

An important direction for age-structured assessment is the use of Bayesian methods. McAllister and Ianelli (1997) showed the use of the sampling-importance resampling (SIR) algorithm in conjunction with the Bayesian approach of treating some model parameters as having prior distributions. As a result, the uncertainty in stock assessment is made explicit by providing posterior probability distributions for quantities of interest such as recent biomass, recruitment, and recommended catch levels. They provided an explicit algorithm for performing the analysis and compared their approach to Markov Chain Monte Carlo (MCMC) and adaptive importance sampling (AIS) methods. They showed that the use of catch-age data in conjunction with relative indices of abundance in such a Bayesian setting can lead to increased precision in estimates of population parameters. In a companion paper (McAllister and Pikitch 1997), this approach was used to address the issue of the design of a survey. The Bayesian approach was used in a decision analytic framework to determine how the survey frequency and precision affected estimated biomass and net present value of a fish population under a variety of stock assessment and management scenarios.

8.2.8. Computer Programs

Most catch-age analyses beyond catch curve and cohort analyses require a computer. Many packages were developed in the 1980s to perform sophisticated analyses. Generally, it is best to contact the author for the most up-to-date version of the program; most of these products are not sold commercially. Further information can be obtained from review articles by Megrey (1989), Anon., Forschungszentrum Jülich (1992), and ICES (1993), and NRC (1998a), which compare features among different methods. There is some confusion between a method and its computer implementation, but the comparisons are generally helpful.

Features of several computer programs from Anon., Forschungszentrum Jülich (1992, table 3.1) are given in table 8.20. The ADAPT approach (section 8.2.7) has a general-purpose program that has been used in assessments done by CAFSAC, NAFO, and ICCAT. CAGEAN implements the approaches described by Deriso et al. (1985, 1989), summarized in sections 8.2.5 and 8.2.6. Tuned VPA methods are summarized by Pope and Shepherd (1985). XSA is extended survivors analysis (Anon., Forschungszentrum Jülich 1992). TSER is the time series approach of Gudmundsson (1987, 1994). Stock synthesis is a versatile catch-age method that incorporates most of the features in section 8.2.5 and section 8.2.6 and also aging errors, yield and average weight, and length information (see chapter 9) (Methot 1989, 1990). Stock synthesis is widely used by scientists on the west coast of the United States. Each program has its advantages and disadvantages, as table 8.20 indicates.

In addition, we have added two columns for two recent approaches. The first is a spreadsheet approach, which simply carries out the calculations for the formulae of any age-structured method. Modern spreadsheets have optimizer software included, which makes it easy to obtain parameter estimates. Somewhat trickier but still possible is the estimation of SEs with Hessian or bootstrap methods. The main advantages are the flexibility of designing an analysis specific to the data set of interest and not being limited by the features of a canned program and the convenience of having all main and auxiliary calculations and graphics readily available in a single spreadsheet. The major disadvantages are that the spreadsheet must be adapted to each new data set, and that calculations can be quite slow with a large enough data set, depending on the power of the computer used.

The second program is associated with the ADMB approach (Fournier 1996). This is a full-featured program and is unique in allowing straightforward incorporation of process errors and Bayesian methods. Unlike the other programs, this package requires learning a programming interface language akin to C++.

8.3. ESTIMATION OF NATURAL MORTALITY

Natural mortality, M , is a key population parameter common to most analyses found in this book. Its estimation has not been presented earlier because some of the methods are found in this chapter. Natural mortality is also one of the most difficult parameters to determine, due to the confounding effects of recruitment, fishing mortality, and natural mortality. In addition, it is difficult to collect specific data to infer or estimate natural mortality values, because rarely is natural mortality observed directly. Good overviews of the estimation of natural mortality have been written by Seber (1982, 1986), Vetter

Table 8.20. Attributes of various age-based assessment methods (modified from Anon., Forschungszentrum Jülich, 1992, table 3.1, to add columns for spreadsheet and AD Model Builder and two new rows at bottom).

	ADAPT	CAGEAN	Tuned VPA	XSA	TSER	Stock synthesis	Spreadsheet	AD Model Builder
Flexibility and operator skill								
Separability	High	Moderate	Low	Low	High	Very high	Moderate	Very high
At fleet/index level	Yes	Yes	Yes	Yes	No	Yes	Option	Option
At total fishery level	No	Yes	No	No	No	Option	Option	Option
Explicit objective function	Least squares	Least squares	None	Least squares	Yes	Max. likelihood	User-defined	User-defined
Allowance for errors								
In catch data	Rarely	Yes	No	No	Yes	Yes	Yes	Yes
In final year indices	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes
Constraint on selectivity on some ages								
Fishing mortality	Usually	No	Yes	No ^a	Weak	No	Option	Option
Catchability	Rarely	Yes	No	Yes	Weak	No	Yes	Yes
Allowance for non-aged data								
Length compositions	Option	No	No	No	No	Yes	With difficulty	Yes
Bulk indices	Yes	Yes	No	No	No	Yes	Yes	Yes
No. of parameters estimated	Low	Moderate	Low	Low	High	High	Low to High	Very high
Computation time	Moderate	Moderate	Low	Low	High	High	High	Moderate
Process errors	No	No	No	No	No	No	User-defined	Yes
Bayesian analysis	No	No	No	No	No	No	Not easily	Yes

^aYes if shrinkage is employed.

(1988), Ralston (1987) for snappers and groupers, and Shepherd and Breen (1992) for abalone. Pope (1975) presented an interesting derivation of the theorem " $M = 0.2$ " starting with the statement " $M = 0.7$ ".

Usually, natural mortality is treated as a fixed constant, M , although in reality it is a random variable over time, age, and year-class. Caddy (in press) proposed an inverse relationship between natural mortality and age based on theoretical considerations. Shepherd and Breen (1992) described variation in natural mortality due to age, density effects, latitude (stock), predation, and habitat for abalone.

In many of the methods below, total mortality, $Z = F + M$, is estimated first rather than natural mortality. To estimate M , either an independent estimate of fishing mortality, F , is needed, or at least two values of fishing effort, E , associated with fishing mortality are needed. In the latter case, the total mortality relationship becomes

$$Z_i = M + q E_i, \quad (8.81)$$

where subscript i denotes each observation. This equation can be viewed as a linear regression relationship, so that the estimate of M is simply the y -intercept of the regression line corresponding to $E = 0$, or equivalently $F = 0$. This method often does not provide good estimates in practice because relatively large measurement errors often occur in Z and E , too few data are obtained, and the contrast in E is too small.

At least six different approaches can be used to estimate natural mortality (Vetter 1988, Shepherd and Breen 1992): (1) catch curve analysis, (2) LFA and related analyses, (3) mark-recapture experiments, (4) collection of dead organisms, (5) fitting population models, and (6) life-history (or meta-) analysis. Due to their unique nature, mark-recapture and life-history analysis are covered in the most depth, with commentary on the other topics.

8.3.1. Catch Curve Analysis

Catch curve analysis was covered in section 8.2.2 and has had a variety of applications to the estimation of natural mortality. Catch curve analysis is frequently applied to age composition data from the early history of a fishery where F is known to be negligible. In this case, the negative of the slope of the catch curve is an estimate of natural mortality. If applied to a "synthetic" cohort, this method requires at least no trend in recruitment, which is usually untestable. An alternative approach is to use (8.81), where Z_i is the negative of the slope of an actual cohort, and E_i is average fishing effort over the same years used in its catch curve analysis.

8.3.2. LFA and Related Analyses

LFA was covered in section 8.1.1 and the estimation of Z was described. The use of (8.81) or auxiliary information about F would be required to obtain M . If fishing effort, and, consequently, fishing mortality varies much over time, LFA is likely to be inaccurate. Its other major limitation is the assumption that recruitment and prerecruit mortality are constant.

Under similar equilibrium assumptions, some simple methods exist to determine total mortality, Z (Beverton and Holt 1957, Shepherd and Breen 1992). If the LVB growth model (see section 4.2.1) for the length-age relationship is assumed, then the following relationship from Beverton and Holt (1957) can be derived:

$$Z = \kappa \frac{L_\infty - \bar{L}}{\bar{L} - L_c}, \quad (8.82)$$

where \bar{L} is average length in a sample, and L_c is length at first capture. In this method, gear selectivity is assumed to be knife-edge at length L_c with constant mortality at larger lengths. Several related methods are reviewed in Hoenig et al. (1983) and Shepherd and Breen (1992).

8.3.3. Mark-recapture Experiments

Mark-recapture is conceptually one of the better approaches for estimating mortality because the known number of fish released and followed over time can only die or emigrate. Most of the basic techniques such as the commonly used Jolly-Seber method, other mark-recapture methods for single and multiple releases for closed and open populations, and various catch-effort methods are described by Seber (1982), but we present some techniques especially useful for fisheries data.

Suppose that a fish population is subject to fishing mortality, F , and constant natural mortality, M , and that N_0 fish are marked at a particular time. Recaptures come from the fishery, which is assumed to have constant catchability, or $F = q e$, where e is fishing effort. Data consist of the numbers $\{m_i\}$ caught in each time period i , the midpoints of the time periods $\{t_i\}$, and the fishing effort $\{e_i\}$ expended in period i . Define cumulative effort, E_i , up to and including period i as $\sum_{x=1}^i e_x$. Chapman (1961) derived the following recaptures per unit effort model, also given in Seber [1982, (8.12)]:

$$\ln \frac{m_i}{e_i} = \ln(qN_0) - M \frac{t_{i-1} + t_i}{2} - q \frac{E_{i-1} + E_i}{2} + \epsilon_i, \quad (8.83)$$

where ϵ_i is an error term.

Seber (1982, section 8.3.1) argued that the dependent variables can be considered independently distributed with approximately constant variance. Estimation of q and M follows from linear regression. Parameter N_0 can either be treated as known or can be estimated from the regression. If treated as known, then nonlinear regression can be used to estimate the other parameters q and M . This approach is advantageous in reducing the number of parameters to be estimated from three to two. If treated as unknown, then a comparison of its estimate with its known value can be used to infer initial tag loss, initial tagging mortality [type I loss of Ricker (1975a)], or an initial change in vulnerability.

Incidentally, (8.83) is a generalization of the well-known DeLury method for estimating abundance, one of the “removal” methods (Seber 1982). As such, it can be used for any population (not just a marked population) not subject to immigration, recruitment, or emigration.

A generalization of this approach for time-dependent behavior follows from a model in Treble et al. (1993). Let $X(t)$ be the disappearance rate of marks from an initially marked population, which combines the losses due to tag loss, natural mortality, and fishing mortality. Further, let α be the type I loss due to tag loss or mortality just after marking. Given N_0 marked members at time t_0 , the number of marked members at any later time is

$$N_t = \alpha N_0 \exp \left[- \int_{t_0}^t X(t) dt \right]$$

$$= \alpha N_0 \exp[-\bar{X}_t(t - t_0)], \quad (8.84)$$

where \bar{X}_t is the average disappearance rate up to time t . Rewriting (8.84) as a proportion, p_t , results in

$$\ln p_t = \ln \alpha - \bar{X}_t(t - t_0), \quad (8.85)$$

where p_t may be thought of as the proportion of marked members in the population at time t or the probability of finding a marked member at time t . Further assumptions can be made about sampling, mortality, and tag loss to provide an estimation framework using (8.85). Treble et al. (1993) gave an experimental design using this framework for detecting changes in tag loss over time. Beinssen and Powell (1979) used a simpler version of this model with constant mortality but also accounted for animal movement.

Another approach is to apply VPA or cohort analysis of section 8.2.3 to tag returns collected over time (Bayliff 1971, Reish et al. 1985, Deriso et al. 1991), where catch is equivalent to tag recoveries, and age is equivalent to time at large. The major advantage of this approach is that it requires only tag recapture data; fishing effort and the numbers of untagged fish are not needed. A value of terminal fishing mortality is selected, and the value of M is estimated as the value that makes the initial abundance equal to the original number tagged. The value of M obtained is made up of natural mortality, tag loss, and nonreporting, so adjustments are necessary to estimate only natural mortality. Methods of estimating tag loss and nonreporting rate are given by Seber (1982). This approach, called the Murphy-Tomlinson method, allows for disappearance of tags after the last reported tag return. It is more fully explained by Bayliff (1971) and applied to yellowfin tuna. Reish et al. (1985) derived the equation

$$N_0 = \sum_{t=1}^{\infty} C_t e^{M(t-1/2)},$$

where N_0 is the number of tags released at reference time 0, C_t is the number of tags recaptured during period t , and 0.5 is a time adjustment to the middle of each period. It follows from (8.45) by noting that parameters r and x in (8.45) correspond to 0 and $t - 1$ and letting $N_a \rightarrow 0$ as $a \rightarrow \infty$. This equation can be readily solved for M .

A related approach uses exact times of recapture (Hearn et al. 1987, Leigh 1988), denoted t_i for the i th recapture. Constants N_0 and t_0 remain as before. Using a stochastic model, Hearn et al. (1987) showed that, for a population with constant natural mortality and possibly variable fishing mortality, that M may be estimated by solving the equation

$$N_0 = \sum_{i=1}^N \exp[M(t_i - t_0)], \quad (8.86)$$

where N is the total number of recaptures. Parameters N_0 , t_0 , t_i , and N in (8.86) are equivalent to N_r , r , a_i , and C_a^- in (8.46); (8.86) then results from (8.46) by letting $N_a \rightarrow 0$. Thus, the experiment is assumed to proceed until no marked fish are alive, in order to derive (8.86). If the experiment does not proceed this long, (8.46) must be used directly, as shown in appendix B of Hearn et al. (1987). Leigh (1988) derived the result that this estimator of M is an MLE and showed that this estimator is superior to a simple method of Gulland (1955).

The general methodology of Hilborn (1990), covered in chapter 10, is also applicable to estimation of natural mortality. Although derived for the purpose of estimating movement, the special case of the method with no movement contains a natural survival parameter, which could be estimated.

8.3.4. Collection of Dead Organisms

The collection of dead organisms approach involves species for which the collection of assemblages of naturally dead organisms is feasible, such as abalone and other such molluscs (Shepherd and Breen 1992). Several mathematical techniques might be applied, including the previously mentioned catch curve and length frequency analyses, empirical estimation if absolute abundance and mortality are estimated, and perhaps change in ratio methods (Seber 1982). The problems with this method include emigration, disappearance of dead organisms, and incomplete or selective sampling.

8.3.5. Use of Population Models; Multispecies VPA

The delay-difference (chapter 5), age-based (chapter 8), and length-based (chapter 9) models in this book all have natural mortality explicitly embedded. These models are frequently fitted to data, and conceivably natural mortality could be estimated. As pointed out in section 8.2.4 for catch-age data, this approach is usually not successful because the objective function often does not vary much as a function of M . MacDonald and Butler (1982) pointed out the related difficulty of simultaneously estimating M and catchability, q , from CPUE data. However, this approach can often be used to determine which values of M are *not* consistent with the data.

Along these lines, information on gut contents indicates the amount of one species being eaten by another, and there are some impressive collections from the Pacific and the Atlantic. It is possible to include this information in population models for a set of species, where the connection is through the natural mortality parameters. This approach is known as multispecies VPA (Pope 1989). If m_{ij} is an index of the consumption of species i by species j , then natural mortality can be modeled as

$$M_i = \beta_0 + \sum_j \beta_j m_{ij},$$

and then included in the population models. If the $\{\beta\}$ are known (so that the total consumption of species i can be determined), then essentially natural mortality is known except for losses caused by disease and other similar factors. If the $\{\beta\}$ are not known, it might be possible to estimate them in the model. However, given the fact that single species analyses are complicated already, attempting joint estimation across species is equivalent to adding another dimension to the problem to be solved.

8.3.6. Life-History or Meta-analysis

The basis of life-history analysis is to use life-history parameters across a variety of species and environments to develop predictive regression relationships with natural mortality as the dependent variable. This approach of examining estimates of various population parameters from a variety of studies and using them in predictive relationships or as statistical distributions is becoming known as *meta-analysis* (NRC 1998a). It is common for species with high natural mortality [r -selected species, as in Gunderson (1980)] to have short lifespans, large gonads in relationship to body size, high

fecundities, fast growth rates, and small asymptotic sizes. This approach exploits the consistency in these life-history characteristics to estimate natural mortality. Four relationships are presented; for others, consult Vetter (1988).

In the Alverson-Carney (1975) procedure, the goal is to approximate the age, t^* , at which an unfished cohort reaches its greatest biomass (often referred to as the “critical age”). From chapter 6, the critical age for the LVB isometric model is

$$t^* = \frac{1}{\kappa} \ln \frac{M + 3\kappa}{M}, \quad (8.87)$$

from which M can be solved as

$$M = \frac{3\kappa}{\exp(t^*\kappa) - 1}. \quad (8.88)$$

If $M \approx \kappa$, then $t^* \approx 0.25 t_m$, where t_m is maximum observed age. However, Alverson and Carney found that the approximation was not warranted and determined empirically that

$$t^* \approx 0.38 t_m, \quad (8.89)$$

based on a regression with 63 values from the literature of species with this information.

Example 8.11. Atka mackerel

Ronholz and Kimura (1986) used the Alverson-Carney approach to estimate M for two stocks of Atka mackerel, one with $\kappa = 0.285$ and one with $\kappa = 0.66$. The maximum age for this species was thought to be from 10 to 12. The estimate of M ranges from 0.10 to 0.47 for the first stock and 0.32 to 0.82 for the second stock, as t_m ranges from 10 to 12 and t^* ranges from 0.25 to 0.38 of t_m . The wide range in M for each stock shows the sensitivity of this approach and the importance of having good information about longevity. ■

For the LVB allometric model, the number 3 in (8.87) and (8.88) can be replaced by the allometric parameter β . However, the Alverson-Carney approach has not been strictly reevaluated in terms of the LVB allometric model.

For molluscs, Hoenig (1983) found appropriate data from 28 stocks and empirically determined that natural mortality was inversely related to longevity. Assuming that the proportion that reach the maximum age is 0.01, a simple rearrangement of the exponential law of population decline (1.18) for an unfished population leads to the formula

$$M = -\ln(0.01)/t_m. \quad (8.90)$$

Shepherd and Breen (1992) noted that some authors prefer the assumption that the proportion surviving to t_m is 0.05.

Example 8.12. Razor clams

Razor clams in eastern Cook Inlet, Alaska, live approximately 12 years. The predicted natural mortality using Hoenig's approach ranges from 0.38 to 0.25 as the proportion surviving ranges from 0.01 to 0.05. ■

Pauly (1980) examined 175 stocks covering 84 species, including both freshwater and marine and both tropical and polar habitats. In addition to growth parameters, he

found that the mean water temperature experienced by the stock was important. His two predictive relationships are

$$\ln M = -0.4852 - 0.0824 \ln W_{\infty} + 0.6757 \ln \kappa + 0.4627 \ln T \quad (8.91a)$$

$$\ln M = -0.0152 - 0.279 \ln L_{\infty} + 0.6543 \ln \kappa + 0.4634 \ln T, \quad (8.91b)$$

where relationships have been converted from originally reported base 10 logarithms. Units for these variables are year⁻¹ for M and κ , grams for W_{∞} , degrees Celcius for T , and centimeters for L_{∞} . In (8.91a) and 8.91b), negative relationships between M and asymptotic sizes occur, and positive relationships between M and growth and between M and temperature occur.

Example 8.13. Canadian haddock

Campana (1987) used Pauly's relationship to estimate M for haddock in two areas. In area 4VW, the life-history parameters were $L_{\infty} = 71.8$, $\kappa = 0.233$, and $T = 3.9$, resulting in $M = 0.20$. In area 4X, the life-history parameters were $L_{\infty} = 68.3$, $\kappa = 0.309$, and $T = 5.24$, resulting in $M = 0.29$. The value $M = 0.2$ was previously used for haddock, which appears too low for area 4X. ■

Gunderson (1980) developed a relationship based on a gonadal index, GI, which is the ratio of gonad weight to total weight. With data from 10 species, he estimated the linear relationship

$$M = -0.37 + 4.64 \text{ GI}, \quad (8.92)$$

which explained 62% of the variability in M . This relationship is sensitive to the measurement of GI, as the value $GI = 0.1$ predicts $M = 0.09$ and the value $GI = 0.2$ predicts $M = 0.56$. To get the commonly used value $M = 0.2$, $GI = 0.125$.

The major limitation with the life-history approach is that the estimates of M and other life-history parameters used in developing the predictive relationships came from a variety of studies using different techniques. If some of the estimates are biased, then the resulting relationships are also biased. It is also important to recognize the limitation imposed by the data sets in the range of life-history parameters examined; the resulting relationships should not be extrapolated beyond this range. In practice, it is advisable to use a variety of approaches to estimate M .

Size-structured Models and Assessment Methods

Recently, much interest has developed in constructing population models based on length, weight, or size of individuals in the population. The reasons for this interest include the difficulty in obtaining accurate ages for a variety of fish species, the ready availability of length and size data, the desire to more accurately reflect the sampling distributions of the data collected, and the goal of integrating various sources of data collected from a fish population. Frequently, length data are the primary information available. Furthermore, population parameters such as mortality, gear selectivity, and maturity may be better related to size rather than to age. Finally, for some populations, it might be desirable to generalize age models to accommodate multiple classifications of an individual (age, length, weight, etc.).

In this chapter we present various approaches applicable to size-structured populations; the resulting models are frequently referred to as length-based models. As several books have been written on this topic, our goal is to provide a broad overview of the types of models available. The reader is referred to Beverton and Holt (1957), Ricker (1975a), Pauly and Morgan (1987), Getz and Haight (1989), Caswell (1989), and Manly (1990) for broader treatment of this topic. A computer package containing several length-based models (including Shepherd's length composition analysis, projection matrix, and Elefan approaches) called LFDA (length frequency distribution analysis) is also available (MRAG 1992). While a major impetus in the development of length-based methods has come from fisheries in tropical areas because of the difficulty in aging tropical species, we agree with Hilborn and Walters (1992) that fishery methods can be developed broadly enough to account for species no matter what particular area they come from.

In chapter 8, we considered various methods for determining age composition using length information: length frequency analysis and the use of age-length keys are the prominent examples. In this chapter, we incorporate length information directly into population models by specifying the growth process. One approach is to directly use a growth model from chapter 4; another approach is to derive transition probabilities from one length class to another from a particular growth model and statistical distribution. Any size or continuous classification variable can be used (length or weight are the

most common). The necessity of incorporating growth into length-based models makes them more complicated than age-structured models. One unresolved issue is whether the advantages of length-based models are outweighed by their complexity; it might be better to perform the conversion from size to age independently and then use age-structured models.

Nevertheless, there is a corresponding length-based method for each of the various age-structured approaches in chapters 6–8. In section 9.1, we present some simple approaches for constructing length-based models. In particular, we describe extensions of the delay-difference models in chapter 5 for size-structured populations. In section 9.2, we present stage-structured models analogous to the Leslie matrix and related approaches from chapter 7. In section 9.3, we present omnibus length–age population models incorporating stochastic growth elements. Finally, in section 9.4, we present size-based analogues to cohort analysis and catch-age analysis.

9.1. BASIC MODELS

Length frequency analysis is a basic model described in section 8.1 for converting length frequency information to age frequency information. It is further used in stock synthesis analysis (section 9.4 below) to perform this conversion.

There are also size-based models that do not perform such a conversion. Because these models implicitly deal with data that cannot be identified by year-class (which is a function of age), most of these methods and models are based on the assumptions of stationary recruitment and growth over time. Several approaches use the average size in the catch as a variable from which to infer mortality. (It is certainly not necessary to assume stationarity to derive size-based statistics: see section 5.3 for such statistics from the delay-difference model.)

9.1.1. Beverton-Holt Approach

The most common model used is the Beverton-Holt “per-recruit” model (Beverton and Holt 1957), which assumes that the LVB growth model applies to length, $L(t)$, and that mortality, Z , is constant beyond age of recruitment, t_c . With these assumptions, mean length, \bar{L} , in the catch can be defined from chapter 6 as

$$\bar{L} = \frac{\int_{t_c}^{t_\infty} L(t)N(t)dt}{\int_{t_c}^{t_\infty} N(t)dt} = \frac{\int_{t_c}^{t_\infty} L(t)e^{-Z(t-t_c)}dt}{\int_{t_c}^{t_\infty} e^{-Z(t-t_c)}dt}, \quad (9.1)$$

where t_∞ is maximum age. By writing the LVB model in terms of t_c and $L_c = L(t_c)$ as

$$L(t) = L_\infty - (L_\infty - L_c) e^{-\kappa(t-t_c)}, \quad (9.2)$$

the closed-form solution to (9.1) is easily shown to be

$$\bar{L} = L_\infty - \frac{(L_\infty - L_c)Z}{Z + \kappa} \left[\frac{1 - e^{-(Z+\kappa)(t_\infty - t_c)}}{1 - e^{-Z(t_\infty - t_c)}} \right]. \quad (9.3)$$

As $t_\infty \rightarrow \infty$, the last ratio in (9.3) approaches 1, so (9.3) becomes

$$\bar{L} = L_\infty - \frac{(L_\infty - L_c)Z}{Z + \kappa}. \quad (9.4)$$

By solving (9.4) for Z , total mortality can be found from LVB growth parameters, length at entry, and average length in the catch as

$$Z = \kappa(L_\infty - \bar{L}) / (\bar{L} - L_c). \quad (9.5)$$

This relationship has been used and investigated by many researchers (Beverton and Holt 1957, essays in Pauly and Morgan 1987, Wetherall et al. 1987, Ralston 1989, Ehrhardt and Ault 1992). An equivalent result as (9.5) but keeping t_∞ finite can be obtained from (9.4), which was derived in Ehrhardt and Ault (1992) and is given by

$$\left(\frac{L_\infty - L_{t_\infty}}{L_\infty - L_c} \right)^{Z/\kappa} = \frac{Z(L_c - \bar{L}) + \kappa(L_\infty - \bar{L})}{Z(L_{t_\infty} - \bar{L}) + \kappa(L_\infty - \bar{L})}, \quad (9.6)$$

where L_{t_∞} is length at maximum age, t_∞ . This nonlinear equation in Z can be solved numerically using standard techniques. Using deterministic and stochastic sensitivity analyses, Ehrhardt and Ault (1992) showed that (9.6) is better to use than (9.5) when exploitable life span is short compared to biological life span. The bias in using (9.5) when this is not true is always positive, though it diminishes with increasing Z . One disadvantage of using (9.6) is the extra variance in Z due to estimation variability of extra parameter L_{t_∞} . For other variations of this approach, see essays in Pauly and Morgan (1987). One obvious generalization of this approach is to consider gear selectivity as a function of length or size, written $s[L(t)]$. In contrast to (9.1), the definition of average length of the catch would then be

$$\bar{L} = \frac{\int_{t_c}^{t_\infty} L s(L) N(t) dt}{\int_{t_c}^{t_\infty} s(L) N(t) dt} = \frac{\int_{t_c}^{t_\infty} L s(L) e^{-Z(L)(t-t_c)} dt}{\int_{t_c}^{t_\infty} s(L) e^{-Z(L)(t-t_c)} dt}, \quad (9.7)$$

in which it is implicitly understood that $L \equiv L(t)$. The term $s(L)N(t)$ is just exploitable abundance, and $Z(L)$ is total mortality as a function of length. If natural mortality is $M(L)$ and full-recruitment fishing mortality is F , then total mortality is

$$Z(L) = s(L) F + M(L).$$

Discrete versions of these per-recruit models can also be constructed.

Example 9.1. Constant mortality and LVB growth

This example illustrates some of the effects of input parameters on the calculations of Z from the Beverton-Holt method and its modification, the Ehrhardt-Ault method (denoted Z_{EA}). Table 9.1 shows a set of LVB growth parameters for a hypothetical population and corresponding lengths at age. Recruitment and entry into the fishery are assumed to occur at age 1 and t_∞ is assumed to be 10, implying that individuals live up to and then die at the start of that age. Recruitment at age 1 is assumed to have an exponential trend with parameter r : $N_{1,t} = N_0 e^{rt}$. Abundance at other ages is found by assuming constant total mortality, Z : $N_{a,t} = N_{1,t-a+1} e^{-Z(a-1)}$. Table 9.1 shows abundance calculations for $Z = 0.2$ and $r = -0.05$. To deal with nonconstant recruitment, integrations in the numerator (n) and denominator (d) of (9.1) are done piecemeal for ages $a = 1, \dots, 9$:

Table 9.1. Input parameters for growth, mortality, and abundance for the case of declining recruitment ($r = -0.05$); length at age, $L(a)$; abundance, $N_{a,t}$; and sample calculations of the numerator (n_a) and denominator (d_a) for years 0 and 8 in illustration of the Beverton-Holt method.

	L_∞	100	Z	0.2						
	κ	0.2	t_c	1						
	t_0	0	t_∞	10						
	N_0	1000	r	-0.05						
		Age, a								
Year, t	1	2	3	4	5	6	7	8	9	10
$L(a)$	18.1	33.0	45.1	55.1	63.2	69.9	75.3	79.8	83.5	86.5
$N_{a,t}$										
0	1000	861	741	638	549	472	407	350	301	259
1	951	819	705	607	522	449	387	333	287	247
2	905	779	670	577	497	427	368	317	273	235
3	861	741	638	549	472	407	350	301	259	223
4	819	705	607	522	449	387	333	287	247	212
5	779	670	577	497	427	368	317	273	235	202
6	741	638	549	472	407	350	301	259	223	192
7	705	607	522	449	387	333	287	247	212	183
8	670	577	497	427	368	317	273	235	202	174
n_a										n
0	23155	30458	33634	34177	33101	31087	28586	25893	23195	263286
8	15521	20416	22546	22910	22188	20838	19162	17357	15548	176486
d_a										d
0	906	780	671	578	497	428	368	317	273	4820
8	608	523	450	387	333	287	247	213	183	3231

$$n_a = \int_a^{a+1} L(t)N(t)dt = \frac{N_a L_\infty}{Z} (1 - e^{-Z}) - \frac{N_a (L_\infty - L_a)}{Z + \kappa} [1 - e^{-(Z+\kappa)}]$$

$$d_a = \int_a^{a+1} N(t)dt = \frac{N_a}{Z} (1 - e^{-Z}),$$

and then added ($n = \Sigma n_a$, $d = \Sigma d_a$). These calculations are illustrated for years 0 and 8 in table 9.1.

Key statistic \bar{L} is then the ratio of these sums of the numerator and denominator terms ($\bar{L} = n/d$). In the Beverton-Holt method, Z is calculated from (9.5). In its modification from Ehrhardt and Ault (1992), Z is calculated by solving (9.6). Relative bias is then calculated as $(Z_x - Z)/Z$, in which Z_x is from method x . These calculations are illustrated in table 9.2 using information similar to that in table 9.1 for combinations of two values of Z and three values of r . In table 9.2, the value of the left-hand side equal to the right-hand side in (9.6) for the Ehrhardt-Ault method is given. The effect of changing t_c from 1 to 3 is also examined for one combination. Other parameters were varied in Ehrhardt and Ault (1992).

For the situation of constant recruitment ($r = 0$), calculations for each year and by year-class are identical when recruitment is constant. The Beverton-Holt method can have substantial bias due to the population having finite longevity. The positive bias is generally larger for lower values of Z and smaller differences between t_∞ and

Table 9.2. Illustration of the Beverton-Holt (BH) and Ehrhardt-Ault (EA) methods of estimating total mortality, Z , from length data.

	t	n	d	\bar{L}	Z_{BH}	Z_{EA}	LHS=RHS	$rb(Z_{BH})$	$rb(Z_{EA})$
$r = 0.0, Z = 0.2$									
	0	218261	4174	52.3	0.279	0.200	0.166	40%	0%
	8	218261	4174	52.3	0.279	0.200	0.166	40%	0%
	yc	218261	4174	52.3	0.279	0.200	0.166	40%	0%
$r = -0.05, Z = 0.2$									
	0	263286	4820	54.6	0.249	0.151	0.257	24%	-25%
	8	176486	3231	54.6	0.249	0.151	0.257	24%	-25%
	yc	218261	4174	52.3	0.279	0.200	0.166	40%	0%
$r = 0.05, Z = 0.2$									
	0	183583	3666	50.1	0.312	0.249	0.106	56%	24%
	8	273874	5468	50.1	0.312	0.249	0.106	56%	24%
	yc	218261	4174	52.3	0.279	0.200	0.165	40%	0%
$r = 0.0, Z = 0.2, t_c = 3$									
	0	166133	2525	65.8	0.331	0.200	0.247	65%	0%
	8	166133	2525	65.8	0.331	0.200	0.247	65%	0%
	yc	166133	2525	65.8	0.331	0.200	0.247	65%	0%
$r = 0.0, Z = 0.4$									
	0	107330	2432	44.1	0.430	0.401	0.027	7%	0%
	8	107330	2432	44.1	0.430	0.401	0.027	7%	0%
	yc	107330	2432	44.1	0.430	0.400	0.027	7%	0%
$r = -0.05, Z = 0.4$									
	0	122635	2671	45.9	0.389	0.351	0.042	-3%	-12%
	8	82204	1791	45.9	0.389	0.351	0.042	-3%	-12%
	yc	107330	2432	44.1	0.430	0.400	0.027	7%	0%
$r = 0.05, Z = 0.4$									
	0	95041	2235	42.5	0.471	0.448	0.018	18%	12%
	8	141784	3334	42.5	0.471	0.448	0.018	18%	12%
	yc	107330	2432	44.1	0.430	0.400	0.027	7%	0%

Calculations are shown using the information analogous to that in table 9.1 for various combinations of r and Z , where except as noted, $t_c = 1$. Calculations are done for years 0 and 8 and the year-class at age 1 in year 0 (labeled yc). Relative bias (rb) is shown for the two methods. LHS, left-hand side; RHS, right-hand side.

t_c . In this situation, the Ehrhardt-Ault method is unbiased. Similar results are found in Ehrhardt and Ault (1992).

For the situation of a recruitment trend, average length is still identical across years but different from that for a given year-class. Using average length from a given year can lead to substantial bias in Z from both methods. A negative trend in recruitment can result in less relative bias without regard to sign in the Beverton-Holt method over the Ehrhardt-Ault method because the inherent positive bias in the Beverton-Holt method is reduced. The use of average length from a given year-class produces identical results to the situation with no recruitment trend because data from only one year-class is used. The magnitude of relative bias is reduced for higher values of Z , as before.

In summary, the Ehrhardt-Ault method eliminates bias in estimating Z due to finite life span. However, it still can produce bias if there is a trend in recruitment. If it is possible to isolate length data from a year-class over time, this type of bias can also be eliminated. ■

9.1.2. Basic Size-based Models

Basic size-based models can be easily derived from their age-based counterparts by changing the metric from age (denoted t) to size (denoted y). For example, the simple cohort model of abundance from section 1.2 adapted for size-specific mortality is

$$\frac{dN}{dt} = -Z(y)N, \quad (9.8)$$

where $Z(y) \equiv Z[y(t)]$ is total instantaneous mortality at size y . If the relation between size and age is $dy/dt = g(y)$ [in which $g(y)$ is one of the instantaneous growth models from chapter 4], then by using the chain rule,

$$\frac{dN}{dy} = \frac{dN}{dt} / \frac{dy}{dt} = -\frac{Z(y)}{g(y)}N. \quad (9.9)$$

Thus, the instantaneous relative change in abundance as a function of size is the negative of the ratio of instantaneous mortality and growth (Beyer 1989). If N_r is abundance at recruitment size $y(t_r) = y_r$, then the solution to (9.9) is

$$N(y) = N_r \exp \left[- \int_{y_r}^y \frac{Z(y)}{g(y)} dy \right]. \quad (9.10)$$

Similarly, the analogous per-recruit models for catch, C , and yield, Y , from chapter 6 as a function of size can be written

$$C = \int_{y_1}^{y_2} \frac{F(y)}{g(y)} N(y) dy \quad (9.11)$$

$$\text{and} \quad Y = \int_{y_1}^{y_2} \frac{F(y)}{g(y)} N(y) W(y) dy, \quad (9.12)$$

where y_1 and y_2 are the sizes of interest, $F(y)$ is instantaneous fishing mortality, and $W(y)$ is average weight as a function of size y .

Such models are developed more fully by Beyer (1989) and Schnute (1987). In particular, Beyer developed a size-based theory to explore recruitment stability and survival. Schnute developed a general class of delay-difference models with respect to fish size. This class is further generalized to include stochastic elements by Fournier and Doonan (1987) and Schnute et al. (1989a,b). Central to Schnute's approach is the development of probability distributions for abundance and related parameters as a function of size. A straightforward delay-difference model applicable to whales was developed by Sampson (1990).

Partial differential equations provide a compact description of how growth rate and mortality rate determine the cohort size distribution at each given age. The Von Foerster (1959) equations for cohort dynamics can be written as

$$\frac{\partial N(y, t)}{\partial t} + \frac{\partial [g(y, t)N(y, t)]}{\partial y} = -Z(y, t)N(y, t)$$

which describes the changes in $N(y, t)$ as the cohort ages for a given initial size distribution, $N(y, 0)$, at coded age 0. Wismer et al. (1985) applied this model to first-year

dynamics of smallmouth bass (*Micropterus dolomieu*). Equivalent integral equation representations, which capture the full life cycle of animals, were derived by Pollard (1973), generalized to a stochastic model by Kirkpatrick (1984), and generalized to nonlinear dynamics by Botsford (1981a).

Example 9.2. Constant mortality and LVB growth

This example illustrates the equivalence between age- and size-structured versions of the single cohort model. Suppose that a population experiences constant natural mortality, Z , past age t_r and follows the LVB growth model of section 4.2. At a given age, t , population abundance is given by

$$N(t) = N_r e^{-Z(t-t_r)}.$$

For the LVB model, $dy/dt = g(y) = \kappa(y_\infty - y)$ with the solution (with respect to t_r)

$$y(t) = y_\infty - (y_\infty - y_r)e^{-\kappa(t-t_r)}.$$

From (9.10), it can be shown that the size-based solution is

$$N(y) = N_r \left(\frac{y_\infty - y}{y_\infty - y_r} \right)^{Z/\kappa}.$$

That this equation is equivalent to the age-based version follows from

$$(y_\infty - y)/(y_\infty - y_r) = \exp[-\kappa(t - t_r)],$$

which comes directly from the LVB solution above. ■

9.2. STAGE-STRUCTURED MATRIX MODELS

The generalization of the Leslie matrix age-structured model from chapter 7 is straightforward. A number of books and essays have covered this generalization, including those by Lefkovitch (1965), Usher (1966), Sainsbury (1982), Caswell (1989), Getz and Haight (1989), Law and Edley (1990), Manly (1990), Sullivan et al. (1990), Sullivan (1992), and Butler et al. (1993). The principal feature of this approach is to use size classes or some other classification variable rather than age classes to represent the characteristics of the population. The classes may also represent some stage of development, sex, or region (for the latter, see chapter 10).

In a one-year transition, individuals in a size class may stay in the same size class or transcend into some larger size class due to growth. Let $P_{x,y}$ be the proportion of individuals surviving that move from size class x to size class y , for which $P_{y,y}$ is the proportion staying in size class y . The constraint $\sum_y P_{x,y} = 1$ is imposed so that survivors appear in some size class. Population abundance in the first class comes from the combination of surviving egg production and surviving individuals in the first class that do not grow out of the class. This combination can be written

$$N_{1,t+1} = S_0 \sum_{x=1}^Y f_x N_{x,t} + S_1 P_{1,1} N_{1,t}, \quad (9.13)$$

where Y is the number of size classes, $N_{x,t}$ is population abundance in size class x at time t , f_x is net fecundity, and S_x is survival. Note that growth and survival are assumed to be independent and that the convention of modeling a female population is being used. For any other size class ($y > 1$), population abundance is the combination of the survivors of size classes that grow into the given size class and the survivors of that size class that do not grow out of it. This combination can be written as

$$N_{y,t+1} = \sum_{x=1}^Y S_x P_{x,y} N_{x,t}, \quad (9.14)$$

where the last term of the sum (y) represents the nongrowing survivors of that class. The pair of equations (9.13) and (9.14) can be written in matrix form as

$$\mathbf{N}_{t+1} = \mathbf{M} \mathbf{N}_t, \quad (9.15)$$

where \mathbf{N}_t is the vector of the $\{N_{y,t}\}$ and projection matrix \mathbf{M} equals

$$\begin{pmatrix} S_1 P_{1,1} + S_0 f_1 & S_0 f_2 & S_0 f_3 & \cdots & S_0 f_{Y-1} & S_0 f_Y \\ S_1 P_{1,2} & S_2 P_{2,2} & 0 & \cdots & 0 & 0 \\ S_1 P_{1,3} & S_2 P_{2,3} & S_3 P_{3,3} & \ddots & \vdots & \vdots \\ \vdots & \vdots & \vdots & \ddots & 0 & \vdots \\ \vdots & \vdots & \vdots & \ddots & S_{Y-1} P_{Y-1,Y-1} & 0 \\ S_1 P_{1,Y} & S_2 P_{2,Y} & \cdots & \cdots & S_{Y-1} P_{Y-1,Y} & S_Y P_{Y,Y} \end{pmatrix},$$

where $P_{Y,Y} = 1$ by definition. Given an initial condition \mathbf{N}_0 , the population can be projected by repeated application of (9.15).

This matrix equation can be written as

$$\mathbf{N}_{t+1} = (\mathbf{PS} + \mathbf{R}) \mathbf{N}_t, \quad (9.16)$$

where projection matrix \mathbf{M} is elaborated as $\mathbf{PS} + \mathbf{R}$. The growth transition matrix \mathbf{P} is the lower triangular matrix

$$\mathbf{P} = \begin{pmatrix} P_{1,1} & 0 & 0 \\ \vdots & \ddots & 0 \\ P_{1,Y} & \cdots & P_{Y,Y} \end{pmatrix},$$

survival matrix \mathbf{S} is the diagonal matrix

$$\mathbf{S} = \begin{pmatrix} S_1 & 0 & 0 \\ 0 & \ddots & 0 \\ 0 & 0 & S_Y \end{pmatrix},$$

and recruitment matrix \mathbf{R} is the matrix

$$\mathbf{R} = \begin{pmatrix} S_0 f_1 & \cdots & S_0 f_Y \\ 0 & \cdots & 0 \\ 0 & \cdots & 0 \end{pmatrix}.$$

An alternative form of this model is

$$\mathbf{N}_{t+1} = \mathbf{PSN}_t + \mathbf{R}_t, \quad (9.17)$$

where \mathbf{R}_t is the vector

$$\mathbf{R}_t = \begin{pmatrix} S_0 N_{0,t} \\ 0 \\ \vdots \\ 0 \end{pmatrix},$$

and $N_{0,t}$ is egg production given by $\sum_{x=1}^Y f_x N_{x,t}$. This form of the model also allows any submodel of recruitment \mathbf{R}_t and/or immigration to be incorporated and has been used by Getz and Haight (1989), Sullivan et al. (1990), and Sullivan (1992); see section 9.4.2.

Special cases and other variations of this stage-structured model exist. The Leslie matrix model is a special case with $P_{y-1,y} = 1$ and all other $P_{x,y} = 0$. The Usher model (Usher 1966, Getz and Haight 1989, Manly 1990) is a special case with $P_{y-1,y} = p_y$, $P_{y,y} = 1 - p_y$, and all other $P_{x,y} = 0$; this model permits growth transitions only one stage at a time. Getz and Haight (1989) derived optimal harvesting results for this model. Butler et al. (1993) determined parameters for this model from northern anchovy and Pacific sardine data to examine how population growth is affected by variations in life-history parameters.

The Lefkovitch model (Lefkovitch 1965, Manly 1990) allows a general projection matrix $\mathbf{M} = \{m_{x,y}\}$ with possibly all nonzero elements. Presumably this model was constructed to permit maximum flexibility in life-history modeling. However, Manly (1990) pointed out that it is difficult to estimate this matrix, and some elements may have estimates that are negative. Indeed, the examples presented by Lefkovitch (1965) do have negative elements, which is counterintuitive. Caswell (1989) showed how to incorporate complicated life histories into a Lefkovitch-type model, for which some of the elements are 0 based on the life history.

Law and Edley (1990) generalized the stage-structured approach to allow elements for both age and size. Caswell (1989) showed that this type of model is also pertinent for multiregional age-structured populations. Further details are given in chapter 10. Getz and Haight (1989) described nonlinear extensions to the stage-structured model.

The linear stage-structured model (9.15) has analogous stability properties to the linear age-structured model in chapter 7; these properties are described fully in Caswell (1989) and Getz and Haight (1989). Briefly, from Caswell (1989), the solution to the projection equation (9.15) can be written in terms of eigenvalues $\{\lambda_i\}$ and right eigenvectors $\{\mathbf{w}_i\}$ as

$$\mathbf{N}_t = \sum_{i=1}^Y c_i \lambda_i^t \mathbf{w}_i.$$

Thus, the long-term behavior of this equation depends on the magnitudes of the eigenvalues. The Perron-Frobenius theorem applies as long as elements of \mathbf{M} are non-negative. This theorem states that if \mathbf{M} is non-negative and primitive, then there exists a positive, real eigenvalue, λ_1 , that dominates all others. As a consequence, if $\lambda_1 > 1$, the population will eventually increase exponentially, and vice versa. If $\lambda_1 = 1$, the

population will eventually stabilize, a condition known as stationarity. The magnitude of increase or decrease each year in the limit is equal to the value of the dominant eigenvalue (i.e., $N_{t+1} = \lambda_1 N_t$), and this result applies to any one stage or the population total. Regardless of the value of λ_1 , the population will tend toward a stable stage distribution that is proportional to the dominant eigenvector, w_1 . One way to check that M is primitive is to determine if M^{Y^2-3Y+2} is positive (meaning all elements are positive). If matrix M is irreducible but imprimitive (all primitive matrices are irreducible), then the Perron-Frobenius theorem states that there are multiple eigenvalues with the same magnitude, which results in cyclic behavior. One way to check that M is irreducible is to determine if $(I + M)^{Y-1}$ is positive. Caswell (1989) pointed out that most linear stage-structured models have both primitive and irreducible projection matrices.

Example 9.3. Hypothetical population with five stages

This hypothetical population has growth transition matrix P , survival matrix S , and recruitment matrix R shown in table 9.3. The growth transition matrix is constructed to mimic rapid growth at the first stage (90% leave the first stage in one year), which is reduced at each subsequent stage. The survival matrix shows low survival (0.3) for the first stage and high survival (0.7) at remaining stages. The recruitment matrix is obtained from the fecundity vector, f , and the early life survival, S_0 , shown in the table. The fecundity vector shows positive fecundity starting at the third stage, which increases for the remaining two stages. (The value for S_0 was selected to give a stationary population.) The nonzero elements of the recruitment matrix are the products of early life survival and fecundity, as shown above (9.17). The projection matrix M shown in the table is then calculated as $PS + R$.

For an arbitrary initial recruitment vector, N_0 , shown in table 9.3, the population is projected over 10 years using (9.15) or (9.16). The relative composition of the population at the end of the time period is also shown. The population at each stage over the 10 years is shown in figure 9.1; it converges to a stationary population with a stable stage distribution.

Corresponding matrix statistics for projection matrix M are given in table 9.4. The dominant eigenvalue is 1, as expected for a stationary population. The two complex and two real subsequent eigenvalues have magnitudes less than the dominant eigenvalue. (The magnitude of the complex roots is $\sqrt{0.127^2 + 0.274^2} = 0.302$.) Thus, the population would be expected to converge to a stationary population level and a stable stage distribution. The dominant eigenvector is equal to the relative composition after 10 years, showing that convergence has occurred. The matrix $M^{5^2-3\times 5+2}$ is positive, so M is primitive, which confirms that a stationary and stable population should occur. The matrix $(I + M)^{5-1}$ is also positive, so M is irreducible. This result is expected because all primitive matrices are irreducible. ■

9.3. STOCHASTIC MODELS

Our description of stochastic models is drawn primarily from Deriso and Parma (1988) and Parma and Deriso (1990). They showed that by making some fairly general assumptions about stochastic growth and survival, in conjunction with some approximations made in the analysis of size-selective fishing mortality, one can write equations to propagate through time the probability density function (PDF) of size of individuals in the population by a recursive update of its parameters. Specifically, they used the

Table 9.3. A hypothetical example showing construction of a five-class length-structured projection matrix \mathbf{M} from growth transition matrix \mathbf{P} , survival matrix \mathbf{S} , and recruitment matrix \mathbf{R} .

\mathbf{P}	$\begin{bmatrix} 0.1 & 0 & 0 & 0 & 0 \\ 0.5 & 0.3 & 0 & 0 & 0 \\ 0.4 & 0.5 & 0.5 & 0 & 0 \\ 0 & 0.2 & 0.3 & 0.7 & 0 \\ 0 & 0 & 0.2 & 0.3 & 1 \end{bmatrix}$																																																																																								
\mathbf{S}	$\begin{bmatrix} 0.3 & 0 & 0 & 0 & 0 \\ 0 & 0.7 & 0 & 0 & 0 \\ 0 & 0 & 0.7 & 0 & 0 \\ 0 & 0 & 0 & 0.7 & 0 \\ 0 & 0 & 0 & 0 & 0.7 \end{bmatrix}$																																																																																								
S_0	0.014																																																																																								
\mathbf{f}'	(0 0 50 100 150)																																																																																								
\mathbf{R}	$\begin{bmatrix} 0 & 0 & 0.7 & 1.4 & 2.1 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$																																																																																								
\mathbf{M}	$\begin{bmatrix} 0.03 & 0 & 0.7 & 1.4 & 2.1 \\ 0.15 & 0.21 & 0 & 0 & 0 \\ 0.12 & 0.35 & 0.35 & 0 & 0 \\ 0 & 0.14 & 0.21 & 0.49 & 0 \\ 0 & 0 & 0.14 & 0.21 & 0.7 \end{bmatrix}$																																																																																								
$N_{l,t}$	<table border="1"> <thead> <tr> <th rowspan="2">l</th> <th colspan="10">Year, t</th> <th rowspan="2">Relative</th> </tr> <tr> <th>0</th> <th>1</th> <th>2</th> <th>3</th> <th>4</th> <th>5</th> <th>6</th> <th>7</th> <th>8</th> <th>9</th> <th>10</th> </tr> </thead> <tbody> <tr> <td>1</td> <td>400</td> <td>334</td> <td>363</td> <td>374</td> <td>374</td> <td>373</td> <td>372</td> <td>372</td> <td>373</td> <td>373</td> <td>373</td> <td>1.000</td> </tr> <tr> <td>2</td> <td>80</td> <td>77</td> <td>66</td> <td>68</td> <td>70</td> <td>71</td> <td>71</td> <td>71</td> <td>71</td> <td>71</td> <td>71</td> <td>0.190</td> </tr> <tr> <td>3</td> <td>140</td> <td>125</td> <td>111</td> <td>105</td> <td>106</td> <td>106</td> <td>107</td> <td>107</td> <td>107</td> <td>107</td> <td>107</td> <td>0.287</td> </tr> <tr> <td>4</td> <td>70</td> <td>75</td> <td>74</td> <td>69</td> <td>65</td> <td>64</td> <td>64</td> <td>64</td> <td>63</td> <td>63</td> <td>63</td> <td>0.170</td> </tr> <tr> <td>5</td> <td>60</td> <td>76</td> <td>87</td> <td>92</td> <td>93</td> <td>94</td> <td>94</td> <td>94</td> <td>94</td> <td>94</td> <td>94</td> <td>0.253</td> </tr> </tbody> </table>	l	Year, t										Relative	0	1	2	3	4	5	6	7	8	9	10	1	400	334	363	374	374	373	372	372	373	373	373	1.000	2	80	77	66	68	70	71	71	71	71	71	71	0.190	3	140	125	111	105	106	106	107	107	107	107	107	0.287	4	70	75	74	69	65	64	64	64	63	63	63	0.170	5	60	76	87	92	93	94	94	94	94	94	94	0.253
l	Year, t										Relative																																																																														
	0	1	2	3	4	5	6	7	8	9		10																																																																													
1	400	334	363	374	374	373	372	372	373	373	373	1.000																																																																													
2	80	77	66	68	70	71	71	71	71	71	71	0.190																																																																													
3	140	125	111	105	106	106	107	107	107	107	107	0.287																																																																													
4	70	75	74	69	65	64	64	64	63	63	63	0.170																																																																													
5	60	76	87	92	93	94	94	94	94	94	94	0.253																																																																													

Recruitment in turn is calculated from early life survival, S_0 , and fecundity vector \mathbf{f}' . The population is then projected over 10 years from the given initial length distribution at time 0. The relative length distribution at time 10 is also shown.

result in probability theory that when a Bayesian update of a normal PDF is made with another normal PDF, the updated PDF is also normal. In the jargon of probability theory, a normal PDF is said to be a “conjugate function” to a normal PDF. Such recursive equations permit a concise description of the size distribution at age based on mean and variance of a transformation of size. That in turns permits a concise description of estimation theory based on likelihood equations.

In the following development of the Deriso-Parma model, fish size, x_a , is defined as the Box-Cox or power transformation $x = (L^\gamma - 1)/\gamma$ of length L of an individual of age a . Size, then, is essentially equivalent to length L when $\gamma = 1$ and to $\ln L$ as

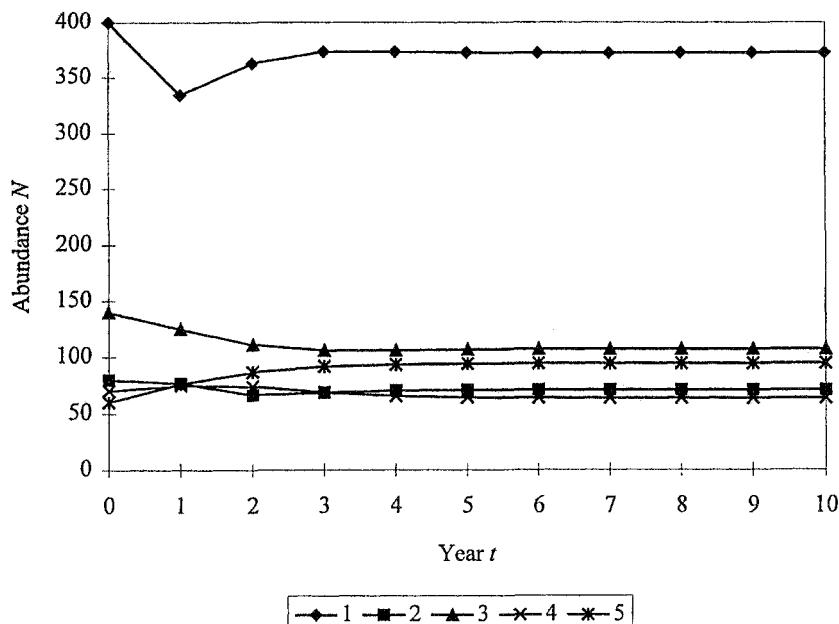


Figure 9.1. Projection of the hypothetical population in example 9.3 from an initial population at time 0 for 10 years using a stage-structured matrix model. Each curve represents a particular stage identified in the legend. All stages are converging to stationary population levels.

$\gamma \rightarrow 0$. Growth in size of an individual in the population is assumed to follow the Cohen-Fishman (1980) stochastic difference equation (4.93) of the form

$$x_{a+1} = \alpha + \rho x_a + \epsilon, \quad (9.18)$$

where $\epsilon \sim N(0, V_\epsilon)$. The power transformation allows one to incorporate any arbitrary degree of skewness in the distribution of size at age. With a logarithmic transformation, the model in (9.18) is a stochastic generalization of the Gompertz growth model applied to length. This can be seen by writing the deterministic Gompertz model (4.27) with $\rho = e^{-\kappa}$ in its integrated form

$$L_a = L_\infty \exp(-\rho^{a-a_0})$$

and then taking logarithms and differences. The parameter L_∞ above is equal to $\exp[\alpha/(1 - \rho)]$. The LVB (von Bertalanffy) length model is obtained for the transformation $\gamma = 1$. Variability in growth rates can be made proportional to expected growth increment by replacing the constant variance term above V_ϵ with $V_\epsilon(a) \propto V_\epsilon(0)\rho^a$. Phenotypic variability in growth can be modeled by allowing the α coefficient to vary among individuals.

The Cohen-Fishman stochastic model (9.18) can be written as an age-dependent model by following the treatment in section 4.7.3. Let $a = 0$ denote the initial coded age that we begin modeling a given cohort and assume that x_0 , the initial size of an

Table 9.4. Matrix statistics for the hypothetical example from table 9.3, including eigenvalue vector λ (the first element of which is the dominant eigenvalue λ_1), the dominant eigenvector w_1 , number of classes $Y = 5$, criterion matrix for a primitive matrix M^{Y^2-3Y+2} , and criterion matrix for an irreducible matrix $(I + M)^{Y-1}$.

λ	$\begin{bmatrix} 1.000 \\ 0.127+0.274 i \\ 0.127-0.274 i \\ 0.113 \\ 0.412 \end{bmatrix}$	(dominant)
w_1	$\begin{bmatrix} 1.000 \\ 0.190 \\ 0.287 \\ 0.170 \\ 0.253 \end{bmatrix}$	
M^{Y^2-3Y+2}	$\begin{bmatrix} 2.501 & 5.412 & 11.992 & 17.668 & 23.839 \\ 0.927 & 2.505 & 1.385 & 2.336 & 3.324 \\ 1.345 & 3.265 & 4.710 & 2.392 & 3.429 \\ 0.509 & 2.218 & 2.613 & 5.307 & 0.557 \\ 0.284 & 1.073 & 2.705 & 3.586 & 8.592 \end{bmatrix}$	
$(I+M)^{Y-1}$	$\begin{bmatrix} 0.180 & 0.532 & 0.794 & 1.015 & 1.263 \\ 0.034 & 0.101 & 0.151 & 0.193 & 0.240 \\ 0.052 & 0.152 & 0.228 & 0.291 & 0.362 \\ 0.031 & 0.090 & 0.135 & 0.173 & 0.215 \\ 0.046 & 0.134 & 0.201 & 0.257 & 0.319 \end{bmatrix}$	

individual aged 0 chosen at random, is distributed normally with mean $E_x(0)$ and variance $V_x(0)$. In the absence of size-specific mortality, the size (x) distribution of the cohort at age a is normal with mean and variance, respectively,

$$E_x(a) = \frac{\alpha}{1 - \rho} + \left[E_x(0) - \frac{\alpha}{1 - \rho} \right] \rho^a \quad (9.19)$$

$$V_x(a) = V_x(0) \rho^{2a} + V_\epsilon \frac{1 - \rho^{2a}}{1 - \rho^2}.$$

These two equations for size are generalizations of (4.96) and (4.97) for length from the LVB model.

Fishing gear is typically selective for specific sizes of fish. A length “separability” assumption is made so as to parameterize size-specific fishing mortality in a given year as the product of a size selectivity factor and full-recruitment fishing mortality. The probability of capture for an individual of size x in year t is given by

$$P(\text{fish captured}|x) = 1 - e^{-F(t,x)}, \quad (9.20)$$

where $F(t, x)$, size-specific fishing mortality rate for year t , is assumed to be separable into a product of a full-recruitment fishing mortality rate, F_t , and a selectivity factor, $S(x)$, which is only a function of size:

Table 9.5. Governing equations for growth and survival of a cohort.

Growth model	$x_{a+1} = \alpha + \rho x_a + \epsilon, \quad \epsilon \sim N(0, V_\epsilon)$
Fishing mortality risk model	$FS(x) = F(b_0 + b_1x + b_2x^2)$
Distribution of x in the cohort	$x_a \sim N[E_x(a), V_x(a)]$
Recursive equation for E_x	$E_x(a+1) = \alpha + \rho \left[\frac{E_x(a) - b_1 F V_x(a)}{2b_2 F V_x(a) + 1} \right]$
Recursive equation for V_x	$V_x(a+1) = \frac{\rho^2 V_x(a)}{2b_2 F V_x(a) + 1} + V_\epsilon$
Probability of avoiding capture	$p(a) = \frac{1}{\sqrt{2b_2 F V_x(a) + 1}}$ $\times \exp\left\{-Fb_0 - F\left[\frac{b_2 E_x(a)^2 + b_1 E_x(a) - b_1^2 V_x(a)F/2}{2b_2 F V_x(a) + 1}\right]\right\}$
Probability of annual survival	$\ell(a+1)/\ell(a) = e^{-M} p(a)$
Probability of survival to age a	$\ell(a) = e^{-Ma} \prod_{j=0}^{a-1} p(j)$

The quadratic selectivity function has coefficients specific to the age of the cohort. Year indices have been dropped from all notation in the table. Fish size, x , is transformed length of a fish. Table modified from Deviso and Parma (1988, table 1).

$$F(t, x) = F_t S(x). \quad (9.21)$$

The probability that an individual of size x survives the fishery in year t can be written as

$$P(\text{fish survives}|x) = e^{-F_t S(x)} \quad (9.22)$$

where P denotes probability that the event in parentheses occurs.

The governing equations for growth and survival of a cohort are listed in table 9.5. In table 9.6, their list is given for the principal assumptions and approximations made in the derivation of the stochastic population model.

The key derivation for the governing equations involves the application of Bayes theorem. Specifically, the PDF of x after a fishing season can be written using Bayes theorem as

Table 9.6. Principal assumptions and approximations made in the development of the Deriso-Parma population model.

Principal Assumptions

1. The year is divided into two parts with fishing taking place in one part, and growth in the other.
2. The PDF of the size distribution of individuals in a cohort at the youngest age of recruitment into the fishery is normal.
3. The size-selective risk of fishing mortality is separable into a product of full-recruitment fishing mortality rate, F_t , and a size-selectivity factor $S(x)$.
4. Growth in size of individual fish is given by (9.18), which is the Cohen-Fishman stochastic growth model.
5. Weight of individual fish is given by an allometric function of size with a multiplicative log-normal random variable.
6. Annual survival of a fish of size x is assumed to be probabilistic. The probability of annual survival is $\exp[-F_t S(x) - M]$, which is composed of size-selective risk of fishing mortality and risk of natural mortality, M .

Principal Approximations

1. Size selectivity of fishing mortality, $S(x)$, is approximated by a quadratic polynomial, which has coefficients specific to each cohort in each year.
2. The expected value of the ratio of age-specific abundance to total population abundance in any given year is approximated by the ratio of their respective expected values.

PDF, probability density function.

$$f(x|a, t) = f(x|\text{fish survives}) = \frac{P(\text{fish survives}|x) \varphi(x|a, t)}{\text{Normalizing Factor}}, \quad (9.23)$$

where $P(\text{fish survives}|x)$ is the conditional probability of a fish surviving the harvest, given that its size is x . The normal PDF $\varphi(x|a, t)$ describes the size distribution of fish of age a prior to fishing in year t ; the corresponding mean and variance are denoted $E_x(a, t)$ and $V_x(a, t)$, respectively. The normalizing factor in the denominator of (9.23) is the probability, $p(a, t)$, that a randomly selected individual in the cohort survives the harvest, given by

$$p(a, t) = \int_{-\infty}^{\infty} P(\text{fish survives}|x) \varphi(x|a, t) dx.$$

The normality of the distribution of x prior to the fishing season can be preserved in the PDF of x after the harvest by approximating the (arbitrary) size-selectivity function by a quadratic polynomial of x as given in table 9.5. The closed-form solution for $p(a, t)$ using the quadratic polynomial is also given there. Figure 9.2 shows the use of quadratic polynomials to approximate a sigmoid-shaped selectivity function, typical of selectivity of longline gear. The recursive equation for expected abundance is then

$$E_N(a + 1, t + 1) = E_N(a, t) p(a, t) e^{-M}.$$

The PDF for size distribution of the catch from a cohort is the complement of the PDF in (9.23); that is,

$$f^c(x|a, t) = \frac{(1 - e^{-F_t S(x)}) \varphi(x|a, t)}{[1 - p(a, t)]}, \quad (9.24)$$

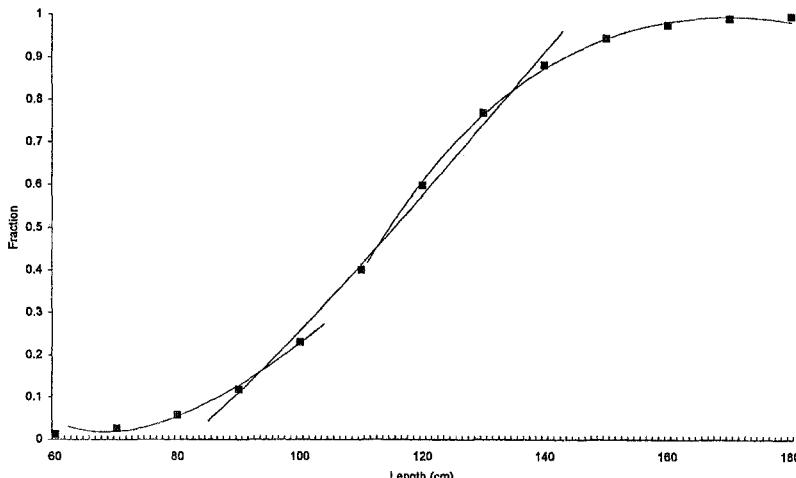


Figure 9.2. Logistic size-selectivity curve and a series of polynomial approximations. The polynomials are of second order and were fitted with least-squares to the logistic curve for three fixed size ranges. The size ranges correspond to mean length ± 1.5 standard deviations for fish of mean length 80, 110, and 140 cm. (After Deriso and Parma 1988, figure 2.)

where $f^c(x|a, t)$ is defined as the PDF for size of a fish chosen randomly from catch of the cohort of age a in year t . The denominator of (9.24) is the probability of being caught.

Size frequency for the total population is given by the marginal distribution

$$f(x|t) = \sum_{a=0}^A \varphi(x|a, t) P_{a,t}, \quad (9.25)$$

where $P_{a,t}$ is the probability that an individual selected at random from the population in year t is of age a . This is approximately the expected abundance of the a year olds divided by expected total abundance:

$$P_{a,t} = \frac{E_N(a, t)}{E_N(t)}$$

to an accuracy of order $o[1/E_N(t)]$, in which $E_N(t) = \sum_{i=0}^A E_N(i, t)$ is expected total abundance. Expected abundance of a given cohort in a given year is calculated recursively by the product of expected abundance of the cohort in the previous year and annual survival probability listed in table 9.5.

Size frequency for total catch in a given year is similar in derivation to the one above in (9.25): the PDF for the size of a fish chosen randomly from the catch is given by

$$f^c(x|t) = \sum_{a=0}^A f^c(x|a, t) P_{a,t}^c,$$

where $P_{a,t}^c$ is the probability that an individual selected at random from the catch in year t is of age a and for which $P_{a,t}^c$ is approximately the ratio of expected catch of the a year olds divided by total expected catch:

$$P_{a,t}^c = \frac{[1 - p(a, t)]E_N(a, t)}{\sum_{a=0}^A [1 - p(a, t)]E_N(a, t)}$$

to an accuracy of order $o[1/(\text{total expected catch})]$. Figure 9.3 shows the stationary probability distribution of size in the catch and in the population for fish of three fixed ages.

Yield-per-recruit analysis for stochastic size-structured models explicitly accounts for the size distribution of fish at each age. The derivation is based on the equations above for growth and survival and, in addition, we assume that weight of an individual fish is allometrically related to its size, x , by $W = m e^{rx + v}$, in which $v \sim N(0, V_v)$. Mean weight of fish of size x is given by

$$E_W(x) = m \exp(rx + V_v/2).$$

Expected yield harvested from a cohort over its life span is given by

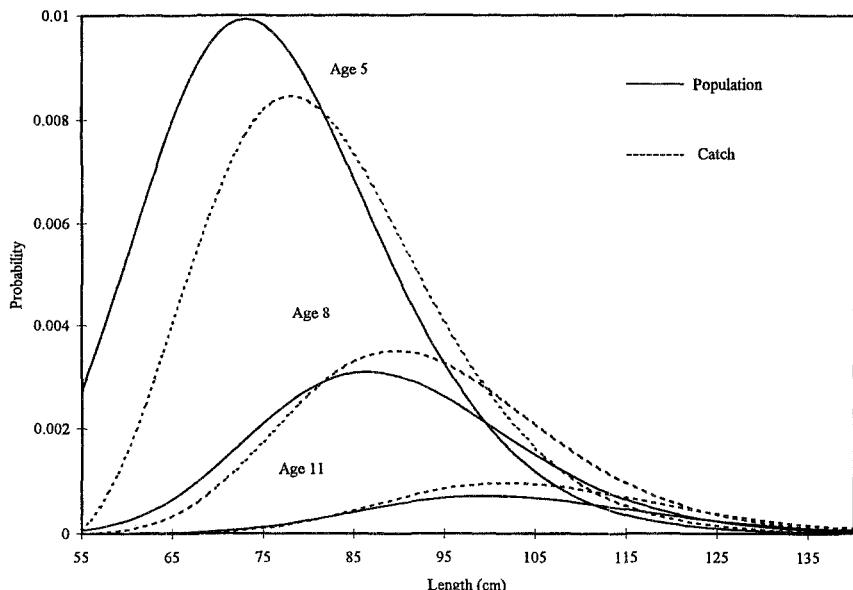


Figure 9.3. Probability that a fish chosen at random from the population (or catch) will be of the length (in 1-cm increments) and age listed. The probabilities shown correspond to the stationary PDF of fish whose dynamics have the parameter values listed below with $F = 0.3$. Parameter values correspond roughly to Pacific halibut: $b_0 = -14.0$, $b_1 = 5.5$, $b_2 = -0.5$, $M = 0.2$, $\alpha = 0.42$, $\beta = 0.92$, $V_x(0, t) = 0.031$, $V = 0.0025$, $x_0 = 4.29$. The selectivity curve is a single quadratic polynomial, which corresponds roughly to the selectivity curve given in Myhre (1969). (After Deriso and Parma 1988, figure 4.)

$$E(Y) = R \sum_{a=0}^A \int_{-\infty}^{\infty} E_W(x) [1 - e^{-FS(x)}] \varphi(x|a) l(a) dx,$$

for a given full-recruitment fishing mortality rate, F , and for R recruits defined to be the fish of coded age 0. The integral equation is tractable. We sketch the derivation: substitute the quadratic selectivity approximation for $S(x)$ and complete the sum of squares of the resultant exponentiated second-order polynomial, as shown in appendix IV of Deriso and Parma (1988). The yield-per-recruit equation above differs from those in chapter 6 mainly by the specific modeling of effects of size-selectivity on mean weight in the catch. Additional size-related effects occur if growth has phenotypic characteristics.

Estimation theory below is based on a typical catch sampling program: (1) a random sample of the catch is measured for size, (2) a stratified random subsample of the measured fish are aged, and (3) the total biomass of the catch is recorded. Maximum likelihood estimates of model parameters can be made from all the sampling data. The logarithm of the likelihood function for all data collected in a given year, Λ_t , can be written as a sum of the three sampling components given approximately, up to additive constants, by

$$\begin{aligned}\Lambda_t = \sum_{i=1}^{NS} \ln[f^c(x_i|t)] & \quad \text{for the first component,} \\ + \sum_{j=1}^{NA} \ln[f^c(x_j|a_j, t) P_{a,t}^c] & \quad \text{for the second component,} \\ + \ln[\varphi(Y_t|E_Y(t), V_Y(t))] & \quad \text{for the third component,}\end{aligned}\tag{9.26}$$

where x_i is the size of the i th sampled fish, which was not aged; (x_j, a_j) is the age and size of subsampled fish; NS is the number of fish measured, but not aged; NA is the number of fish measured and aged; and Y_t is the biomass of total catch in year t .

The first two likelihood components were described earlier. The last one relates observed biomass of catch to a normal approximation, which in turn depends on the expected biomass of catch, $E_Y(t)$, and variance, $V_Y(t)$; equations for mean and variance of biomass of catch are lengthy (Deriso and Parma 1988, appendix IV).

When there are aging errors, the second component of the log-likelihood function needs to be generalized with a misclassification matrix. Let $\theta(i, a)$ be the probability that a fish of true age i is said to be age a . The second component in (9.26) is changed to

$$\sum_{j=1}^{NA} \ln \left[\sum_{i=0}^A \theta(i, a_j) f^c(x_j|i, t) P_{i,t}^c \right];$$

the rest of Λ_t is the same as given in (9.26).

The joint log-likelihood of several years of data can be approximated by summing Λ_t , a single year log-likelihood, across the T years of data being analyzed. Parameter estimates for growth, abundance, and mortality can be obtained by maximizing

$$\Lambda = \sum_{t=1}^T \Lambda_t.$$

To add auxiliary information to the likelihood criteria, we can add to Λ the likelihood functions corresponding to that information.

9.4. LENGTH-BASED ASSESSMENT METHODS

9.4.1. Length Cohort Analysis

The extension of cohort analysis in section 8.2.3 to length data was first developed by Jones (1981) and has been used in some stock assessments in the northern Atlantic. Lai and Gallucci (1988) explored the properties of length cohort analysis. The goal of the method is to use length frequency data of catches in a back-calculation algorithm to estimate population abundance and fishing mortality in a manner similar to cohort analysis. The assumptions of the method are (1) catches in length are measured without error, (2) the assumptions for cohort analysis of age data are met (i.e., the approximations in section 8.2.3 can be used), and (3) growth can be modeled using the deterministic LVB model.

Recall from (8.38) that the backward equation for cohort analysis (with constant M) is

$$N_a = N_{a+1} e^M + C_a e^{M/2}.$$

This equation can be generalized for an arbitrary age $a + \tau$ as

$$N_a = N_{a+\tau} e^{M\tau} + C_a e^{M\tau/2}. \quad (9.27)$$

We now think of a and $a + \tau$ as the ages corresponding to two ends, l_l and l_u , of a length class l . Thus, l_u is the start of length class $l + 1$. From (4.10), it can be shown that time increment $\tau \equiv \tau_l$ can be expressed as

$$\tau_l = \frac{1}{\kappa} \ln \left(\frac{L_\infty - l_l}{L_\infty - l_u} \right). \quad (9.28)$$

By substituting (9.28) into (9.27) and replacing age-based subscripts with length-based subscripts, the corresponding backward equation for length cohort analysis is

$$N_l = (N_{l+1} X_l + C_l) X_l \quad \text{where} \quad X_l = \left(\frac{L_\infty - l_l}{L_\infty - l_u} \right)^{M/(2\kappa)}, \quad (9.29)$$

and where N_l is the abundance at the start of length class l (corresponding to actual length, l_l). Note that (9.29) is a function of asymptotic length, L_∞ , and the ratio M/κ .

The algorithm for conducting the back-calculation starts with the last length class, L , which represents all fish larger than a particular size. A value for F_L/Z_L is assumed, from which population abundance at the start of the class is calculated as

$$N_L = C_L / (F_L/Z_L).$$

This form of the Baranov equation is used because this length class covers all ages older than a particular age [cf. (8.40b)]. Then (9.29) is used to back-calculate abundance at the start of the other length classes. The exploitation fraction F/Z for the other length classes is then found from

$$F_l/Z_l = C_l / (N_l - N_{l+1}),$$

where the denominator is simply the total number of deaths D_l . The quantities $Z_l \tau_l$ and $F_l \tau_l$ are then calculated as

$$Z_l \tau_l = -\ln(N_{l+1}/N_l) \quad \text{and} \quad F_l \tau_l = (F_l/Z_l)(Z_l \tau_l).$$

Calculations of Z_l and F_l require explicit values of M (or κ). Then,

$$Z_l = M / (1 - F_l/Z_l) \quad \text{and} \quad F_l = (F_l/Z_l)(Z_l).$$

Finally, average number, \bar{N}_l , in the length class l is given by

$$\bar{N}_l = (N_l - N_{l+1}) / (Z_l \tau_l).$$

Ideally, length cohort analysis would be applied by isolating catch-length data from a year-class over its life span. This would require knowing the ages corresponding to lengths, which defeats the purpose of applying length cohort analysis rather than regular cohort analysis. The alternative of applying length cohort analysis to length

frequency data from a single year requires the assumption that the length frequency distribution in a year is representative of the catch of a year-class over its lifetime. This can occur only if recruitment and growth are constant over time, which are quite stringent assumptions. By analogy to catch-curve analysis in section 8.2.2, severe bias in estimation can occur if these assumptions are not met. Jones (1981) recommended using length cohort analysis on average data over several years to minimize variations due to growth and recruitment. In that situation, an indication of average abundance and mortality over the span of data averaging might be gained if the two stationarity assumptions are met, but there is little information from length frequency data alone to validate those assumptions. Another limitation of length cohort analysis is that it is based on a deterministic LVB growth model.

Lai and Gallucci (1988) investigated the magnitude of error caused by incorrect specification of input parameters in length cohort analysis. Like cohort analysis, errors in abundance due to incorrect specification of F/Z for the last length class L diminished as the back-calculation proceeded. Incorrect specification of M led to large errors in abundance and fishing mortality, particularly at smaller sizes. Large coefficients of variation for abundance and fishing mortality estimates occurred even when growth parameter estimates had low coefficients of variation. Lai and Gallucci concluded that the greater dependence of length cohort analysis upon steady-state conditions and the LVB growth model and its generally greater relative error suggests that results from length cohort analysis are much less reliable than those from cohort analysis.

Example 9.4. Numerical example from Jones (1981)

This example illustrates the calculations for length cohort analysis. The example is from table 4 of Jones (1981); the species and location are unspecified. The calculations here deviate slightly from Jones's in some cases, perhaps due to rounding error. Some additional variables are calculated here as well. Values of the input parameters L_∞ , M/κ , F_L/Z_L , and catches $\{C_L\}$ in 11 length categories are shown in table 9.7, along with subsequent calculations. First the values of X_l are calculated from the input parameters, and then values of N_l follow directly from (9.29). Then values of F_l/Z_l , $Z_l \tau_l$, and $F_l \tau_l$ are calculated as described above. For $M = 0.2$, values of Z_l , F_l , and \bar{N}_l can be calculated. Two calculations of τ_l are then made: the first by dividing $Z_l \tau_l$ by Z_l , the second from (9.28). The slight discrepancy is due to the cohort analysis approximation used (see section 8.2.3). ■

9.4.2. Catch-Length Analysis and Length-Based Stock Synthesis Analysis

Length-based models (Methot 1990, Sullivan et al. 1990, Sullivan 1992, Sigler 1993, Gudmundsson 1995, Hampton and Fournier 1996) have been developed to avoid the assumptions of recruitment stationarity and deterministic growth made in length cohort analysis. Essentially, these models start with catch-age analysis (section 8.2) and then incorporate distributions of length for each age. An extension and generalization of catch-age analysis of Deriso et al. (1985, 1989), called catch-length analysis (Sullivan et al. 1990, Sullivan 1992, Gudmundsson 1995), uses a stochastic growth model (section 4.7.3). An extension and generalization of the stock synthesis analysis of Methot (1989, 1990), which we call length-based stock synthesis analysis, is described in Methot (1990) and Sigler (1993). It uses the structure of length frequency analysis (section 8.1) to transform age to length. Kimura (1990) developed a similar extension and called it

Table 9.7. Example of length cohort analysis from Jones (1981, table 4).

l	l_l	C_l	X_l	N_l	$F_{l,l}/Z_l$	$Z_l\tau_l$	$F_l\tau_l$	Z_l	F_l	\bar{N}_l	$(Z_l\tau_l)/Z_l$	$\tau_l =$	τ_l from (9.12)
1	20	0.10	1.044	50.48	0.023	0.089	0.002	0.205	0.005	48.30	0.435	0.435	
2	25	0.47	1.049	46.18	0.101	0.106	0.011	0.223	0.023	43.82	0.477	0.477	
3	30	3.88	1.054	41.53	0.495	0.209	0.104	0.396	0.196	37.48	0.528	0.527	
4	35	5.54	1.061	33.70	0.618	0.309	0.191	0.523	0.323	28.99	0.591	0.589	
5	40	5.37	1.069	24.73	0.662	0.398	0.263	0.591	0.391	20.41	0.673	0.668	
6	45	4.62	1.080	16.62	0.695	0.511	0.355	0.655	0.455	13.01	0.781	0.771	
7	50	3.03	1.095	9.97	0.684	0.587	0.402	0.634	0.434	7.54	0.927	0.912	
8	55	1.68	1.118	5.54	0.644	0.637	0.410	0.561	0.361	4.10	1.136	1.116	
9	60	1.02	1.155	2.93	0.631	0.802	0.506	0.543	0.343	2.01	1.478	1.438	
10	65	0.46	1.225	1.31	0.566	0.966	0.546	0.460	0.260	0.84	2.098	2.027	
11	70	0.25		0.50	0.500								

Input information includes length interval definitions, LVB growth parameters, natural mortality M , catch C for each length class, and F/Z for the last length class. Calculations of other quantities in the table are described in text. Length is in centimeters and abundances are reported in millions. $L_\infty = 80$; $M = 0.2$; $K = 0.2$; $M/K = 1$.

length-based separable sequential population analysis. Hampton and Fournier (1996) developed an age-structured, likelihood-based catch-at-length model, which builds on their earlier method of length frequency analysis (Fournier et al. 1990).

Both types of models allow for variations in length as a function of age and have length-based parameters. Both models also have computer programs that can be used to estimate parameters.

Catch-length analysis

Our description of catch-length analysis is drawn from Sullivan et al. (1990) and Sullivan (1992). The form of the population model used in catch-length analysis is an extension of (9.17); the extension allows for additive process error, w_t , in the population dynamics:

$$\mathbf{N}_{t+1} = \mathbf{PS}_t \mathbf{N}_t + \mathbf{R}_{t+1} + \mathbf{w}_t, \quad (9.30)$$

where the vectors represent length classes. In addition, survival, \mathbf{S}_t , is allowed to vary over time. Here recruitment, \mathbf{R}_{t+1} , is added in at the start of time $t + 1$ rather than at time t and is not necessarily specified as a Leslie matrix progression. Rather, it is assumed that recruitment, $R_{l,t}$, can be separated into a temporal component, R_t , and a length-based component, p_l , as

$$R_{l,t} = R_t p_l. \quad (9.31)$$

To reduce the number of proportions to be estimated, Sullivan et al. (1990) suggested using a gamma distribution with parameters α_r and β_r (see the growth submodel below).

The Baranov catch equation formulation is used as a mortality submodel with natural mortality, $M_{l,t}$, fishing mortality, $F_{l,t}$, total mortality, $Z_{l,t} = M_{l,t} + F_{l,t}$, survival, $S_{l,t} = \exp[-Z_{l,t}]$, and exploitation fraction, $\mu_{l,t} = (F_{l,t}/Z_{l,t})(1 - S_{l,t})$. To reduce the number of parameters to be estimated, the separability assumption for fishing mortality as a function of length and time is made:

$$F_{l,t} = s_l F_t \quad (9.32)$$

where F_t is full-recruitment fishing mortality, and s_l is selectivity as a function of length. Selectivity may be parameterized in terms of parameters α_s and β_s from a gamma or logistic function to further reduce the number of estimated parameters. The matrix \mathbf{S}_t in (9.30) is the diagonal matrix with elements $\{S_{l,t}\}$ for each time t .

To obtain the lower triangular growth transition matrix \mathbf{P} in (9.30), a stochastic LVB growth model (cf. section 4.7.3) is used, although in principle any stochastic growth model could be used. The goal is to find the proportion, $P_{m,l}$, of fish in length class l at the start of a time period that survive and are in length class m at the start of the next time period. If l_l and l_u are the two ends of length class l and l^* is the midpoint $(l_l + l_u)/2$, then the expected length change or growth increment, $\bar{\Delta}_l$, over one time period for an individual at mid-length, l^* , from the LVB model is

$$\bar{\Delta}_l = (L_\infty - l^*) (1 - e^{-\kappa}). \quad (9.33)$$

Hence, the expected length, $E(x)$, of a fish of mid-length l^* one time unit later is

$$E(x) = l^* + \bar{\Delta}_l. \quad (9.34)$$

Stochasticity is incorporated for a fish of mid-length l^* by assuming that its length, x , one time unit later can be modeled as a gamma distribution

$$g(x|\alpha_l, \beta) = \frac{1}{\beta^{\alpha_l} \Gamma(\alpha_l)} x^{\alpha_l-1} e^{-x/\beta}, \quad (9.35)$$

with expected length $E(x)$, for which α_l is the scale parameter for class l , and β is a shape parameter common to all length classes (for reasons of parsimony and to avoid confounding). The mean and variance of this gamma distribution are

$$E(x) = \alpha_l \beta \quad \text{and} \quad \text{Var}(x) = \alpha_l \beta^2 = \beta E(x). \quad (9.36)$$

By equating the two expressions (9.34) and (9.36) for $E(x)$, the parameters α_l of the gamma distribution are calculated as $(l^* + \bar{\Delta}_l)/\beta$. Essentially, the parameters α_l are functions of L_∞ and κ , given l^* and β . The variance of length one time unit later is proportional to expected length in (9.36). Finally, if m_l and m_u are the two ends of length class m , the growth transition probabilities (from length class l to length class m) can be computed as

$$P_{m,l} = \int_{m_l}^{m_u} g(x|\alpha_l, \beta) dx \quad (9.37)$$

and then placed in the matrix \mathbf{P} .

The predicted catch by length each year is simply the product of the exploitation fraction and abundance, or $C_{l,t} = \mu_{l,t} N_{l,t}$. This can be written in matrix form as

$$\mathbf{C}_t = \boldsymbol{\mu}_t \mathbf{N}_t,$$

where $\boldsymbol{\mu}_t$ is the diagonal matrix of the $\{\mu_{l,t}\}$. Observed catch is assumed to differ from predicted catch with additive error, which can be written in matrix form as

$$\mathbf{C}'_t = \mathbf{C}_t + \mathbf{v}_t, \quad (9.38)$$

where \mathbf{v}_t is a vector of additive measurement errors. There are $L \times T$ observations of catch at length, $C'_{l,t}$.

Parameters of the catch-length model include recruitments, R_t , and initial population vector, \mathbf{N}_0 , recruitment-by-length proportions, p_l (or recruitment proportion parameters α_r and β_r), natural mortalities, $M_{l,t}$, fishing mortalities, F_t , selectivities, s_l (or selectivity parameters α_s and β_s), and growth parameters, L_∞ , κ , and β . In practice, natural mortalities and shape parameter β are generally specified. Sullivan et al. (1990) further reduced the number of estimated parameters by using a single parameter N_0 for initial total abundance and calculating the initial abundance vector from initial catch-length and length-specific fishing mortality information.

Like catch-age analysis, successful estimation usually requires auxiliary information. If fishing effort, E_t , information is available, then the typical assumption from section 8.2 is that full-recruitment fishing mortality deviates from the constant catchability assumption by lognormal error, or

$$F_t = q E_t e^{\epsilon_q}. \quad (9.39)$$

If absolute abundance, N'_t , information from surveys is available, then the typical assumption from section 8.2 is that survey abundance deviates from model abundance by lognormal error, or

$$N'_t = N_t e^{\epsilon_N}. \quad (9.40)$$

Other auxiliary information described in section 8.2 can be used as well.

The combination of the process-error abundance model (9.30), the measurement-error catch-length model (9.38), and the models for auxiliary information form the complete catch-length analysis. Estimation follows from Kalman filter methodology (see section 5.4.4); an explicit algorithm for its implementation is given in Sullivan (1992). If process error is assumed negligible ($\mathbf{w}_t = \mathbf{0}$), then least squares can be used to minimize

$$\text{RSS}_L = \sum_l \sum_t (C'_{l,t} - C_{l,t})^2 + \text{RSS}_{\text{aux}}. \quad (9.41)$$

The computer program CASA (Sullivan et al. 1990) takes this approach. Other error structures (such as lognormal or multinomial) could be used as well; see Sullivan et al. (1990), Sullivan (1992), and section 8.2 for discussion of these alternatives. The process of fitting the catch-length model to data using least squares is similar to that for catch-age analysis, illustrated in chapter 8.

In application to several real and simulated data sets, Sullivan et al. (1990) found that the measurement-error model worked reasonably well when the recruitment distribution was carefully modeled. They also found that the shape parameter β should be fixed and that good auxiliary information improves the estimation results.

Example 9.5. Hypothetical population with five length classes

This example illustrates only the underlying model for catch-length analysis rather than performing a complete catch-length analysis, which is done similarly to catch-age analysis. For a more complete illustration, the reader should consult the examples in Sullivan et al. (1990) and Sullivan (1992). Only the deterministic part of the model is illustrated; hence \mathbf{w}_t and \mathbf{v}_t are zero in the following example.

LVB growth parameters and gamma parameter β for a hypothetical population are given in table 9.8. Parameter t_0 is not needed for the analysis, but the length-age relationship is given in the table to guide selection of length classes and to provide a means for relating length to age. The start of the first length class corresponds to length at age 1; other length classes are chosen to provide contrast in growth transitions. Calculations of mean growth increments, $\bar{\Delta}_l$, from (9.33) and the expected length, $E(x)$, from (9.34) are shown in the table. Parameters α_l are obtained by dividing $E(x)$ by β , and the standard deviations, $SD(x)$, are square roots of the variance formula in (9.36). The gamma distribution (9.35) for length x one time unit later is shown for the first midlength ($l^* = 24.1$) in figure 9.4. The various areas under the curve correspond to the growth transition probabilities $P_{m,1}$ for the first length class shown in table 9.8, calculated from (9.37). Similar curves can be constructed for the other length classes. The resulting growth transition matrix \mathbf{P} is shown in table 9.8.

Calculations related to recruitment and mortality are shown in table 9.9. In this illustration, gamma distributions are not used for p_l and s_l for simplicity's sake. This example has oscillations in R_t and F_t over time. Recruitment proportions, p_l , are 0.8 for the first length class, 0.2 for the second, and 0 for the last three. A constant natural mortality, M , of 0.2 occurs, and selectivity, s_l , increases with length class. The

Table 9.8. Hypothetical example with five length classes showing growth calculations for the model used in catch-length analysis.

		Age, a					
		1	2	3	4	5	6
$L(a)$		18.1	33.0	45.1	55.1	63.2	69.9
Length l	l_l	l_u	l^*	$\bar{\Delta}_l$	$E(x)$	α_l	$SD(x)$
1	18.1	30	24.1	13.8	37.8	18.9	8.7
2	30	45	37.5	11.3	48.8	24.4	9.9
3	45	55	50.0	9.1	59.1	29.5	10.9
4	55	75	65.0	6.3	71.3	35.7	11.9
5	75	125	100.0	0.0	100.0	50.0	14.1

		Length l					
		Length m	1	2	3	4	5
\mathbf{P}							
1		0.186	0.000	0.000	0.000	0.000	
2		0.617	0.371	0.000	0.000	0.000	
3		0.162	0.377	0.374	0.000	0.000	
4		0.035	0.243	0.547	0.639	0.000	
5		0.000	0.009	0.079	0.361	1.000	

Input quantities include LVB growth parameters L_∞ and κ , gamma growth parameter β , and length classes $l = [l_l, l_u]$. From these, class midlengths, l^* , growth increments, $\bar{\Delta}_l$, expected values, $E(x) = l^* + \bar{\Delta}_l$, and standard deviations, $SD(x) = \sqrt{\beta E(x)}$ of length x one time unit later, gamma parameters α_l , and growth transition matrix \mathbf{P} are calculated as described in text. Corresponding lengths at age $L(a)$ for a t_0 of 0 are also shown for comparison. $L_\infty = 100$; $\kappa = 0.2$; $t_0 = 0$; $\beta = 2$.

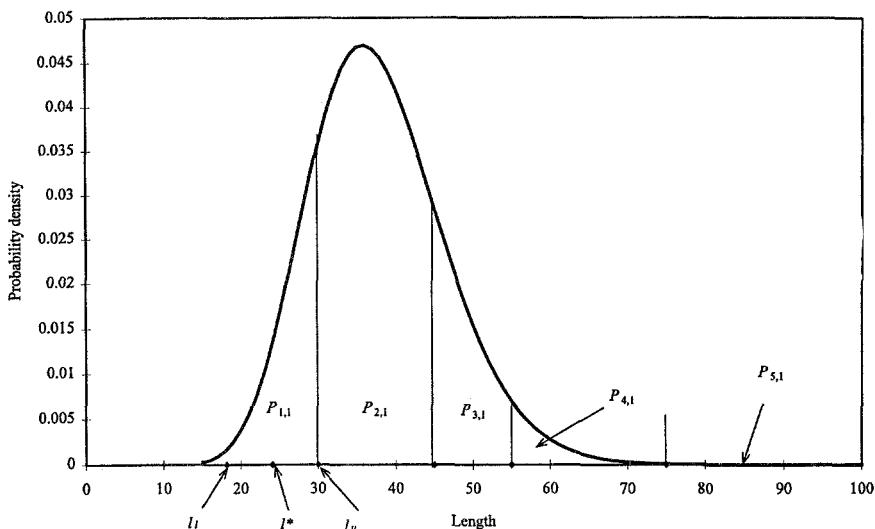


Figure 9.4. The gamma distribution for length x one time unit later of the first length class $l = [l_l, l_u]$ with mid-length l^* for the hypothetical population in example 9.5, used in catch-length analysis. Also shown are the areas under the curve corresponding to growth transition probabilities $P_{m,l}$, $m = 1, \dots, 5$.

corresponding recruitment distributions, $R_{l,t}$, from (9.31) and fishing mortalities, $F_{l,t}$, from (9.32) by length and time are shown in the table. The exploitation fractions, $\mu_{l,t}$, and survivals, $S_{l,t}$, shown in the table follow from the traditional Baranov equations given above (9.32).

The final set of calculations shown in table 9.10 relates to abundance and catch. Construction of the diagonal matrices, S_t , is not shown but simply involves taking survivals by length for each time and placing them on the diagonals. The combined growth and survival matrix PS_1 for the first time period is shown; the others follow analogously. Abundances, $N_{l,t}$, by length and time now follow from (9.30), in which N_0 is the given set of values at time 1. The diagonal matrices μ_t are not shown but are easily constructed. Catches, $C_{l,t}$, by length and time then follow from (9.38). ■

Length-based stock synthesis analysis

Our description of length-based stock synthesis analysis is drawn from Methot (1989, 1990), Kimura (1990), and Sigler (1993). As Kimura (1990) noted, all catch-age and catch-length methods can be thought of as a family of models, and our description of the approach below as stock synthesis analysis is based on precedence in the literature. Our presentation is similar to Kimura's (1990), who used a form of length frequency analysis applied to a general catch-age framework. Details pertinent exclusively to stock synthesis analysis as published by Methot (1989, 1990) are described at the end of this section.

Unlike catch-length analysis in the previous section, the population dynamics in length-based stock synthesis analysis remain fundamentally age based. Thus, the Baranov-type equations [(8.56)–(8.60)] can be used to specify abundance, $N_{a,t}$, and catch, $C_{a,t}$. Average abundance can be calculated as

Table 9.9. Continuation of the hypothetical example from table 9.8 showing recruitment and mortality calculations for the model used in catch-length analysis. Input quantities include natural mortality, $M(0.2)$, annual recruitments, R_t , annual full-recruitment fishing mortalities, F_t , recruitment proportions by length, p_l , and selectivities, s_l (from these, recruitments, $R_{l,t}$, fishing mortalities, $F_{l,t}$, exploitation fractions, $\mu_{l,t}$, and survivals, $S_{l,t}$, by length and time are calculated as described in text).

		Time, t					
Length, l		1	2	3	4	5	6
R_t			1000	800	1000	1200	1000
F_t		0.1	0.2	0.3	0.2	0.1	
$R_{l,t}$							
1	p_l	0.8		800	640	800	960
2		0.2		200	160	200	240
3		0.0		0	0	0	0
4		0.0		0	0	0	0
5		0.0		0	0	0	0
$F_{l,t}$							
1	s_l	0.1	0.010	0.020	0.030	0.020	0.010
2		0.4	0.040	0.080	0.120	0.080	0.040
3		0.7	0.070	0.140	0.210	0.140	0.070
4		1.0	0.100	0.200	0.300	0.200	0.100
5		1.0	0.100	0.200	0.300	0.200	0.100
$\mu_{l,t}$							
1			0.009	0.018	0.027	0.018	0.009
2			0.036	0.070	0.103	0.070	0.036
3			0.061	0.119	0.172	0.119	0.061
4			0.086	0.165	0.236	0.165	0.086
5			0.086	0.165	0.236	0.165	0.086
$S_{l,t}$							
1			0.811	0.803	0.795	0.803	0.811
2			0.787	0.756	0.726	0.756	0.787
3			0.763	0.712	0.664	0.712	0.763
4			0.741	0.670	0.607	0.670	0.741
5			0.741	0.670	0.607	0.670	0.741

$$\bar{N}_{a,t} = N_{a,t}[1 - \exp(-Z_{a,t})]/Z_{a,t}, \quad (9.42)$$

which is used below. An extension to this model that specifies both vulnerability and selectivity is also described below.

A length-age matrix, ψ , also used in development of length frequency analysis (section 8.1.1), provides the mechanism to determine abundance in length classes, for which $\psi_{l,a}$ represents the proportion of age a fish which are in length class l . The average abundance in a length class l at time t is then given by

$$\bar{N}_{l,t} = \sum_a \psi_{l,a} \bar{N}_{a,t}. \quad (9.43)$$

Thus, growth does not come from a stochastic model, but variation in length as a function of age is explicitly allowed. As in length frequency analysis, it is assumed that the distribution of lengths for a given age is normal, so (8.4) can be used to calculate

Table 9.10. Continuation of the hypothetical example from tables 9.8 and 9.9 showing calculations of joint growth and survival matrix \mathbf{PS}_1 for time 1 and abundances, $N_{l,t}$, and catches, $C_{l,t}$, by length and time for the model used in catch-length analysis.

		Length, m				
Length, l		1	2	3	4	5
\mathbf{PS}_1	1	0	0.000	0.000	0.000	0.000
	2	0.500	0.292	0.000	0.000	0.000
	3	0.131	0.296	0.286	0.000	0.000
	4	0.028	0.191	0.418	0.474	0.000
	5	0.000	0.007	0.060	0.267	0.741

		Time, t					
		1	2	3	4	5	6
$N_{l,t}$	1	1000	951	782	916	1097	965
	2	800	934	892	824	924	1018
	3	600	540	533	477	480	555
	4	400	621	674	634	634	709
	5	200	297	387	416	465	550
Total		3000	3342	3268	3266	3601	3797

$C_{l,t}$	1	2	3	4	5	6
	9	17	21	16	10	
	28	65	92	57	33	
	37	64	92	57	29	
	35	102	159	105	55	
	17	49	91	69	40	
Total	126	298	455	304	167	

$\psi_{l,a}$. Growth parameters L_∞ , κ , and $\{\sigma_a\}$ pertain to the population and not to fish in the catch because of size selectivity, described below. The gamma distribution used in catch-length analysis, as well as other distributions, could also be used here.

Gear selectivity is assumed to be a function of length alone, written s_l . Selectivity may be further parameterized with a set of selectivity parameters $\{\eta_s\}$. The length distribution of the catch in a given year t can then be approximated as

$$\alpha_{l,t} \approx s_l \bar{N}_{l,t} / \sum_l s_l \bar{N}_{l,t}, \quad (9.44)$$

where $\alpha_{l,t}$ is the proportion of fish in year t that are in length class l . (Similar notation is used in section 8.1.) Mean selectivity as a function of age can then be determined as

$$s_a = \sum_l s_l \psi_{l,a}, \quad (9.45)$$

which is then used in the Baranov equations for abundance and catch. The age distribution in the catch can also be approximated as

$$\theta_{a,t} \approx s_a \bar{N}_{a,t} / \sum_a s_a \bar{N}_{a,t}. \quad (9.46)$$

Because of size selectivity, average length, L_a , and weight, W_a , at age a in the catch differ from those in the population. If L_l is the average length and W_l is the average weight of fish in length class l , then average length and weight at age in the catch can be found from

$$L_a = \sum_l s_l \psi_{l,a} L_l / s_a \quad \text{and} \quad W_a = \sum_l s_l \psi_{l,a} W_l / s_a. \quad (9.47)$$

The term $s_l \psi_{l,a}$ is approximately the proportion of age a fish in the population that are of length l in the catch. Thus, the sizes of fish in the population are determined from the LVB model, and corresponding sizes in the catch are obtained by (9.47) and related statistics.

From (9.44), catch-length can be determined as

$$C_{l,t} = C_t \alpha_{l,t}, \quad (9.48)$$

where C_t is total catch in numbers in year t (see section 8.1.3 for its estimation). Objective functions for catch-length and auxiliary information can then be defined, in analogy to catch-age analysis (sections 8.2.5, 8.2.7) and catch-length analysis (see also Beddington and Cooke 1981 and Kimura 1990).

A method called IMMAGE (inverse method for mortality and growth estimation), developed in Somerton and Kobayashi (1992), is conceptually similar to the length-based stock synthesis model and has been useful for stock assessment of Hawaiian bottomfish (D.R. Kobayashi, personal communication, 1992). The LVB model with asymptotic variance as a function of age is used for length, and the conversion to age uses a discrete form of the normal density function. Selectivity is modeled with a logistic function, and the objective function is the sum of squared catch-length deviations. No auxiliary information is used. The population is assumed to be in equilibrium, however, so that data from a single year can be used. If the equilibrium assumption holds, the method produces reasonable results. When the equilibrium assumption does not hold, substantial bias found in other equilibrium methods is likely to occur.

Some technical details about stock synthesis analysis

The computer program and literature for stock synthesis analysis contain some technical specifications which deserve mention. Although these specifications are not necessary for carrying out the length-based stock synthesis approach, they are features found in the literature and in the computer implementation.

Nominally, the procedure is based on a likelihood approach as in Fournier and Archibald (1982) rather than on least squares. However, except as described below for composition data, most likelihood components turn out to be sums of squares.

Observed total yield, Y'_t , is a primary data source (catch in weight units). Predicted yield, Y_t , can be calculated as

$$Y_t = \sum_a C_{a,t} W_a = \sum_l C_{l,t} W_l.$$

These average weights W_a and W_l may also be functions of time, t . In practice, full-recruitment fishing mortalities are not estimated but adjusted so that predicted and observed yield are identical. This has the advantage of reducing the total number of parameters to be estimated. When some data are missing (e.g., missing length composition data in some years, or no auxiliary fishing effort information), a likelihood component for yield deviations can be included. When observed total catch, C'_t , rather than yield is a primary data source, this type of approach can still be used to obtain full-recruitment fishing mortalities.

Estimates of catch-age or catch-length are not directly used; the age or length composition is a primary data source. As most sampling procedures estimate composition, this feature is a natural one and lends itself to incorporation of aging error through a correction matrix. The default error structure for composition data is the multinomial, based on simple random sampling. In practice, the log-likelihood component $\sum_t \lambda_t \sum_a \theta'_{a,t} \ln \theta_{a,t}$ for age or $\sum_t \lambda_t \sum_l \alpha'_{l,t} \ln \alpha_{l,t}$ for length is used in the overall objective function, in which λ_t is a weighting term (such as sample size) and a prime denotes an estimate from data (observed age or length composition). The lack of a prime indicates a variable obtained from the model. Multinomial-type objective functions can also be used in catch-age analysis (see section 8.2.5). As in catch-age or catch-length analysis, various weighting terms for objective function components must be specified.

The age-structured component of the model can be generalized to separately handle the concepts of vulnerability, v (fish present in the fishing area) and selectivity, s (fish susceptible to the gear in a fishing area). The recursive equation for abundance is generalized to

$$N_{a+1,t+1} = N_{a,t} \left[(1 - v_a) e^{-M_{a,t}} + v_a e^{-Z_{a,t}} \right], \quad (9.49)$$

where v_a is the proportion of age a fish that could be caught if infinite fishing effort were expended. Vulnerability is assumed constant over time. Note that if $v_a = 1$, then the Baranov recursive equation results. The separability assumption $F_{a,t} = s_a F_t$ is still made, and $Z_{a,t} = F_{a,t} + M_{a,t}$ still applies. The catch equation in this situation is generalized to

$$C_{a,t} = N_{a,t} v_a \frac{F_{a,t}}{Z_{a,t}} \left(1 - e^{-Z_{a,t}} \right). \quad (9.50)$$

However, Methot (1990) pointed out that joint estimation of vulnerability and selectivity is difficult unless there are survey data to indicate the proportion of a stock in a given area.

Gear selectivity is parameterized with a four-parameter double logistic function (a combination of an increasing and a decreasing logistic curve) given by

$$s_a = \left[\frac{1}{1 + e^{-\eta_2(a - \eta_1)}} \right] \left[1 - \frac{1}{1 + e^{\eta_4(a - \eta_3)}} \right] \frac{1}{x}, \quad (9.51)$$

where η_1 and η_3 are inflection points for the (increasing) first and (decreasing) second logistic curves, η_2 and η_4 are slopes for the curves, and x is the maximum of the first two terms of the right-hand side of (9.51) over the range of ages, so that selectivity is equal to 1 for at least one age. This function allows great flexibility in the shape

of selectivity curves. The first curve is just the standard logistic curve and a special case of (9.51) with $\eta_4 \rightarrow \infty$. The second curve allows for dome-shaped selectivity curves, such as found in trawl and gillnet surveys. How much is saved by specifying a selectivity function versus estimating selectivity parameters probably depends on the specific example (involving perhaps the number of ages, variability in the data, confounding with natural mortality, etc.) Comparison of different selectivity functions (or sets of selectivity parameters) can easily be done with F tests or likelihood ratio tests, as in chapter 4.

To reduce the number of year-class parameters, the stock synthesis program allows the use of a single pristine recruitment parameter, which leads to an equilibrium pristine distribution of age for a given value of total mortality at that time. Whether it is worth making the equilibrium assumption which may be incorrect in order to reduce the number of parameters estimated is unknown.

Size-specific survival is not included in current model specifications, even though the presence of length selectivity suggests that it should be. Methot (1990) discussed further desirable modifications in this direction, such as including the model formulations of Deriso and Parma (1988) and Parma and Deriso (1990).

Example 9.6. Hypothetical population with 5 length classes and 10 age classes

This example illustrates only the underlying model for length-based stock synthesis analysis. The hypothetical population has similar characteristics to the one used for catch-length analysis (example 9.5), so similarities and differences between the models can be illustrated. For a more complete illustration, the reader should consult the examples in Methot (1989, 1990), Kimura (1990), Sigler (1993), and stock assessment documents of the North Pacific and Pacific Fishery Management Councils.

LVB growth parameters for the hypothetical population given in table 9.11 are the same as in example 9.5. The corresponding length-age relationship is centered at the middle of the age (ages 1.5, 2.5, etc.) because L_a was used in the previous example to define the start of the length interval. The oldest age used is age 10, which is chosen to cover the main extent of length in the length-age relationship. The same variance relationship, $\text{var}(x) = \beta E(x)$, for length x is used for each age. Standard deviations, σ_a , shown in the table are square roots of the variance. The normal distribution for age 3 is shown in figure 9.5.

The same length classes as before are used, except that the start of the first length class is set to 0 and the end of the last length class is set to 150 to encompass the entire length distribution. The various areas under the curve that correspond to the length-age proportions $\psi_{l,a}$ for age 3 are also shown in the figure, calculated from (8.2) and (8.4). Similar curves can be constructed for the other ages, and the resulting proportions are given in table 9.11.

The same length-selectivity values, s_l , are used as before and given in table 9.11. In this illustration, s_l is not parameterized as a gamma or logistic distribution for the sake of simplicity. Calculations related to mortality are shown in table 9.12. The values of age-selectivity in table 9.12 from (9.45) come from s_l and $\psi_{l,a}$ given in table 9.11. The same oscillating fishing mortality values, F_t , and natural mortality, M , of 0.2 are used as before. The corresponding fishing mortalities, exploitation fractions, and survivals by age and time, shown in table 9.12, follow from the traditional Baranov equations for age.

Table 9.11. Hypothetical example with 5 length classes and 10 ages showing growth calculations for the model used in length-based stock synthesis analysis.

Length, l	Age, a									
	1	2	3	4	5	6	7	8	9	10
L_a	25.9	39.3	50.3	59.3	66.7	72.7	77.7	81.7	85.0	87.8
σ_a	7.2	8.9	10.0	10.9	11.6	12.1	12.5	12.8	13.0	13.2
	l_l	l_u	s_l							
1	0.0	30	0.1							
2	30	45	0.4							
3	45	55	0.7							
4	55	75	1.0							
5	75	150	1.0							
$\psi_{l,a}$										
1	0.715	0.146	0.021	0.004	0.001	0.000	0.000	0.000	0.000	0.000
2	0.281	0.592	0.276	0.090	0.029	0.011	0.004	0.002	0.001	0.001
3	0.004	0.223	0.382	0.251	0.125	0.060	0.030	0.016	0.010	0.006
4	0.000	0.039	0.314	0.580	0.608	0.503	0.380	0.281	0.210	0.161
5	0.000	0.000	0.007	0.075	0.237	0.426	0.585	0.701	0.779	0.832
Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Input quantities include LVB growth parameters $L_\infty(100)$, $\kappa(0.2)$, and $t_0(0)$, variance parameter $\beta(2)$, and length classes $l = [l_l, l_u]$. From these, expected lengths $E(L_a)$ centered at the middle of the age ($a + 0.5$), standard deviations $\sigma_a = \sqrt{\beta E(L_a)}$, and length-age proportions $\psi_{l,a}$ are calculated as described in text. Length selectivities, s_l , are also given.

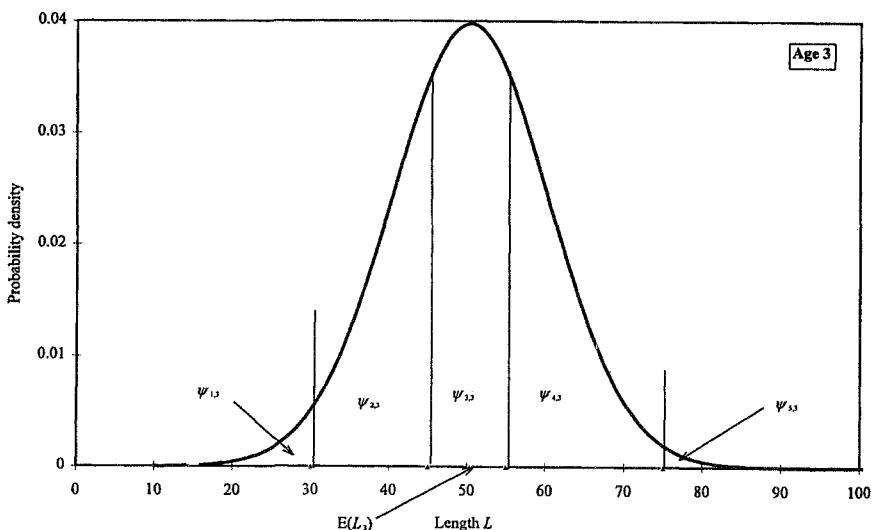


Figure 9.5. The normal distribution for length of age 3 fish for the hypothetical population in example 9.6, used in length-based stock synthesis analysis. The mean and SD of the distribution are given in table 9.11. Also shown are the areas under the curve corresponding to length-age proportions $\psi_{l,3}$, $l = 1, \dots, 5$.

Table 9.12. Continuation of the hypothetical example from table 9.11 showing mortality calculations for the model used in length-based stock synthesis analysis.

Time, t	Age, a										Total
	1	2	3	4	5	6	7	8	9	10	
s_a	0.187	0.446	0.701	0.867	0.944	0.976	0.988	0.994	0.996	0.998	
$F_{a,t}$											
1	$F_t, 0.1$	0.019	0.045	0.070	0.087	0.094	0.098	0.099	0.099	0.100	0.100
2	0.2	0.037	0.089	0.140	0.173	0.189	0.195	0.198	0.199	0.199	0.200
3	0.3	0.056	0.134	0.210	0.260	0.283	0.293	0.297	0.298	0.299	0.299
4	0.2	0.037	0.089	0.140	0.173	0.189	0.195	0.198	0.199	0.199	0.200
5	0.1	0.019	0.045	0.070	0.087	0.094	0.098	0.099	0.099	0.100	0.100
$\mu_{a,t}$											
1	0.017	0.040	0.061	0.075	0.082	0.084	0.085	0.086	0.086	0.086	
2	0.033	0.078	0.119	0.145	0.156	0.161	0.163	0.164	0.164	0.165	
3	0.049	0.114	0.172	0.209	0.225	0.231	0.234	0.235	0.235	0.236	
4	0.033	0.078	0.119	0.145	0.156	0.161	0.163	0.164	0.164	0.165	
5	0.017	0.040	0.061	0.075	0.082	0.084	0.085	0.086	0.086	0.086	
$S_{a,t}$											
1	0.804	0.783	0.763	0.751	0.745	0.743	0.742	0.741	0.741	0.741	
2	0.789	0.749	0.712	0.688	0.678	0.674	0.672	0.671	0.671	0.671	
3	0.774	0.716	0.663	0.631	0.617	0.611	0.609	0.608	0.607	0.607	
4	0.789	0.749	0.712	0.688	0.678	0.674	0.672	0.671	0.671	0.671	
5	0.804	0.783	0.763	0.751	0.745	0.743	0.742	0.741	0.741	0.741	
$N_{a,t}$											
1	1225	400	1100	65	60	50	40	30	20	10	3000
2	1100	984	313	840	49	45	37	30	22	15	3435
3	1000	868	737	223	578	33	30	25	20	15	3529
4	1100	774	621	489	141	356	20	18	15	12	3547
5	1200	868	580	442	337	95	240	14	12	10	3798
6	1100	964	679	442	332	251	71	178	10	9	4037

Input quantities include natural mortality, $M(0.2)$, annual full-recruitment fishing mortalities, F_t , and length-selectivities, s_t (from table 9.10). From these, age selectivities, s_a , fishing mortalities, $F_{a,t}$, exploitation fractions, $\mu_{a,t}$, and survivals, $S_{a,t}$, by age and time are calculated as described in text. Also given are abundances, $N_{a,t}$. Abundances at age 1 for all times and at all ages for time 1 are input and all other abundances are obtained from previous cohort abundance multiplied by corresponding survival.

As in catch-age analysis, abundances for the first age (recruitments) for all times and for all ages at the first time must be specified. The values shown in table 9.12 are chosen to approximate those from the catch-length analysis example, although it was not possible to do this exactly due to the different treatment of recruitment and growth. Other abundances in the table are calculated as usual by multiplying previous cohort abundance by survival. These abundances pertain to the start of the time (or age) period.

Calculations in table 9.13 are abundances and catches by age and time which are pertinent to length-based stock synthesis analysis. Average abundance, $\bar{N}_{a,t}$, over the time or age interval comes from (9.42) and is also expressed as population proportions, $\theta(N)_{a,t}$. Catches by age and time can be obtained by multiplying exploitation fractions by corresponding starting abundances or by multiplying fishing mortalities by average abundances. These are also expressed as catch proportions, $\theta(C)_{a,t}$. A comparison of population and catch proportions shows that older ages have higher proportions in the catch than in the population, as expected due to increasing age selectivity.

The final set of calculations shown in table 9.14 relates to abundance and catch by length. For comparison to catch-length analysis, starting abundances, $N_{l,t}$, by length

Table 9.13. Continuation of the hypothetical example from tables 9.11 and 9.12 showing calculations of average abundances, $\bar{N}_{a,t}$, and catches, $C_{a,t}$, by age and time for the model used in length-based stock synthesis analysis, along with the corresponding proportions, $\theta(N)_{a,t}$, for average abundance and $\theta(C)_{a,t}$ for catch at age a for each time t .

Time, t	Age, a										Total
	1	2	3	4	5	6	7	8	9	10	
$\bar{N}_{a,t}$	1100	355	964	57	52	43	35	26	17	9	2657
1	979	855	265	701	40	37	31	24	18	12	2963
2	882	738	605	179	458	26	24	20	16	12	2958
3	979	672	527	408	117	294	17	15	12	10	3051
4	1078	770	508	384	292	82	208	12	11	9	3353
$\theta(N)_{a,t}$	0.414	0.134	0.363	0.021	0.020	0.016	0.013	0.010	0.007	0.003	1.000
1	0.330	0.288	0.090	0.236	0.014	0.012	0.010	0.008	0.006	0.004	1.000
2	0.298	0.249	0.204	0.060	0.155	0.009	0.008	0.007	0.005	0.004	1.000
3	0.321	0.220	0.173	0.134	0.038	0.097	0.005	0.005	0.004	0.003	1.000
4	0.321	0.230	0.152	0.115	0.087	0.025	0.062	0.004	0.003	0.003	1.000
$C_{a,t}$	21	16	68	5	5	4	3	3	2	1	127
1	37	76	37	122	8	7	6	5	4	2	304
2	49	99	127	46	130	8	7	6	5	4	480
3	37	60	74	71	22	57	3	3	2	2	331
4	20	34	36	33	28	8	21	1	1	1	183
$\theta(C)_{a,t}$	0.162	0.125	0.534	0.039	0.039	0.033	0.027	0.020	0.014	0.007	1.000
1	0.121	0.251	0.123	0.400	0.025	0.024	0.020	0.016	0.012	0.008	1.000
2	0.103	0.206	0.265	0.097	0.270	0.016	0.015	0.012	0.010	0.007	1.000
3	0.110	0.181	0.223	0.214	0.066	0.173	0.010	0.009	0.008	0.006	1.000
4	0.110	0.188	0.195	0.183	0.151	0.044	0.112	0.006	0.006	0.005	1.000

Table 9.14. Continuation of the hypothetical example from tables 9.11–9.13 showing calculations of starting abundances, $N_{l,t}$, average abundances, $\bar{N}_{l,t}$, and catches $C_{l,t}$, by length and time for the model used in length-based stock synthesis analysis, along with the corresponding proportions, $\alpha(N)_{l,t}$, for average abundance and $\alpha(C)_{l,t}$ for catch at length class l for each time t .

Length, l	Time, t					
	1	2	3	4	5	6
$N_{l,t}$						
1	958	940	858	914	998	943
2	893	1057	1036	991	1063	1121
3	543	565	611	577	586	652
4	490	705	788	792	824	916
5	116	168	236	273	326	405
Total	3000	3435	3529	3547	3798	4037
$\bar{N}_{l,t}$						
1	859	833	752	811	895	
2	793	920	882	862	944	
3	476	481	504	490	514	
4	428	590	634	662	717	
5	101	139	187	226	282	
Total	2657	2963	2958	3051	3353	
$\alpha(N)_{l,t}$						
1	0.323	0.281	0.254	0.266	0.267	
2	0.298	0.310	0.298	0.283	0.282	
3	0.179	0.162	0.170	0.161	0.153	
4	0.161	0.199	0.214	0.217	0.214	
5	0.038	0.047	0.063	0.074	0.084	
Total	1.000	1.000	1.000	1.000	1.000	
$\alpha(C)_{l,t}$						
1	0.068	0.055	0.047	0.049	0.049	
2	0.251	0.242	0.220	0.208	0.207	
3	0.263	0.222	0.220	0.207	0.197	
4	0.338	0.389	0.396	0.400	0.393	
5	0.080	0.092	0.117	0.136	0.154	
Total	1.000	1.000	1.000	1.000	1.000	
$C_{l,t}$						
1	9	17	23	16	9	
2	32	74	106	69	38	
3	33	67	106	69	36	
4	43	118	190	132	72	
5	10	28	56	45	28	
Total	127	304	480	331	183	

and time follow from (9.43) by replacing average abundances, $\bar{N}_{a,t}$, with starting abundances, $N_{a,t}$. These abundances are similar to those in table 9.10, suggesting that different model structures can have similar results, even though they are based on different assumptions.

Average abundances, $\bar{N}_{l,t}$, by length and time in table 9.14 follow from (9.43) and are also expressed as population proportions, $\alpha(N)_{l,t}$. Unlike catch-length analysis,

abundances by length are derived from abundances by age and the length–age proportions $\psi_{l,a}$ rather than from an initial abundance vector by length and a growth transition matrix. Then catch proportions by length, $\alpha(C)_{l,t}$, are determined from length selectivities, s_l , and average abundances, $\bar{N}_{l,t}$, using (9.44). Catches, $C_{l,t}$, by length and time are then obtained by multiplying these proportions by total catches, C_t , using (9.48). A comparison of population and catch proportions by length, previously done by age, shows the same result: that length classes with larger fish have higher proportions in the catch than in the population, as expected due to increasing length selectivity.

Due to the disparate length intervals of classes used in this example (in order to keep the number of calculations small enough for presentation), average length in the catch by age is not calculated using (9.47). To use that formula, this example would need to be repeated using a finer scale of length classes (say, 1-cm length classes). ■

Migration, Movement, and Other Spatiotemporal Considerations

Many fish populations exhibit migration or movement during some phase of their life histories. Migration is considered to be consistent, directional movement of some component of a population. Movement refers more generally to any change in the location of individuals in a population. Migrations may be seasonal, such as movement from summer feeding grounds to winter spawning areas, as for Pacific halibut. Or migrations may be annual or longer, such as the movement of young fish from nursery areas to areas where adults are found. Homing of salmon to natal streams after some years in the marine environment is the best known example. For species where eggs and larvae drift far from spawning grounds, compensatory movement is clearly needed to maintain population viability. We use the terms *movement* and *migration* interchangeably and leave the specification of terms to the interpretation of data from a given population. Mathematically, consistency in movement can be handled by making movement parameters constant over some time dimension.

Incorporating the migration of a population into its assessment is not frequently undertaken, and the array of techniques is fairly limited. One reason is that many populations are resident, especially in the adult stage, or that the migration rate is low enough that it can be ignored. However, some notable exceptions include species such as Pacific halibut (*Hippoglossus stenolepis*), Pacific salmon (*Oncorhynchus* sp.), tuna (*Thunnus* sp.), and sablefish (*Anoplopoma fimbria*). Another reason is that instantaneous assessments of a migratory population are often possible, especially when a population passes a location where it can be encountered. For other populations, analysis of the combined population suffices, or simple techniques are used for apportioning abundance and yield among geographic regions (see section 10.5). Finally, the dynamics for migratory populations can be complicated, and sufficient data are frequently unavailable.

Models for non-age-structured and age-structured migratory populations are described in section 10.1. Estimation of migration is explored in section 10.2. Extensions to cohort analysis and catch-age analysis (chapter 8) for migratory populations are given in section 10.3. Run reconstruction of salmon populations, a technique for separating mixed stocks, is presented in section 10.4. Run reconstruction is an extension

of migratory cohort analysis. Methods of apportioning biomass and yield based on catch-per-unit-effort and survey data are given in section 10.5. Finally, necessary modifications to per recruit studies are given in section 10.6.

10.1. POPULATION MODELS

As with other population models, models for migratory populations can be based on either instantaneous or annual (or some other unit time) rates, depending on whether the dynamics are based on a continuous or discrete time frame. In terms of migration or movement, we parameterize the instantaneous rate of movement from region i to region j as $\psi_{i \rightarrow j}$. We refer to the total instantaneous rate of movement from region i as the instantaneous exit rate and write it as

$$\psi_i^* = \sum_{j \neq i} \psi_{i \rightarrow j}. \quad (10.1)$$

The annual rate of movement from region i to region j is denoted $\theta_{i \rightarrow j}$ and represents the probability or proportion of individuals in region i that move to region j . The corresponding annual exit rate is

$$\theta_i^* = \sum_{j \neq i} \theta_{i \rightarrow j}. \quad (10.2)$$

We can write the probability or proportion of individuals remaining in region i as $\theta_{i \rightarrow i}$ and note that

$$\theta_{i \rightarrow i} = 1 - \theta_i^* = 1 - \sum_{j \neq i} \theta_{i \rightarrow j}. \quad (10.3)$$

The matrix of the $\{\theta_{i \rightarrow j}\}$ is denoted Θ .

The population is distributed across R regions. A graphical depiction of annual movement is shown in figure 10.1 for three regions where movement occurs in both directions between any two regions.

10.1.1. Deterministic Model, Non-Age-structured Populations

In this model, the time dimension is continuous, so instantaneous rates are used. The population within a region may be affected by recruitment, mortality, immigration (into the region), and emigration (out of the region). Let N_i be the abundance in region i , r_i be the intrinsic rate of increase in region i , and K_i be the carrying capacity in region i . The intrinsic rate of increase is understood to represent the combined processes of recruitment and growth decremented by natural and fishing mortalities.

The multispecies extension of the logistic from section 1.1.4 can be adapted for multiregion dynamics as

$$\frac{dN_i}{dt} = r_i N_i \left(1 - \frac{N_i}{K_i}\right) - \sum_{j \neq i}^R \psi_{i \rightarrow j} N_i + \sum_{j \neq i}^R \psi_{j \rightarrow i} N_j. \quad (10.4)$$

The first term represents the simple logistic, the second term represents emigration from the area, and the third term represents immigration into the area. This model is

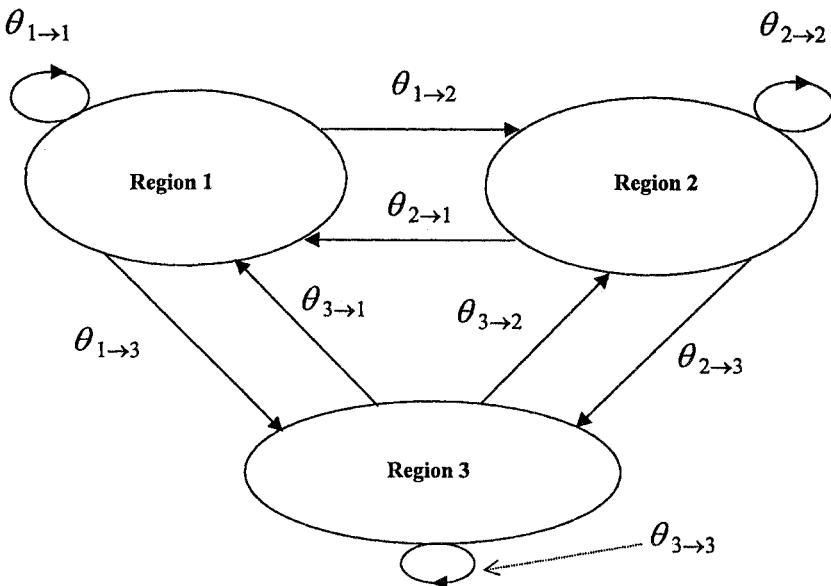


Figure 10.1. A conceptual diagram for a population found in three regions, showing the rates of movement, $\theta_{i \rightarrow j}$, between regions.

simply a geographical generalization of the logistic model of section 1.1.2. Written in terms of the exit rate using (10.1), (10.4) becomes

$$\frac{dN_i}{dt} = (r_i - \psi_i^*) N_i - \frac{r_i}{K_i} N_i^2 + \sum_{j \neq i}^R \psi_{j \rightarrow i} N_j. \quad (10.5)$$

Phase-plane analysis can be used to find joint equilibrium solutions. Numerical techniques can be used to obtain time-dependent solutions. As in chapters 1 and 2, this type of model can also be formulated as a set of difference equations. Other parameterizations are possible, such as using relative rates or productivity parameters.

This model is a deterministic example from a class of models known as compartmental models, where modeling of a process is undertaken with compartments representing subprocesses or components. A large literature exists for compartmental models (Matis et al. 1979, Grant et al. 1991). A stochastic compartmental model is described in the next section. An important assumption of this model, called the “Markovian” assumption, is that the rate of movement is a function solely of the region individuals are in at a given time. This lack of “memory” may be unrealistic for some populations that exhibit homing or have fidelity to certain locations.

A geographical generalization of the exponential model of section 1.1.1 is obtained as a special case of (10.5) by letting $K_i \rightarrow \infty$. By denoting $\kappa_i = r_i - \psi_i^*$ as the difference between the intrinsic rate of increase and exit rate, (10.5) simplifies to

$$\frac{dN_i}{dt} = \kappa_i N_i + \sum_{j \neq i}^R \psi_{j \rightarrow i} N_j. \quad (10.6)$$

As shown by Gordon et al. (1970, 1995), this model can be written in matrix form as

$$\begin{pmatrix} \frac{dN_1}{dt} \\ \vdots \\ \frac{dN_n}{dt} \end{pmatrix} = \begin{pmatrix} \kappa_1 & \psi_{2 \rightarrow 1} & \cdots & \psi_{n \rightarrow 1} \\ \vdots & \vdots & \vdots & \vdots \\ \psi_{1 \rightarrow n} & \psi_{2 \rightarrow n} & \cdots & \kappa_n \end{pmatrix} \begin{pmatrix} N_1 \\ \vdots \\ N_n \end{pmatrix}$$

or $\frac{d\mathbf{N}}{dt} = \tilde{\Psi}\mathbf{N}.$ (10.7)

Given initial conditions $\mathbf{N}_0 = \mathbf{N}(0)$, the solution of the system (10.7) is

$$\mathbf{N}(t) = e^{\tilde{\Psi}t} \mathbf{N}_0, \quad (10.8)$$

which is analogous to the simple exponential model. The exponential term in (10.8) can be calculated from the series expansion

$$e^{\tilde{\Psi}t} = \mathbf{I} + \tilde{\Psi}t + \frac{1}{2}\tilde{\Psi}^2 t^2 + \cdots + \tilde{\Psi}^x \frac{t^x}{x!} + \cdots. \quad (10.9)$$

By calculating the matrix $\mathbf{R} = \exp(\tilde{\Psi})$ of annual rates, one can calculate abundance sequentially for discrete times $t = 1, 2, \dots$ using

$$\mathbf{N}_t = \mathbf{R} \mathbf{N}_{t-1}. \quad (10.10)$$

Example 10.1. Hypothetical population

Table 10.1 shows a hypothetical population in three regions with movement rates ranging from 0.10 to 0.20 and intrinsic rates of increase ranging from 0.05 to 0.15. The values for ψ_i^* , κ_i , and the corresponding matrix $\tilde{\Psi}$ from (10.7) are also shown. Terms up to order 3 in the series expansion (10.9) with $t = 1$ are also given, leading to the matrix \mathbf{R} . For an initial population of 50, 100, and 50 individuals in the three regions at time $t = 0$, the population is projected for the next five years, using (10.10). After five years, the annual rate of increase among the regions ranges from 6% in region 2 to 13% in region 1, with a rate of increase for the overall population of 10%. ■

Difference models

Hilborn (1990) developed a difference model for dynamics of a migratory population. By assuming that the order of dynamics in a time period is harvest, followed by natural mortality, followed by movement, the dynamics of a population of $\{N_{i,0}\}$ for areas i at time 0 in later time periods, t , can be written

$$N_{i,t+1} = \sum_{j=1}^R N_{j,t} (1 - \mu_{j,i}) \ell_j \theta_{j \rightarrow i} + R_{i,t}, \quad (10.11)$$

where ℓ is natural survival, θ is annual (rather than instantaneous) movement rate, $R_{i,t}$ represents new additions to the population, and μ is harvest rate. Because movement rates are now annual, they sum to 1 for each region as in (10.2) and (10.3). (Hilborn used parameter $p_{i,j}$ in place of $\ell_j \theta_{j \rightarrow i}$ because in his applications, natural mortality and movement were confounded.) Similar models can be written for different orderings

Table 10.1. Hypothetical population in three regions following Gordon's model with given instantaneous movement rates and rates of increase.

From i	To j	1	2	3	ψ_i^*	r_i	κ_i
$\Psi_{i \rightarrow j}$							
	1		0.10	0.10	0.20	0.05	-0.15
	2	0.15		0.15	0.30	0.10	-0.20
	3	0.20	0.20		0.40	0.15	-0.25
$\tilde{\Psi}$		$\begin{bmatrix} -0.15 & 0.15 & 0.20 \\ 0.10 & -0.20 & 0.20 \\ 0.10 & 0.15 & -0.25 \end{bmatrix}$			\mathbf{I}	$\begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix}$	
$\tilde{\Psi}^2/2$		$\begin{bmatrix} 0.02875 & -0.01125 & -0.02500 \\ -0.00750 & 0.04250 & -0.03500 \\ -0.01250 & -0.02625 & 0.05625 \end{bmatrix}$					
$\tilde{\Psi}^3/6$		$\begin{bmatrix} -0.00265 & 0.00094 & 0.00325 \\ 0.00063 & -0.00496 & 0.00525 \\ 0.00163 & 0.00394 & -0.00727 \end{bmatrix}$					
\mathbf{R}		$\begin{bmatrix} 0.876 & 0.140 & 0.178 \\ 0.093 & 0.838 & 0.170 \\ 0.089 & 0.128 & 0.799 \end{bmatrix}$					
			t				
	i	0	1	2	3	4	5
$N_{i,t}$							Ratio
	1	50	67	82	97	112	126
	2	100	97	97	100	105	111
	3	50	57	64	71	78	86
	Sum	200	221	243	268	294	323

of the harvest, natural mortality, and movement processes. In some situations, harvest rate might be assumed proportional to fishing effort, or

$$\mu_{i,t} = q_i E_{i,t}, \quad (10.12)$$

where q_i is the catchability coefficient.

Diffusion models

A different approach is the use of partial differential equations to model movement (Beverton and Holt 1957, section 10; Okubo 1980, Hilborn 1990, Deriso et al. 1991, Mullen 1994). The population is considered to be continuous in three dimensions: two position dimensions, x and y , and the time dimension, t . As summarized by Hilborn (1990), a simple partial differential equation for population change subject to natural mortality, M , and movement is then

$$\frac{\partial N(x, y, t)}{\partial t} = -MN + D \left[\frac{\partial^2 N(x, y, t)}{\partial x^2} + \frac{\partial^2 N(x, y, t)}{\partial y^2} \right], \quad (10.13)$$

where D is a coefficient of dispersion. A difference equation approximation of (10.13) from Hilborn (1990) is

$$N_{i,j,t+1} = \ell [N_{i,j,t}(1 - 4d) + d(N_{i-1,j,t} + N_{i,j-1,t} \\ + N_{i+1,j,t} + N_{i,j+1,t})], \quad (10.14)$$

where individuals are located in squares indexed by i and j ; d is an analogous coefficient of dispersion representing the proportion of individuals moving to an adjacent square. Equation (10.14) is better regarded as a difference equation analogue to (10.13) rather than as a method for solving the partial differential equation (PDE). The problem with (10.14), as a method of solution to a PDE, is that it is a numerically unstable method because it involves an explicit scheme for approximation of derivatives. Explicit schemes are those in which the right-hand side of the PDE is approximated by functions dependent only on current or previous states of the system. Implicit schemes are numerically stable [see, for example, chapter 17 of Press et al. (1989) for theory and Sibert and Fournier (1994) for an application of such methods to a model of movement of tagged fish]. See section 10.1.2 for Deriso's alternative approach to representing diffusion as a discrete process.

Basin model

MacCall (1990) developed a theory of dynamic geography for marine fish populations that combines principles from theoretical ecology with those from population dynamics theory. The basis of the theory is that some areas are more suitable than others in terms of habitat for fish populations, so the locations and movement of fish are related to habitat suitability as modified by the population density in the area. A population at low levels will occupy the most suitable habitats; as population size increases, those habitats become less suitable, and the population will expand into less suitable habitats. In the basic model, MacCall assumes that the overall population dynamics can be described by the logistic model (as in section 1.2):

$$\frac{1}{N} \frac{\partial N}{\partial t} = r^* - F = r - bN - F, \quad (10.15)$$

where realized habitat suitability or per capita growth rate, $r^* = r - bN$ (in the absence of fishing), is determined by basic habitat suitability and abundance; r is the intrinsic rate of population increase, $b = r/K$, K is carrying capacity; and F is fishing mortality. The spatial dynamics in one spatial dimension, x , are assumed to follow a diffusion process where rate of migratory flow is proportional to the gradient in realized habitat suitability ($\partial r^*/\partial x$), which leads to

$$\frac{\partial N}{\partial t} = \mathcal{K} \frac{\partial^2 N}{\partial x^2} - V^{-1} \frac{\partial r^*}{\partial x} \frac{\partial N}{\partial x}, \quad (10.16)$$

where \mathcal{K} is a coefficient of diffusivity and V is a constant for population flow rate (e.g., viscosity). The combination of temporal dynamics in (10.15) and spatial dynamics in (10.16) is the complete basic model, given by

$$\frac{\partial N}{\partial t} = r^* N - FN + \mathcal{K} \frac{\partial^2 N}{\partial x^2} - V^{-1} \frac{\partial r^*}{\partial x} \frac{\partial N}{\partial x}. \quad (10.17)$$

Realized habitat suitability, r^* , affects both the rate of population growth and the amount of movement in (10.17), which MacCall asserted is a natural evolutionary consequence of individuals responding to better habitat.

MacCall (1990) used the basin model to explore conceptually the impact of differential habitat suitability on population dynamics and fisheries management. He extended the model to consider nonlinear growth models, territoriality, multiple habitats, stock-recruitment relationships, optimal harvesting, and spatial modeling. He also developed an application of the basin model to the California northern anchovy population, which has a long time series of life-history information from CALCOFI surveys. The model has to date received much attention and provides a heuristic first step in understanding spatial dynamic processes, but there are differing views of the model's usefulness (e.g., Power 1991, Quinn 1991).

10.1.2. Stochastic Model, Non-Age-structured Populations

Stochastic compartmental models have been developed by Grant et al. (1991) and Deriso et al. (1991). In Grant et al. (1991), recruitment and mortality dynamics are considered negligible, time is continuous, and the focus is on movement. In a stochastic model, interest is in the probability of movement. Let $\psi_{i \rightarrow j}$ and ψ_i^* be, as before, instantaneous movement and exit rates expressed as probabilities, and let $N_{j \rightarrow i}(t)$ be the abundance in region i at time t from region j at time 0, and $P_{j \rightarrow i}(t)$ be the probability of being in region i at time t given in region j at time 0. The standard assumptions of Markov processes are now made—namely, that individuals move independently and that the probability that an individual in region j at time t will be in region i at time $t + \Delta t$ for $i \neq j$ is $\psi_{j \rightarrow i} \Delta t$. Markov processes are characterized by the same lack of memory as found in the models in the previous section. That is, the transition probability depends only on where an individual is at the given time and is independent of previous locations of the individual.

The set of R^2 differential equations that results may be written in matrix form as

$$\frac{d\mathbf{P}}{dt} = \Psi^* \mathbf{P}, \quad (10.18)$$

where Ψ^* is the so-called transition matrix made up of the $\psi_{j \rightarrow i}$ off the diagonal and the $-\psi_j^*$ on the diagonal, where i is row and j is column. The solution (10.8) for \mathbf{N} of the previous section with Ψ^* in place of $\tilde{\Psi}$ applies here to \mathbf{P} . As shown by Grant et al., this solution can be expressed as a sum of exponentials involving the eigenvalues of Ψ^* . The number of fish moving from j to i by time t is then a binomial random variable with expected value

$$E[N_{j \rightarrow i}(t)] = N_j(0) P_{j \rightarrow i}(t). \quad (10.19)$$

As a consequence of the Markovian assumptions, the transit or sojourn time of a random fish in area j before its movement to area i is an exponential random variable with parameter $\psi_{j \rightarrow i}$. Hence, the expected conditional and unconditional transit times are $\psi_{j \rightarrow i}^{-1}$ and $(\psi_j^*)^{-1}$, respectively. Grant et al. also derived variances for these transit times and determine expected number of visits to a region and residence time in the region during the visits.

The approach of Deriso et al. (1991) also uses a Markov process. It differs from that of Grant et al. in that time is discrete, mortality is included, and a continuous diffusion

process is used to determine transition probabilities. With mortalities F , M , and Z and fishing effort, E , defined as usual, let $\theta_{i \rightarrow j}$ and $\theta_{i \rightarrow i}$ again be annual movement and nonmovement rates expressed as probabilities, and during time t , let

$P_{j,t}$ = probability of being in region j (at the start of time t),

$P'_{j,t}$ = probability of being in region j after movement,

$S_{j,t} = e^{-Z \cdot t}$ = probability of survival in region j after movement,

$\mu_{j,t} = \frac{F_{j,t}}{Z_{j,t}}(1 - e^{-Z \cdot t})$ = exploitation probability in region j ,

$f_{j,t}$ = probability of capture in region j after movement, and

$F_{j,t} = q_{j,t} E_{j,t}$ = typical fishing mortality–fishing effort relationship.

Movement is assumed to occur just after the start of the time interval, after which fishing and natural mortality occur simultaneously. Three equations govern the movement, capture, and survival processes:

$$P'_{j,t} = \sum_{i=1}^R P_{i,t} \theta_{i \rightarrow j} \quad (10.20)$$

$$f_{j,t} = \mu_{j,t} P'_{j,t} \quad (10.21)$$

$$P_{j,t+1} = S_{j,t} P'_{j,t}. \quad (10.22)$$

Given an initial distribution of abundances $\{N_{j,0}\}$, population abundance and catch can be calculated sequentially in time using these equations by multiplying by total abundance, N_t , at the start of time t .

To compute movement probabilities, Deriso et al. approximated a continuous diffusion model from Okubo (1980) with components for velocity, direction, and diffusion. The population area is divided into equal-sized square quadrats, and fish are assumed to be distributed uniformly over each quadrat. As shown in figure 10.2 (see example 10.2), the fish in a given quadrat are assumed to move with velocity R , angle α , and diffusion D , where the resulting movement box has length \sqrt{D} . Movement probabilities are then calculated from the relative area occupied in each quadrat, as follows. Suppose that the coordinates of the center quadrat are at $(0, 0)$; then the center of the movement box is at $(x, y) = (R \cos \alpha, R \sin \alpha)$. For a particular quadrat for which the movement probability is to be found, let i_l and i_u be the lower and upper coordinates on the x -axis, and j_l and j_u be the lower and upper coordinates on the y -axis. For the movement box, the same coordinates are denoted x_l , x_u , y_l , and y_u . The movement probabilities are:

$$\theta_{i,j} = 0 \quad \text{if } y_u < j_l \text{ or } x_u < i_l \text{ or } y_l > j_u \text{ or } x_l > i_u;$$

otherwise,

$$\theta_{i,j} = D^{-1}[\min(x_u, i_u) - \max(x_l, i_l)][\min(y_u, j_u) - \max(y_l, j_l)]$$

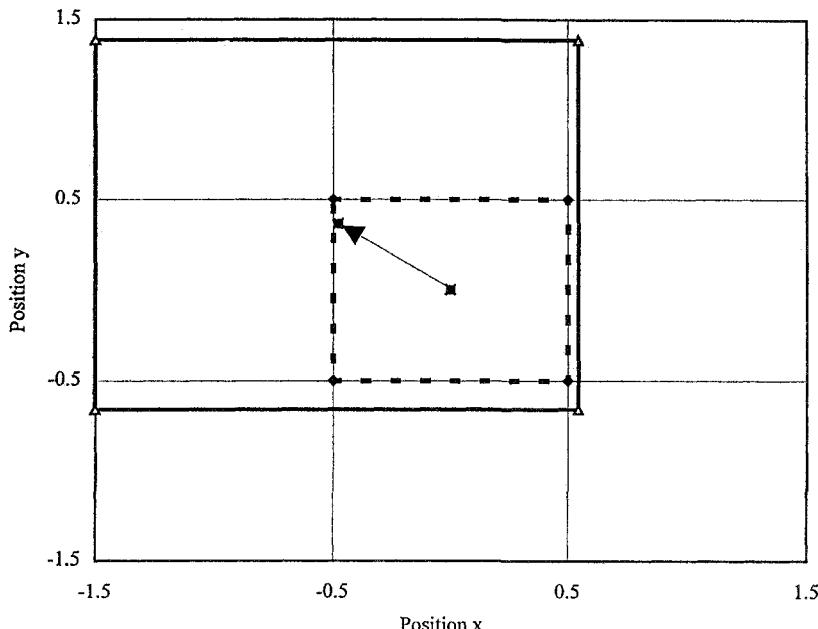


Figure 10.2. Movement of fish from the center box (dashed lines) to the box in thick solid lines. Movement parameters are $R = 0.6$, $\alpha = -3.79$ radians (about -217°), and $D = 4.19$. The arrow shows the net direction and distance of movement at the centers of the two boxes.

for any quadrat adjacent to the center one. Deriso gave further restrictions for biological realism and to improve parameter estimation and also gave an alternate foraging model for predicting movement.

Example 10.2. Yellowfin tuna

Yellowfin tuna can move great distances, and the Inter-American Tropical Tuna Commission has conducted several tagging experiments to assess the magnitude and direction of their movement. Deriso et al. (1991) applied the above model (labeled iv in his paper) to experiment 1084. For season 2 and quadrats with islands, they obtained parameter estimates for R , α , and D of 0.6 (relative to a distance of 5°), -3.79 radians, and 4.19 (relative to an area of $5^{\circ}2$), respectively. These values produce the movement box shown in figure 10.2. The definitions of the vertices of the donor and movement boxes and calculations of movement probabilities are illustrated in table 10.2. ■

Non-Markovian processes

If movement follows a Markovian process, then an individual's current location depends only on its most recent previous location. Therefore, if movement does not follow a Markovian process, then at least some of an individual's previous locations must be known. The failure of the Markovian assumption is most likely to occur for homing species such as Pacific salmon. However, even then the Markovian assumption may be a reasonable approximation. Alternative models for homing populations are described in section 10.4.

Table 10.2. Diffusion parameters from experiment 1084, model iv of Deriso et al. (1991) and calculation of corresponding movement probabilities and vertices of movement boxes.

	Center quadrat		Movement box		
	x	y	x	y	
Vertices					
	-0.5	0.5	-1.50	1.39	
	0.5	0.5	0.55	1.39	
	0.5	-0.5	0.55	-0.66	
	-0.5	-0.5	-1.50	-0.66	
Centers	0	0	-0.48	0.36	
			($R \cos \alpha$)	($R \sin \alpha$)	
Quadrats	i_l	i_u	j_l	j_u	θ
	-1.5	-0.5	0.5	1.5	0.211
	-1.5	-0.5	-0.5	0.5	0.239
	-1.5	-0.5	-1.5	-0.5	0.038
	-0.5	0.5	0.5	1.5	0.211
	-0.5	0.5	-0.5	0.5	0.239
	-0.5	0.5	-1.5	-0.5	0.038
	0.5	1.5	0.5	1.5	0.010
	0.5	1.5	-0.5	0.5	0.011
	0.5	1.5	-1.5	-0.5	0.002
	x_l	x_u	y_l	y_u	Sum
	-1.50	0.55	-0.66	1.39	0.999

$$R = 0.6; \alpha = -3.79; D = 4.19.$$

10.1.3. Age-structured Populations

The Leslie matrix model of section 7.1 can be extended for migratory populations, as we now show. The extension is analogous to that for stage-structured models (section 9.2). One approach, mentioned by Getz and Haight (1989, p.36), is to consider a single population of interest with immigration and emigration. The dynamic equation for an age-structured population, $\mathbf{N}_t = \{N_{a,t}\}$ for ages $a = 1, \dots, A$ at time t can be written

$$\mathbf{N}_{t+1} = \mathbf{G} \mathbf{N}_t + \mathbf{R}_t, \quad (10.23)$$

where \mathbf{G} is a projection matrix with off-diagonal elements $G_{a,a-1} = S_a$ and other elements $G_{a,j} = 0$, $j \neq a - 1$, and S_a is survival during age a . The vector \mathbf{R}_t represents net additions or subtractions from the population, given by

$$\mathbf{R}_t = \begin{pmatrix} S_0 \sum_{a=1}^A f_a N_{a,t} + R_1 \\ R_2 \\ \vdots \\ R_A \end{pmatrix}, \quad (10.24)$$

where R_a represents net additions or subtractions during age a . The first term of the first element $R_{1,t}$ is simply the production of eggs during year t that survive to age

1. The advantages of this form of the Leslie matrix are described by Getz and Haight (1989), one of which is its adaptability to stage-structured models.

A different extension of the Leslie matrix method for migratory populations, thoroughly described by Caswell (1989, chapter 3), considers the dynamics of an age-structured population stratified (or classified) by different regions. Pertinent to stage-structured models and age-size models as well, the extension is made by simply stacking the age-specific vectors for the regions and augmenting the projection matrix with consideration of movement. For age $a = 1, \dots, A$, time $t = 1, \dots, T$, and region $i = 1, \dots, R$, let

- $N_{a,t,i}$ = population abundance in region i
- $S_{a,i}$ = survival in region i
- $S_{0,i}$ = early life survival at age 0 in region i
- $f_{a,i}$ = net fecundity and region i
- $\theta_{a,i \rightarrow j}$ = migration proportion from region i to region j .

We assume that migration occurs just after the start of the year, followed by survival.

To derive this extension, we first consider a population made up of two regions, i and j , derive the dynamic equations, and then show the corresponding matrix representation. We make use of previous results for the Leslie matrix from section 7.1. A pair of recursive equations (one for age 1, one for age $a + 1$) describes population abundance for year $t + 1$ in region i . For age 1, the recursive equation follows directly from the single-area Leslie matrix and is given by

$$N_{1,t+1,i} = S_{0,i} \sum_{a=1}^A f_{a,i} N_{a,t,i}. \quad (10.25)$$

This equation simply expresses the number of individuals that age 1 abundance is the number of individuals that survive from egg production the previous year. The second equation is analogous to (10.4) for a non-age-structured population and is given by

$$N_{a+1,t+1,i} = S_{a,i} (N_{a,t,i} - N_{a,t,i} \theta_{a,i \rightarrow j} + N_{a,t,j} \theta_{a,j \rightarrow i}) \quad (10.26)$$

$$= S_{a,i} [N_{a,t,i} (1 - \theta_{a,i \rightarrow j}) + N_{a,t,j} \theta_{a,j \rightarrow i}] \quad (10.27)$$

$$= S_{a,i} (N_{a,t,i} \theta_{a,i \rightarrow i} + N_{a,t,j} \theta_{a,j \rightarrow i}) \quad (10.28)$$

The second term in parentheses in (10.26) represents movement of fish from area i to area j , and the third term represents movement from area j to area i . Equivalently in (10.28), the first term represents continuing residence in area i and the second term represents movement from area j . The two equations for area j follow directly from (10.25) and (10.28) by replacing i with j and j with i .

Combined over areas, these two equations become

$$N_{1,t+1} = \sum_{a=1}^A (S_{0,i} f_{a,i}) N_{a,t,i} + \sum_{a=1}^A (S_{0,j} f_{a,j}) N_{a,t,j} \quad (10.29)$$

$$\begin{aligned} N_{a+1,t+1} &= (S_{a,i} \theta_{a,i \rightarrow i} + S_{a,j} \theta_{a,i \rightarrow j}) N_{a,t,i} \\ &\quad + (S_{a,i} \theta_{a,j \rightarrow i} + S_{a,j} \theta_{a,j \rightarrow j}) N_{a,t,j}. \end{aligned} \quad (10.30)$$

It is fairly easy to show that (10.29) and (10.30) become equivalent to those for the Leslie matrix model:

$$N_{1,t+1} = S_0 \sum_{a=1}^A f_a N_{a,t} \quad (10.31)$$

$$N_{a+1,t+1} = S_a N_{a,t}, \quad (10.32)$$

if and only if $S_{0,i} = S_{0,i} = S_0$, $f_{a,i} = f_{a,j} = f_a$, and $S_{a,i} = S_{a,j} = S_a$. Thus, if these population parameters are constant over region, the regional Leslie matrix model reduces to the single-region model.

This multiregional model can be written in matrix form analogous to a Leslie matrix. The vector of abundances is made up of the two vectors by region, and the projection matrix has four different subsections to account for movement and non-movement between regions. By using (10.25) and (10.28), the matrix form is

$$\mathbf{N}_{t+1} = \mathbf{MN}_t. \quad (10.33)$$

where the column vector \mathbf{N}_t is

$$\mathbf{N}_t = \begin{pmatrix} \mathbf{N}_{t,i} \\ \mathbf{N}_{t,j} \end{pmatrix} = \begin{pmatrix} N_{1,t,i} \\ N_{2,t,i} \\ \vdots \\ N_{A-1,t,i} \\ N_{A,t,i} \\ N_{1,t,j} \\ N_{2,t,j} \\ \vdots \\ N_{A-1,t,j} \\ N_{A,t,j} \end{pmatrix},$$

and the projection matrix \mathbf{M} is

$$\mathbf{M} = \begin{pmatrix} M_{i,i} & M_{i,j} \\ M_{j,i} & M_{j,j} \end{pmatrix}, \quad (10.34)$$

with submatrices on the diagonal given by

$$\mathbf{M}_{i,i} = \begin{pmatrix} S_{0,i} f_{1,i} & S_{0,i} f_{2,i} & \cdots & S_{0,i} f_{A-1,i} & S_{0,i} f_{A,i} \\ S_{1,i} \theta_{1,i \rightarrow i} & 0 & \cdots & 0 & 0 \\ 0 & S_{2,i} \theta_{2,i \rightarrow i} & \ddots & \vdots & \vdots \\ \vdots & \ddots & \ddots & 0 & 0 \\ 0 & \cdots & 0 & S_{A-1,i} \theta_{A-1,i \rightarrow i} & S_{A,i} \theta_{A,i \rightarrow i} \end{pmatrix} \quad (10.35)$$

and with submatrices off the diagonal given by

$$\mathbf{M}_{i,j} = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ S_{1,i}\theta_{1,j \rightarrow i} & 0 & \cdots & 0 & 0 \\ 0 & S_{2,i}\theta_{2,j \rightarrow i} & \ddots & \vdots & \vdots \\ \vdots & \ddots & \ddots & 0 & 0 \\ 0 & \cdots & 0 & S_{A-1,i}\theta_{A-1,j \rightarrow i} & S_{A,i}\theta_{A,j \rightarrow i} \end{pmatrix}. \quad (10.36)$$

If the last age group A does not represent a pooled age group of ages A and older, then $S_{A,i} = S_{A,j} = 0$, which results in a 0 in the (A,A) position of each submatrix.

The generalization to multiple regions is straightforward. The modification to (10.28) follows from (10.4) and is given by

$$N_{a+1,t+1,i} = S_{a,i} \left(N_{a,t,i}\theta_{a,i \rightarrow i} + \sum_{j \neq i} N_{a,t,j}\theta_{a,j \rightarrow i} \right). \quad (10.37)$$

In matrix form, this is accomplished by adding additional submatrices for additional regions and noting that $\theta_{a,i \rightarrow i} = 1 - \sum_{j \neq i} \theta_{a,i \rightarrow j}$.

Caswell (1989, pp.45–68) described the time-dependent behavior, stability of the age distribution, and stationarity of the population for any projection matrix with non-negative elements (see chapter 7 for age-structured models and chapter 9 for length-structured models). The projection matrix \mathbf{M} is always non-negative and usually primitive (unless too many of the f_a are zero). Non-negative, primitive matrices are irreducible, and as a consequence, the population will reach a stable age distribution across ages and regions regardless of initial conditions. This stable age distribution is proportional to the eigenvector corresponding to the dominant eigenvalue (say, λ_1). The population will grow or diminish asymptotically at a rate proportional to λ_1 . Hence, a stationary population is one in which $\lambda_1 = 1$. If the projection matrix is non-negative and irreducible but imprimitive, then the population will oscillate and not converge to a stable condition. However, if the population should start out initially proportional to the dominant eigenvector, it will remain stable. If the projection matrix is non-negative and reducible, then some regions do not communicate. The population may reach a stable population level, but this depends on initial conditions.

Example 10.3. Hypothetical population

Consider a population with $A = 3$ ages and $R = 2$ regions with the following parameters:

$$\begin{aligned} N_{a,1,x} &= \{100, 80, 72\} \text{ for } a = \{1, 2, 3\}, \text{ for } x = 1, 2; \\ S_{a,x} &= \{0.8, 0.9\} \text{ for } a = \{1, 2\}, \text{ for } x = 1, 2; \\ f_{a,x} &= \{1, 2, 3\} \text{ for } a = \{1, 2, 3\}, \text{ for } x = 1, 2; \\ \theta_{a,1 \rightarrow 2} &= \{0.4, 0.2\}, \text{ for } a = \{1, 2\}; \\ \theta_{a,2 \rightarrow 1} &= \{0.5, 0.3\}, \text{ for } a = \{1, 2\}. \end{aligned}$$

Assume that $S_{0,1} = S_{0,2} = S_0$.

The value of S_0 that makes the population stationary is 0.21. This value can be found using a spreadsheet program by projecting the population forward for, say, $T = 20$ years and altering the value of S_0 until the population becomes stationary (table 10.3).

Table 10.3. Computation of the generalized Leslie matrix for a population with three ages and two regions.

		Region 1 ($S_0 = 0.21$)			Region 2 ($S_0 = 0.21$)												
		Age			Age												
		1	2	3	1	2	3										
S		0.8	0.9		0.8	0.9											
f		1	2	3	1	2	3										
θ		0.4	0.2		0.5	0.3											
M		Region 1			Region 2												
Region 1	1	$\begin{bmatrix} 0.21 & 0.42 & 0.63 \end{bmatrix}$			$\begin{bmatrix} 0.00 & 0.00 & 0.00 \\ 0.40 & 0.00 & 0.00 \\ 0.00 & 0.27 & 0.00 \end{bmatrix}$												
	2	$\begin{bmatrix} 0.48 & 0.00 & 0.00 \end{bmatrix}$			$\begin{bmatrix} 0.21 & 0.42 & 0.63 \end{bmatrix}$												
	3	$\begin{bmatrix} 0.00 & 0.72 & 0.00 \end{bmatrix}$			$\begin{bmatrix} 0.40 & 0.00 & 0.00 \\ 0.00 & 0.63 & 0.00 \end{bmatrix}$												
Region 2	1	$\begin{bmatrix} 0.00 & 0.00 & 0.00 \end{bmatrix}$			$\begin{bmatrix} 0.21 & 0.42 & 0.63 \end{bmatrix}$												
	2	$\begin{bmatrix} 0.32 & 0.00 & 0.00 \end{bmatrix}$			$\begin{bmatrix} 0.40 & 0.00 & 0.00 \\ 0.00 & 0.63 & 0.00 \end{bmatrix}$												
	3	$\begin{bmatrix} 0.00 & 0.18 & 0.00 \end{bmatrix}$			$\begin{bmatrix} 0.00 & 0.63 & 0.00 \end{bmatrix}$												
		<i>t</i>															
		<i>a</i>	0	1	2	3	4	5	6	7	8	9	10	...	15	...	20
<i>N</i>																	
Region 1	1	100	100	108	112	113	113	114	114	114	114	114	114	114	114	113	
	2	80	88	88	89	89	89	89	89	89	89	89	89	89	89	89	
	3	72	79	83	83	83	83	83	83	83	83	83	83	83	83	83	
Region 2	1	100	100	92	88	87	86	86	86	86	86	86	86	86	86	86	
	2	80	72	72	71	71	71	71	71	71	71	71	71	71	71	71	
	3	72	65	61	61	61	61	61	61	61	61	61	61	61	61	60	
Sum	1	200	200	200	200	200	200	200	200	200	200	200	200	200	199	199	
	2	160	160	160	160	160	160	160	160	160	160	160	160	160	160	159	
	3	144	144	144	144	144	144	144	144	144	144	144	144	144	144	144	

The value of early life survival, S_0 , is the one that keeps the population stable. Population projections are given for $T = 20$ years. Also given are the eigenvalues and eigenvectors for projection matrix \mathbf{M} .

With this value of S_0 , the projection matrix \mathbf{M} can be formed; it has $p = AR = 6$ rows and columns. It is irreducible [$(\mathbf{I} + \mathbf{M})^{p-1}$ is positive] and primitive (\mathbf{M}^{p^2-3p+2} is positive), which implies that the population will converge to a stable age distribution. The eigenvalues and first eigenvector of the projection matrix computed using the mathematical software MATHCAD are also given in table 10.3. As expected, the dominant eigenvalue $\lambda_1 = 1$, implying stationarity, and the dominant eigenvector is proportional to the stable age distribution of the population at $T = 20$. That the remaining eigenvalues are small compared to the dominant one suggests that the convergence to the stable age distribution should be rapid. ■

The time-dependent behavior of this density-independent Leslie matrix model is not realistic because the population can decrease to extinction or increase without bound at an exponential rate (unless the dominant eigenvalue = 1). The necessary change to the model necessary to obey the limits seen in actual populations is density dependence. Thus the term S_0 would need to be replaced with a density-dependent function as in chapter 7. Other changes that would increase the realism of the model for short-term projections include making migration, survival, and fecundity time-dependent

functions and incorporating stochasticity, especially in the term S_0 . Some work along these lines is in Heifetz (1996).

10.2. ESTIMATION OF MIGRATION

Mark-recapture studies are the primary technique for determining migration rates (Seber 1982). In some circumstances, mark-recapture analysis can also be used to estimate abundance of a migratory population, as presented by Seber (1982). There are also a variety of techniques related to analysis of survival and capture of tag recoveries that may be applicable to migratory populations (Burnham et al. 1987). Major problems with mark-recapture estimation applied to commercial fisheries data are tag loss, lack of information on reporting rates, probability estimates that are less than 0 or greater than 1, and failure to meet the other stringent assumptions of mark-recapture methodology. We present two techniques in depth that have been extensively used in the fisheries literature and briefly mention some other approaches.

10.2.1. Darroch's Method and Extensions

An extension of the simple Petersen mark-recapture method, which entails a single release of marks and a subsequent single capture of fish, is available for populations stratified geographically (Seber 1982, chapter 11). Maximum likelihood theory for the extension was developed by Darroch (1961), and this approach often bears his name. This technique requires temporal and/or spatial marking and recapturing but does not require constant probability of capture. The extension is also based on two time points for release and capture, only that releases and captures are made in geographic strata. Let

a_i = number of marked releases at time 1 in region i , $i = 1, \dots, R$

n_j = number examined for marks at time 2 in region j

$m_{i \rightarrow j}$ = marked recaptures in region j originally marked in region i

p_j = probability of capture in region j

$\theta_{i \rightarrow j}$ = probability that a marked release from region i moves to region j .

It is assumed that (1) the population is closed, so that $\sum_j \theta_{i \rightarrow j} = 1$ for all i ; (2) all individuals in region j have the same probability p_j of being captured; (3) each fish behaves independently of others in regard to movement and capture; (4) movement and capture are independent; and (5) the matrix Θ of the θ 's is nonsingular. Note that the matrix Θ is for marked fish; it must also be assumed that marking does not alter fish behavior, in order to interpret Θ as the probability of movement for the population as a whole.

If ρ is the column vector of the inverses of the capture probabilities ($\rho_j = 1/p_j$), maximum likelihood estimates of ρ and Θ are

$$\widehat{\rho} = \mathbf{M}^{-1} \mathbf{a} \quad \text{and} \quad \widehat{\Theta} = \mathbf{D}_a^{-1} \mathbf{M} \mathbf{D}_{\rho},$$

where \mathbf{M} is the matrix of the $m_{i \rightarrow j}$, \mathbf{a} is the column vector of the a_i , and \mathbf{D} is a diagonal matrix with entries corresponding to the given symbol (Darroch 1961, Seber 1982). Hence, the estimate of $\theta_{i \rightarrow j}$ can be written simply as $\widehat{\theta}_{i \rightarrow j} = m_{i \rightarrow j} \widehat{\rho}_j / a_i$. Note that the

Darroch method can estimate probability of capture and migration rates simultaneously without the need of auxiliary information. However, auxiliary information on fishing effort can improve estimates of capture probability (see Hilborn's method in section 10.2.2).

The variance–covariance matrix for ρ from Seber (1982) is

$$\Sigma_\rho = \mathbf{D}_\rho \Theta^{-1} \mathbf{D}_\mu \mathbf{D}_a^{-1} \Theta'^{-1} \mathbf{D}_\rho,$$

where the diagonal matrix D_μ has diagonal elements $\mu_i = \sum_j \theta_{i \rightarrow j} \rho_j - 1$ (or in matrix form: $\mu = \Theta \rho - 1$). This matrix is estimated by replacing parameters by their estimates. The estimated variance of $\theta_{i \rightarrow j}$ is not given in Seber (1982) but can be derived using the delta method, which results in

$$\widehat{\text{var}}(\widehat{\theta}_{i \rightarrow j}) = \left(\frac{m_{i \rightarrow j}}{a_i} \right)^2 \widehat{\text{var}}(\widehat{\rho}_j) + \widehat{\rho}_j^2 \widehat{\text{var}} \left(\frac{m_{i \rightarrow j}}{a_i} \right),$$

where $\widehat{\text{var}} \left(\frac{m_{i \rightarrow j}}{a_i} \right) = \left(\frac{m_{i \rightarrow j}}{a_i} \right) \left(1 - \frac{m_{i \rightarrow j}}{a_i} \right) / a_i.$

Darroch and Seber also derived estimates of abundance, discussed validity of assumptions, considered variable number of strata, described hypothesis tests, and generalized the method to account for natural mortality in an open population. Darroch's method has also been extended to the situation where a proportion of the marked population strays out of the region of interest (Eames et al. 1981). Dorazio and Rago (1991) evaluated Darroch's method with simulation studies and found that unrealistic or biased parameter estimates could occur for some populations. They derived an estimator incorporating probabilities of tag retention, survival from tagging, and reporting of tags to examine sensitivity to these factors. Dempson and Stansbury (1991) applied Darroch's method successfully to a population of migrating salmon smolts. Schwarz and Dempson (1994) extended Darroch's method by deriving the probability of movement from expected travel time parameters.

Arnason (1972, 1973) extended Darroch's approach to three time intervals and multiple recaptures (described by Seber 1982), and gave recommendations regarding sample size based on simulation studies. Schwarz et al. (1993) derived the likelihood for Arnason's extension by application of a general tag-recovery model of Brownie et al. (1985). They showed how to derive emigration, immigration, harvest rate, and net survival from basic survival, capture, and movement parameters. Schweigert and Schwarz (1993) applied this approach to Pacific herring tagging data from several years. Brownie et al. (1993) further explored this approach by relaxing the assumption of Markovian movement and giving some reduced-parameter models. In application to bird data, they found that Markovian movement was not a tenable assumption, suggesting that models that allow memory are desirable. Several other applications of Darroch's approach are cited in these papers.

Example 10.4. Gulkana River grayling

Grayling in the three sections (main stem, middle fork, upper reaches) of the Gulkana River in Alaska were tagged over several years to determine if fish in these areas could be treated as separate management units or stocks (Bosch 1995). Natural mortality of

grayling was ignored in the following calculations, so migration rates are probably lower than estimated. Thus, this analysis represents a worst case scenario. The vector of marked releases, \mathbf{a} , and the matrix of marked recaptures, \mathbf{M} , is given in table 10.4. Necessary calculations, mainly using matrix arithmetic, that lead to estimates of probability of capture, p_j , and migration rate, $\theta_{i \rightarrow j}$, are also given. Estimates of p_j range from 8% to 16% among the three areas. The variance estimates on the diagonal of the estimated matrix $\hat{\Sigma}_\rho$ are small, suggesting that the inverses of the probability of capture are estimated precisely. Migration rates between areas (the off-diagonal elements of $\hat{\Theta}$) range between 0% and 4%. The migration rates between the main stem and the other two areas are significantly different from 0 (CVs are less than 50% in table 10.4), but small enough in magnitude to be insignificant for management purposes. The migration rate between the middle fork and the upper reaches is not even significantly different from 0. These results, along with other information in Bosch (1995), suggest that grayling in these three areas can be treated as separate management units. ■

10.2.2. Hilborn's Method and Extensions

Hilborn (1990) developed a general framework for estimating movement and population parameters from mark–recapture data which synthesizes several earlier approaches (including the important work in Ishii 1979). The framework consists of a population dynamics model, an observation model for recaptured marks or tags, and maximum likelihood theory to estimate parameters. Any of the models in section 10.1 can be used for the population dynamics model, which is then used to describe the population dynamics of a group of marked individuals. This tag group is usually defined as the number of tagged individuals released at a given time, t , and place, i . Let $N_{i,j,t}$ be the number of individuals of group i in area j at time t after initial release. By allowing additions to the population [as in (10.11) with $T_{i,j,t}$ in place of $R_{i,t}$], new batches of marked members in a region or several regions can be accommodated. In general, one can write the population dynamics model as

$$\mathbf{N}_t = f(\mathbf{N}_{t-1}, \mathbf{N}_{t-2}, \dots | \gamma, \mathbf{T}, \mathbf{E}), \quad (10.38)$$

where f is an arbitrary function, \mathbf{N}_t is the vector of abundances of the tag group in different regions at time t , γ is a vector of movement and population parameters, \mathbf{T} is a vector of tag releases in different areas for group i , and, if available, \mathbf{E} is a vector of fishing effort or auxiliary data affecting harvest rate.

The observation model specifies the recapture process for marks. In general, the observation model can be written

$$\mathbf{C}_t = g(\mathbf{N}_t | \nu, \mathbf{E}) \quad (10.39)$$

where ν is a vector of parameters related to mark recovery (tag shedding, misreporting, reading error, differential catchability of marked members, etc.). Harvest rate parameters are already included in γ , because they affect population dynamics.

If all marked members recaptured are reported and harvest rate is constant among tag groups, then the predicted number of marked recaptures is

$$C_{i,j,t} = \mu_{j,t} N_{i,j,t}, \quad (10.40)$$

Table 10.4. Calculations using Darroch's method for Arctic grayling in the Gulkana River, Alaska (MS, main stem; MF, middle fork; UR, upper reaches).

		MS	MF	UR
	a'	26621	3344	1598
\mathbf{D}_a	MS	26621	0	0
	MF	0	3344	0
	UR	0	0	1598
\mathbf{M}	MS	2169	11	12
	MF	10	522	0
	UR	0	1	171
\mathbf{M}^{-1}	MS	0.000461	-9.7×10^{-6}	-3.2×10^{-5}
	MF	-8.8×10^{-6}	0.001916	6.2×10^{-7}
	UR	5.17×10^{-8}	-1.1×10^{-5}	0.005848
$\hat{\rho}'$		12.19	6.17	9.31
\mathbf{D}_p	MS	12.19	0.00	0.00
	MF	0.00	6.17	0.00
	UR	0.00	0.00	9.31
$\hat{\Theta}$	MS	0.9933	0.0026	0.0042
	MF	0.0365	0.9635	0.0000
	UR	0.0000	0.0039	0.9961
\mathbf{D}_μ	MS	11.1632	0.0000	0.0000
	MF	0.0000	5.3920	0.0000
	UR	0.0000	0.0000	8.2968
Σ_p	MS	0.0632	-0.0015	-0.0025
	MF	-0.0015	0.0662	-0.0003
	UR	-0.0025	-0.0003	0.4534
$\{m_{i-j}/a_i\}$	MS	0.0815	0.0004	0.0005
	MF	0.0030	0.1561	0.0000
	UR	0.0000	0.0006	0.1070
$\{\text{SE}(m_{i-j}/a_i)\}$	MS	0.0017	0.0001	0.0001
	MF	0.0009	0.0063	0.0000
	UR	0.0000	0.0006	0.0077
$\{\text{SE}(\hat{\theta})\}$	MS	0.0289	0.0008	0.0012
	MF	0.0115	0.0558	0.0000
	UR	0.0000	0.0039	0.1019
$\{\text{CV}(\hat{\theta})\}$	MS	2.91%	30.43%	29.75%
	MF	31.64%	5.79%	N/A
	UR	N/A	100.06%	10.22%

where $\mu_{j,t}$ is the harvest rate in region j at time t . If fishing effort information is available, then a common model assumes that harvest rate is proportional to fishing effort, or $\mu_{j,t} = q_j E_{j,t}$, where q_j is catchability (see section 10.1.1).

The likelihood component of the model specifies a suitable error structure for observations of mark recoveries. Hilborn presented both the Poisson and multinomial error structures. For a given marked recapture observation, $C'_{i,j,t}$, following the Poisson distribution, the likelihood can be written

$$\mathcal{L}(C_{i,j,t}|C'_{i,j,t}) = e^{-C_{i,j,t}} C_{i,j,t}^{C'_{i,j,t}} / C'_{i,j,t}!, \quad (10.41)$$

and the total likelihood is the product of the individual likelihoods. The total likelihood (or its logarithm) is then maximized as a function of parameters μ and ν to obtain maximum likelihood estimates.

Hilborn (1990) compared this approach to others in the literature and applied it to a two-area set and to a seven-area set of tag recaptures from skipjack tuna fisheries. Each tag group consisted of tagged fish released from a given country's fishery in a given month. He also described extensions and problems of parameter confounding related to size-specific probability of capture, tag mortality, tag shedding, and nonreporting.

This approach has proven to be a versatile one used by several authors (e.g., Deriso et al. 1991, Heifetz and Fujioka 1991, Anganuzzi et al. 1994). Heifetz and Fujioka (1991) developed a tag recovery model based on the Baranov catch equation and incorporated auxiliary estimates of natural and fishing mortality, tag shedding, and reporting rate. They also used alternative parameterizations and applied their model to tagged sablefish recoveries in the northern Pacific Ocean. Deriso et al. (1991) combined Hilborn's approach with a diffusion model (see section 10.1.2) to estimate movement parameters. They also used the Baranov catch equation and auxiliary information about natural mortality and showed how to use the multinomial distribution to model observation errors. Anganuzzi et al. (1994) generalized Hilborn's approach to estimate size-specific vulnerability and movement simultaneously, while also allowing for growth and natural mortality. They also used the multinomial distribution and included tag mortality and loss. Bayley (1993) suggested that Hilborn's model (as well as many others) can be extended to incorporate additional variability caused by heterogeneity in distribution (overdispersion) by using quasi-likelihood methods. Cormack and Skalski (1992) handled overdispersion in a general mark–recapture setting by using a scaled Poisson distribution and compared this approach to using negative binomial and lognormal distributions.

Example 10.5. Hypothetical population

Consider a population with two regions and a mark–recapture experiment that occurs over four time periods. Population parameters are given in table 10.5. In region 1, 1000 tagged fish are released at times 1 and 3; in region 2, 2000 tagged fish are released at time 1. For simplicity, tags are assumed not to contain information about region of origin; thus equations above are modified to have only a single region subscript denoting region of capture. More complicated models can be easily developed if this information is available.

In region 1, 20% of the (tagged) population moves to region 2 each year; in region 2, 30% moves to region 1. Natural survival, ℓ , is 0.9 in both regions; harvest rates, μ_j , are 0.2 and 0.1 in regions 1 and 2, respectively. The population dynamics model is

Table 10.5. Calculations using Hilborn's method for a hypothetical population found in two regions.

		i	t				
			1	2	3	4	
True Parameters: Θ		$N_{i,t}$					
$(\begin{array}{cc} 0.8 & 0.2 \\ 0.3 & 0.7 \end{array})$; $\ell=0.9$			1	1000	1062	1922	
			2	2000	1278	878	
	μ	$C_{i,t}$					
$(\begin{array}{cc} 0.2 & 0.2 \\ 0.2 & 0.2 \end{array})$			1	200	212	384	
			2	200	128	88	
						77	
Estimated Parameters: $\hat{\Theta}$		$N_{i,t}$					
$(\begin{array}{cc} 0.757 & 0.243 \\ 0.279 & 0.721 \end{array})$			1	1000	1000	1853	
			2	2000	1368	990	
	$\hat{\mu}$	$C_{i,t}$					
$(\begin{array}{cc} 0.211 & 0.079 \\ 0.079 & 0.211 \end{array})$			1	211	211	392	
			2	158	108	78	
						72	
		$C'_{i,t}$					
				210	199	407	
				160	115	67	
						73	
	$\ln L$						
				-3.60	-3.92	-4.22	
				-3.47	-3.51	-3.86	
						-3.07	
	Sum			-29.38			

given by (10.11); the abundances of tagged animals in the two regions using this model are shown in table 10.5. The numbers of tagged fish caught, $C_{i,t}$, from (10.40) are also shown.

One set of simulated data from this model is given in table 10.5, obtained by generating random Poisson variates with parameters $\lambda = C_{i,t}$. Also shown are the maximum likelihood estimates of μ_j and $\theta_{i,j}$; ℓ was assumed to be known (because it is difficult to estimate). To obtain the maximum likelihood estimates, the population dynamics model above was recalculated with a trial set of estimates, leading to estimates of $N_{i,t}$ and $C_{i,t}$. Then the log likelihood for each time and region was calculated from (10.41) and summed to get the total. The total log likelihood was then maximized with respect to the parameters. Model calculations at the maximum likelihood solution are shown in table 10.5. Variance estimates for the parameter estimates could be made using Hessian or bootstrap methodology. ■

Hilborn's approach is applicable to any situation where a population dynamics model for tag recoveries can be constructed. Thus, it need not only be used for tagging experiments with geographical stratification. The example below describes an actual experiment where the interest is in estimating population parameters over time, not space. While Darroch's method in the previous section can often be used for temporal

stratification as well (see Seber 1982, chapter 11), it is often more straightforward to use Hilborn's approach.

Example 10.6. Emergence and loss of salmon eggs

Colored pink salmon eggs were planted into the redds of a study area in Auke Creek near Juneau, Alaska, in 1994 to determine egg loss rates (Fukushima 1996). Some eggs are dislodged from the redds and are then eventually washed out of the study area by the flow of the creek. There were three mark groups released on successive days (days 0, 1, and 2) with 5000 eggs each (different colors for different groups); eggs were distributed across the study area in proportion to spawning abundance. Samples of emerged eggs were made on days 1, 2, and 3; both colored and normal (unmarked) eggs were sampled. For the purpose of determining egg loss rate, only the data from marked recaptures is of use. This experiment was repeated through the spawning season. From one of these experiments (no. 4), the numbers of eggs caught for the tag groups and days of sampling, $m_{i,t}$, are given in table 10.6.

To estimate the number of eggs still in the redds, $N_{i,t}$, for the i th group, a single-area version of (10.11) is used:

$$N_{i,t+1} = N_{i,t} \ell_{i,t}, \quad (10.42)$$

where $\ell_{i,t}$ is the proportion not emerging on day t . The initial abundance, N_{i,t_0} , is the number of eggs planted on day t_0 . To reduce the number of parameters estimated and to connect information among the tagging groups, it is assumed that the rate of emergence is a function of the time elapsed since planting. Thus $\ell_{1,t} = \ell_{2,t+1} = \ell_{3,t+2}$. Then the number of eggs from a particular tag group that emerged in a given day must be the difference between two successive values of N , or

$$\mathcal{E}_{i,t+1} = N_{i,t} - N_{i,t+1} = N_{i,t}(1 - \ell_{i,t}). \quad (10.43)$$

For the values of ℓ shown in table 10.6 and the three groups of 5000 eggs released on successive days, the corresponding number of eggs in the redds from (10.42) and those that emerged from (10.43) are shown. If p_t is the probability of capture of emerged eggs on day t (assuming that all eggs have the same capture probability), then the number of eggs sampled is $C_{i,t} = p_t \mathcal{E}_{i,t}$. For the set of p 's in table 10.6, the number of eggs caught is shown.

To estimate parameters $\{\ell\}$ and $\{p\}$ under the Poisson assumption, the likelihood function (10.41) can be maximized given the actual number of eggs caught in a manner similar to the previous example. However, in this situation, there are six observation equations and six parameters to be estimated. An exact solution is not obtained because not all equations are independent. To reduce the number of parameters further, we note that the ratio of two successive diagonal terms in the \mathbf{C} matrix is the ratio of the probabilities of capture (i.e., $C_{2,2}/C_{1,1} = p_2/p_1$ and $C_{3,3}/C_{2,2} = p_3/p_2$). We constrain the maximum likelihood solution by forcing these ratios to equal those observed. The results shown in table 10.6 are those from that constrained maximum likelihood estimation. Without the constraints, any number of different solutions give approximately the same likelihood. ■

Table 10.6. Estimation of egg loss rates for pink salmon in Auke Creek, Alaska, using Hilborn's method.

		<i>t</i>		
		0	1	2
<i>m_{i,t}</i>			125	9
<i>i</i>	1			7
	2		104	9
	3			72
$p_2/p_1 = 0.832, p_3/p_2 = 0.692$				
<i>l_{i,t}</i>			0.674	0.951
<i>i</i>	1		0.674	0.951
	2			0.951
	3			0.674
<i>N_{i,t}</i>				
<i>i</i>	1	5000	3369	3203
	2		5000	3369
	3			3203
			5000	3369
<i>E_{i,t}</i>			1631	159
<i>i</i>	1		1631	159
	2			167
	3			1631
<i>p_t</i>			0.077	0.064
<i>C_{i,t}</i>			125.0	10.6
<i>i</i>	1		125.0	7.0
	2			7.4
	3			72.0
ln <i>L</i>			-3.33	-2.16
<i>i</i>	1		-3.33	-1.90
	2			-2.20
	3			-3.06
Sum			-15.89	

10.2.3. Miscellaneous Methods

Differential equation approaches

Beverton and Holt (1957) developed a variety of population models that include dispersion. Hampton (1991b) developed a differential equation model for southern bluefin tuna for three regions. He gave the solution to the differential equations and derived the likelihood for a set of tag recoveries assuming an underlying multinomial distribution. A population dynamics model links the observations, similar to Hilborn's model, with parameters for movement and natural mortality.

An analogous method from the NRC (1994a) for estimating migration is available for a two-area population, which involves determining the instantaneous rate of transfer, T_1 , from one area to the other. The population in each area, i , is subject to natural

mortality, M (assumed constant for simplicity), and fishing mortality, F_i . Tagged fish are also assumed to shed tags at an instantaneous rate, T_i . The combination of natural mortality and tag shedding is denoted $M^* = M + T_i$. For the population of fish tagged at time 0 in area 1, denoted $N_{1,0}$, the differential equations of population change in the two areas are written

$$\frac{dN_1}{dt} = -(M^* + F_1 + T_1)N_1 \quad (10.44)$$

$$\frac{dN_2}{dt} = -(M^* + F_2)N_2 + T_1 N_1 \quad (10.45)$$

No transfers back from area 2 to area 1 are assumed to occur. The solution to this system from NRC (1994a) is

$$N_1(t) = N_{1,0} e^{-(M^* + F_1 + T_1)t} \quad (10.46)$$

$$N_2(t) = N_{1,0} \frac{T_1}{F_1 - F_2 + T_1} \left[e^{-(M^* + F_2)t} - e^{-(M^* + F_1 + T_1)t} \right]. \quad (10.47)$$

The catches in the two areas from the Baranov catch equation are

$$C_1(t) = N_{1,0} \frac{F_1}{M^* + F_1 + T_1} \left[1 - e^{-(M^* + F_1 + T_1)t} \right] \quad (10.48)$$

$$C_2(t) = N_{1,0} \frac{T_1}{F_1 - F_2 + T_1} \left\{ \frac{F_2}{M^* + F_2} \left[1 - e^{-(M^* + F_2)t} \right] - \frac{F_2}{M^* + F_1 + T_1} \left[1 - e^{-(M^* + F_1 + T_1)t} \right] \right\}. \quad (10.49)$$

The ratio of catches for large t is then

$$\frac{C_2}{C_1} = \frac{T_1 F_2}{F_1 (F_2 + M^*)}.$$

If not all tags are reported and P_1 and P_2 are the reporting rates for areas 1 and 2, the ratio of catches is modified to be

$$\frac{C_2}{C_1} = \frac{P_2 T_1 F_2}{P_1 F_1 (F_2 + M^*)}. \quad (10.50)$$

If the fishing mortalities, natural mortality, and reporting rates are known (or estimated from other information), then (10.50) can be solved for transfer rate, T_1 .

Analogous equations with subscripts reversed can be written to estimate the transfer rate from area 2 to area 1. Because the models (10.44) and (10.45) do not allow round-trip movement, the transfer rates from (10.50) will be underestimates of actual migration rates. Also, if fishing mortality decreases with age, the rates will be underestimated with this method. These rates are instantaneous rates and are not strictly comparable to annual rates of migration in other sections. However, they should be approximately equal, if they are small in magnitude (as they usually are).

These equations can also be used to describe the common phenomenon of movement of fish from near-shore coastal fisheries to off-shore fisheries such as occurs for tiger flathead in southeastern Australia (Rowling 1994). Related differential equation models for populations exhibiting movement are given by Beverton and Holt (1957), Clark (1976a), and Polacheck (1990).

Example 10.7. Atlantic bluefin tuna

Atlantic bluefin tuna move from the western Atlantic to the eastern and vice versa. By performing cohort analysis of tag recoveries from fish originally tagged in the east and originally tagged in the west, it is possible to get combinations of estimated reporting rate and average fishing mortality (NRC 1994a). One set of these combinations is $P_e = 0.1330$, $F_e = 0.2606$, $P_w = 0.4400$, and $F_w = 0.0710$. Natural mortality is thought to be $M = 0.14$, and the estimated tag shedding rate is $L = 0.26$, for a total loss rate of $M^* = 0.40$. For fish tagged with a single tag in the west between 1960 and 1981 (considered to be the most consistent data), the western catch was $C_w = 3037$ and the eastern catch was $C_e = 65$. By using (10.50), the estimated transfer rate from west to east is $T_w = 0.0127$. For fish tagged in the east between 1976 and 1991, the eastern catch was $C_e = 339$ and the western catch was $C_w = 17$. By using (10.50) with subscripts reversed, the estimated transfer rate from east to west is $T_e = 0.0262$.

■

Advection-diffusion approach

Salvado (1993) developed a theory for analyzing mark–recapture data that uses partial differential equations for advection and diffusion. The use of empirical Green functions associated with the population field equations derived from the Rayleigh transport theorem permits parameter estimation. Although the approach requires that dynamics be linear, he showed how to extend the approach to nonlinear dynamic situations. An application to skipjack tuna in the eastern tropical Pacific illustrated how to build the population model.

10.3. MIGRATORY COHORT AND CATCH-AGE ANALYSES

Extensions of cohort analysis (section 8.2.3) and catch-age analysis (section 8.2.5) for migratory populations are given in this section. Data requirements for migratory cohort and catch-age analyses are fairly extensive. The population must be divided into geographic regions and data must be available for each region. Catch-age data must be available from several years, and auxiliary information should be available from each region, such as catch-effort, a spawner-recruit relationship, or survey estimates. Natural mortality is usually assumed to be known. The major data requirement for these analyses is information on migration rates among regions, the estimation of which was described in section 10.2. It is possible to treat migration rates as parameters in these analyses, but confounding of migration and mortality can make estimation overwhelming if not impossible. Let there be data from A ages, T years, and R regions, with corresponding subscripts a , t , and i .

10.3.1. Migratory Cohort Analysis

Migratory cohort analysis was developed by Deriso and Quinn (1983) and treated further in Quinn et al. (1990a). The model is a backward recursion of the population from

terminal abundances in different regions, using migration rates, natural mortality, and catches from a cohort of fish across regions. Catch is assumed to be measured without error. We use a constant value of natural mortality, M , for simplicity of development, but the model is easily modified for variable natural mortality as a function of age, year, and/or area. Migration is assumed to occur at the end of the year, and catch is assumed to occur in the middle; other placements of migration and catch can be easily constructed in analogous fashion, as in section 10.1.2. The population dynamics equations are derived for age-specific migration rate matrices $\Theta_a = \{\theta_{a,j \rightarrow i}\}$. Analogous equations can be obtained for migration rates that vary from year to year.

We derive equations for the cohort $t - a$ (i.e., at age a in year t), which will be useful for migratory catch-age analysis in section 10.3.2. Given the vector of regional abundances, $\mathbf{N}_{a,t}$, at the start of the year, the vector of regional abundances at the start of the next year is then

$$\mathbf{N}_{a+1,t+1} = \Theta_a \left(\mathbf{N}_{a,t} e^{-M} - \mathbf{C}'_{a,t} e^{-M/2} \right), \quad (10.51)$$

where C' is observed catch. This equation follows from consideration of (8.37), (10.10), and the models in section 10.1. A recurrence relation is now written in closed form that expresses abundance at any time as a function of terminal abundances. From (10.51),

$$\mathbf{N}_{a,t} = \Theta_a^{-1} \mathbf{N}_{a+1,t+1} e^M + \mathbf{C}'_{a,t} e^{M/2}. \quad (10.52)$$

Given terminal abundances $\{\mathbf{N}_{A,t}\}$, then (10.52) can be used to back-calculate abundances at all earlier ages. Terminal abundance can be calculated using one of the approaches in section 8.2.3.

The recursive process can be repeated for x years as shown in Quinn et al. (1990), which for a migration matrix Θ constant over age yields

$$\mathbf{N}_{a,t} = \Theta^{-x} \mathbf{N}_{t+x,a+x} e^{xM} + \sum_{i=0}^{x-1} \Theta^{-i} \mathbf{C}'_{t+i,a+i} e^{M/2+iM}, \quad (10.53)$$

where by definition $\Theta^{-0} = \mathbf{I}$, the identity matrix. Equation (10.53) is exact because catch is assumed measured without error. Given terminal abundances, $\mathbf{N}_{a,T}$, for all a and $\mathbf{N}_{A,t}$ for all t , any abundance, $N_{a,t,i}$, can be determined from (10.53) as

$$N_{a,t,i} = \sum_{j=1}^R \theta_{i,j}^{-I} N_{a+I,t+I,j} e^{IM} + \sum_{z=0}^{I-1} \left(\sum_{j=1}^R \theta_{i,j}^{-z} C'_{a+z,t+z,j} \right) e^{M/2+zM} \quad (10.54)$$

where $\theta_{i,j}^{-z}$ is the (i, j) th element of Θ^{-z} and $I = \min(A - a, T - t)$. In practice, it is easier to use the recursive relationship (10.52) to generate abundances for a year-class, but (10.54) is used in calculations for migratory catch-age analysis described in the next section.

To generalize (10.54) for an age-specific migration-rate matrix Θ_a , it follows from the preceding development that the powers of the inverse of Θ are replaced with the product of the inverses of age-specific migration matrices. It can be shown that the term Θ^{-x} in (10.53) should be replaced with the matrix product

$$\Theta_a^{-1} \dots \Theta_{a+x-1}^{-1},$$

and that the term Θ^{-i} in (10.53) should be replaced with the matrix product

$$\Theta_a^{-1} \dots \Theta_{a+i-1}^{-1} \quad \text{for } i > 0$$

and should remain equal to \mathbf{I} for $i = 0$. The analogue to (10.54) follows by substituting the corresponding elements of the matrix products for the elements of Θ^{-x} and Θ^{-i} .

Example 10.8. Pacific halibut

The Pacific halibut population area has been divided into regulatory areas 2A, 2B, 2C, 3A, 3B, and 4 for management purposes (Quinn et al. 1985, 1990a). Sufficient data to estimate migration and catch-age parameters are available for four larger regions: 1 (areas 2A+2B), 2 (area 2C), 3 (area 3A), and 4 (areas 3B+4). The age range of Pacific halibut is 8–20, but we use only data for ages 8–11 to illustrate calculations for migratory cohort analysis. Estimated migration rates for age 8 and ages 9–11, along with catch-age data for ages 8–11 from 1981 to 1984, for these four regions from Quinn et al. (1990a) are shown in table 10.7. The inverses of the migration matrices, used in calculations, are also shown. Natural mortality is assumed to be 0.2 for all ages, years, and regions. Estimated terminal fishing mortalities for age 11 in 1984 in table 10.7 are chosen to give results similar to Quinn et al. (1990a) for these ages. Estimated abundance at age 11 in 1984 for each region is calculated from the Baranov catch relationship (8.33), as shown in table 10.7. Abundance at other ages in that table is calculated using the migratory cohort analysis relationship (10.52). Exploitation rates are then calculated by dividing catch by abundance. ■

10.3.2. Migratory Catch-Age Analysis

Measurement error model

The measurement error model, presented by Quinn et al. (1985, 1990a), is an extension of the measurement error model of Deriso et al. (1985), which details assumptions and equations relating catch and population dynamics. The model uses a forward recursion of abundance from starting values of abundance for all ages in the first year and the first age in all years. Thus there are $T + A - 1$ year-class parameters for each region. In this development, uppercase letters are used for original parameters and variables. Lowercase letters are used for corresponding logarithms.

For model simplicity, it is assumed that migration rates are known and occur instantaneously at the start of the year. Alternative formulations to model the migration process are conceivable; such as an instantaneous rate of migration occurring throughout the year analogous to instantaneous rates of fishing or natural mortality or a seasonal process occurring over a short time period. This development is analogous to that in section 8.2.5 for catch-age analysis in a single region.

As before, the $R \times R$ matrix of annual migration rates is denoted $\Theta_a = \{\theta_{a,j \rightarrow i}\}$. The vector of abundance after migration, $\mathbf{N}_{a,t}^*$, is

$$\mathbf{N}_{a,t}^* = \Theta_a \mathbf{N}_{a,t}, \quad (10.55)$$

where $\mathbf{N}_{a,t}$ is the vector of size $R \times 1$ containing the regional abundances $\{N_{a,t,i}\}$ at the start of the year t for age a . For a given region i , abundance at the start of the next year is then

Table 10.7. Migratory cohort analysis of Pacific halibut in four regions (1 = regulatory areas 2A and 2B, 2 = 2C, 3 = 3A, 4 = 3B and 4), for ages 8–11 between 1981 and 1984 given catch-age data, migration matrices, and values for terminal fishing mortality and natural mortality.

	To region	Θ_a From region				Θ_a^{-1} From region				
		1	2	3	4	1	2	3	4	
Migration matrices	Age 8	1	0.9982	0.0200	0.0095	0.0099	1.0018	-0.0205	-0.0095	-0.0098
		2	0.0013	0.9768	0.0108	0.0210	-0.0013	1.0238	-0.0111	-0.0231
		3	0.0005	0.0032	0.9672	0.0743	-0.0005	-0.0034	1.0351	-0.0859
		4	0.0000	0.0000	0.0125	0.8948	0.0000	0.0000	-0.0145	1.1188
	Ages 9–11	1	0.9961	0.0122	0.0061	0.0064	1.0040	-0.0124	-0.0061	-0.0064
		2	0.0029	0.9858	0.0070	0.0138	-0.0029	1.0145	-0.0071	-0.0146
		3	0.0010	0.0020	0.9788	0.0481	-0.0010	-0.0021	1.0221	-0.0527
		4	0.0000	0.0000	0.0081	0.9317	0.0000	0.0000	-0.0089	1.0738
Catch, $C'_{a,t}$			1981	1982	1983	1984				
			age 8	age 9	age 10	age 11				
	1	31540	37198	38177	47763					
	2	15522	14883	32991	29584					
	3	27119	31008	63895	100007					
	4	7180	34166	75887	47146					

Natural mortality, M (all years, ages, and regions) 0.2

		1984		
		age 11		
Fishing mortality, F	1		0.15	
	2		0.07	
	3		0.14	
	4		0.22	
		1981	1982	1983
		age 8	Age 9	age 10
Abundance, $N_{a,t}$	1	751642	620184	489303
	2	939746	766588	620620
	3	1714979	1383360	1103995
	4	769580	575226	418932
		1984		
		age 11		
Exploitation rate, $\mu_{a,t}$	1	0.042	0.060	0.078
	2	0.017	0.019	0.053
	3	0.016	0.022	0.058
	4	0.009	0.059	0.181

$$N_{a+1,t+1,i} = N_{a,t,i}^* e^{-Z_{a,t,i}}, \quad (10.56)$$

where $Z_{a,t,i} = F_{a,t,i} + M_{a,t,i}$, $F_{a,t,i}$ is fishing mortality, and $M_{a,t,i}$ is natural mortality. Because natural mortality is difficult to estimate from catch-age data, we assume that natural mortality is known.

The catch predicted from the model is calculated from the Baranov catch equation

$$C_{a,t,i} = \frac{F_{a,t,i}}{Z_{a,t,i}} N_{a,t,i}^* \left(1 - e^{-Z_{a,t,i}}\right), \quad (10.57)$$

for each age, year, and region. The observed catch, $C'_{a,t,i}$, is assumed to have a log-normal error structure with median $C_{a,t,i}$. To estimate parameters, fishing mortality is assumed to be separable into an age factor and a year factor for each region,

$$F_{a,t,i} = S_{a,i} G_{t,i}, \quad (10.58)$$

where age selectivity, $S_{a,i}$, is equal to 1 for at least one fully recruited age, and $G_{t,i}$ is full-recruitment fishing mortality. Let D be the number of ages for which selectivity parameters are to be estimated.

To incorporate auxiliary information, full-recruitment fishing mortality is related to fishing effort, $E_{t,i}$, as a lognormal variable with median $Q_i E_{t,i}$, where Q_i is catchability for region i . A straightforward extension for fisheries with multiple gear types can be incorporated into this approach with separate parameters for selectivity, catchability, and fishing mortality for each gear type, as shown in section 8.2.6.

For each region, the residual sum of squares (RSS) criterion from Deriso et al. (1985) is (with logarithms of appropriate relations substituted as lowercase letters),

$$\text{RSS}_i = \sum_a \sum_t (c'_{a,t,i} - c_{a,t,i})^2 + \lambda \sum_t (g_{t,i} - q_i - e_{t,i})^2, \quad (10.59)$$

where λ is a specified constant determining the influence of fishing effort. For each region there are $T + A - 1$ year-class parameters, D parameters $s_{a,i}$, T parameters $g_{t,i}$, and one parameter q_i to be estimated from $T \times A$ observations of catch and T observations of effort, using a nonlinear least squares procedure. It is possible to have λ be a function of i to implement different regional weightings.

As explained in Quinn et al. (1985, 1990a), it is fairly straightforward to modify catch-age analysis programs to accommodate different regions. However, results to date have not been satisfactory because results are sensitive to initial conditions and convergence to the lowest sum of squares cannot often be guaranteed.

Process error model

The process error model assumes that the catch is measured without error and that process error, or stochastic variation, occurs in the dynamics of the population. In this section, the process error model presented in Deriso et al. (1985) is extended for migration. The basic population dynamics equations follow from migratory cohort analysis in section 10.3.1, equations (10.51) to (10.54). It suffices then to determine an estimation procedure for the terminal abundances.

Terminal abundances can be estimated only from additional model structure. It is assumed that the exploitation rate, $U_{a,t,i}$, the ratio of catch to abundance, is lognormally

distributed with median $S_{a,i}V_{t,i}$. The term $S_{a,i}$ is age selectivity as before, and $V_{t,i}$ is full-recruitment exploitation rate. The process error approach uses a separability assumption for exploitation rate rather than for fishing mortality as in the measurement error model because this permits a tractable solution. For this model, the median catch is

$$C_{a,t,i} = S_{a,i}V_{t,i}N_{a,t,i}. \quad (10.60)$$

Substituting (10.54) into (10.60) produces the model equation in terms of its parameters, which is then log transformed for use in nonlinear least squares. The log transformation produces an almost-linear model,

$$c_{a,t,i} = s_{a,i} + v_{t,i} + n_{a,t,i}, \quad (10.61)$$

which simplifies the estimation process. To incorporate auxiliary information, full-recruitment exploitation rate is related to fishing effort, $E_{t,i}$, as a lognormal variable with median $Q_i E_{t,i}$.

The appropriate sum of squares criterion from Deriso et al. (1985) extended over all regions is given by

$$\text{RSS} = \sum_r \left[\sum_a \sum_t (c'_{a,t,i} - c_{a,t,i})^2 + \lambda \sum_t (v_{t,i} - q_i - e_{t,i})^2 \right]. \quad (10.62)$$

As before, there are $T \times A$ observations of catch and T observations of effort for each region i . The RSS is minimized as a function of the terminal abundances for all regions, using nonlinear least squares.

The other parameters for each region i — D parameters $s_{a,i}$, T parameters $v_{t,i}$, and q_i —are found directly. By taking partial derivatives of RSS in (10.62) with respect to the parameters and setting them equal to zero, as shown by Quinn et al. (1990a), the parameter estimates for each region are obtained as the solution to a linear system of equations. Thus, it is possible to jointly estimate abundance for all regions because the number of parameters to be estimated from nonlinear least squares has been reduced substantially from the measurement error model.

In summary, the process error model uses migratory cohort analysis to project abundance backward in time from terminal values of abundance, catch, migration rates, and natural mortality. Many nonlinear least squares routines require analytical derivatives of the dependent variable with respect to the parameters; these are derived by Quinn et al. (1990a). The dependent variable in the nonlinear least squares algorithm is composed of the logarithm of catch for each time, age, and region from (10.61) and logarithm of auxiliary effort (multiplied by $\sqrt{\lambda}$) for each time and region. Independent variables are time, age, and region. Parameters estimated by the nonlinear least squares algorithm are logarithms of terminal abundances. The linear system of equations given in Quinn et al. (1990a) is then solved for each region to estimate parameters $s_{a,i}$, $v_{t,i}$, and q_i within each iteration, allowing the computation of RSS in (10.62). The terminal abundances are updated in subsequent iterations of the nonlinear least squares algorithm until convergence occurs. Quinn et al. (1990a) illustrated this method by application to Pacific halibut data.

One common problem in these migratory models is that negative estimates of abundance can occur if the redistribution of population due to migration is too severe. Such a problem would indicate an inconsistency in the data sources or a model deficiency.

Other constructions of migratory catch-age analysis have been made. An extension to the ADAPT program (see section 8.2.7) is described by Butterworth and Punt (1993) and by the NRC (1994). The stock synthesis program (see section 8.2.8) has also been modified to incorporate migration (R. Methot, personal communication, 1996). Tuning approaches using spreadsheet software have also been used successfully (V. Wespestad, personal communication, 1995). Migratory age-structured models have been generalized to age-structured likelihood-based catch-length models with one-dimensional diffusionlike movement between spatial strata, as described by Hampton and Fournier (1996) in their application to South Pacific albacore tuna.

10.4. RUN RECONSTRUCTION

Although run reconstruction is a widely used technique to estimate stock-specific exploitation and run size of Pacific salmon populations, few studies have been published (Schnute and Sibert 1983, Starr and Hilborn 1988, Mundy et al. 1993, Templin et al. 1996). The spatial and/or temporal distribution of a stock is determined with only catch, escapement, and migration data, and the catch data usually obtained does not contain stock-specific information. Schnute and Sibert (1983) projected a single stock forward in time in a single area to develop comprehensive information on temporal distributions and to estimate descriptive parameters in the fishery. Starr and Hilborn (1988) and Mundy et al. (1993) used a backward reconstruction in time with migration among areas to differentiate stocks and to assess the fishing effects on each of the stocks, which were subject to mixed-stock fisheries. Movement was assumed to follow a “box-car” distribution: a daily cohort of fish in a stock spends a fixed amount of time in an area and then moves as a unit to another area. Templin et al. (1996) used a Markovian movement model with backward projection to differentiate stocks and to assess fishing effects. We give an overview of this method.

The total population consists of stocks labeled n , which can be found in districts labeled d . On a given day, the order of events is assumed to be exploitation, followed by escapement, followed by migration. Migration among districts is represented by a migration matrix, Θ_n , for each stock, n , with an element $\theta_{n,i,j}$ equal to the probability that a fish is in district i on day t given that it is in district j on day $t+1$. This redefinition of migration is necessary to accommodate the backward projection. Given the vector of abundances, $\mathbf{P}_{t+1,n}$, in districts for stock n on day $t+1$, then the backward projection of the stock one day earlier is

$$\mathbf{P}_{t,n} = \Theta_n \mathbf{P}_{t+1,n} + \mathbf{c}_{t,n} + \mathbf{s}_{t,n}, \quad (10.63)$$

where vectors \mathbf{c} and \mathbf{s} are district-specific catches and escapements (fish leaving the fishery area), respectively.

Given the district-wide catch, $C_{t,d}$, on day t , it is assumed that stock-specific catch is proportional to the relative abundance of each stock in the fishing area, or

$$c_{t,n,d} = C_{t,d} \left(P_{t,n,d} / \sum_n P_{t,n,d} \right). \quad (10.64)$$

Thus, the exploitation rate, $\mu_{t,d} = c_{t,n,d} / P_{t,n,d}$, is constant for all stocks n .

Equation (10.63) cannot be used directly for back-calculation because catch depends on population abundance, which in turn depends on catch. By substituting (10.64) into (10.63) and simplifying, a useful back-calculation equation is

$$\mathbf{P}_{t,n} = (\mathbf{I} - \mathbf{U}_t)^{-1} (\Theta_n \mathbf{P}_{t+1,n} + \mathbf{s}_{t,n}) = (\mathbf{I} - \mathbf{U}_t)^{-1} \mathbf{P}_{t,n}^*, \quad (10.65)$$

where I is the identity matrix, U_t is a diagonal matrix with elements $\mu_{t,d}$ on the diagonal, and $\mathbf{P}_{t,n}^*$ is the population after harvest on day t . In the back-calculation, \mathbf{P}^* is calculated as an intermediate quantity from migration, escapement, and previously obtained abundance information, from which harvest rate can be calculated as

$$\mu_{t,d} = C_{t,d} / (C_{t,d} + P_{t,d}^*), \quad (10.66)$$

where $P_{t,d}^* = \mathbf{1}' \mathbf{P}_{t,n}^*$. Stock-specific catch is then obtained directly by multiplying daily abundance and exploitation rate, so that $c_{t,n,d} = \mu_{t,d} P_{t,n,d}$. Total run size, R_n , of each stock is then

$$R_n = \mathbf{1}' \mathbf{c}_{t,n} + \mathbf{1}' \mathbf{s}_{t,n},$$

and seasonal harvest rate is then $\mu_n = \sum_d \sum_t c_{t,n,d} / R_n$.

Example 10.9. Hypothetical population

This simple hypothetical example of a returning Pacific salmon population shows the details of calculations in run reconstruction. For each of the two stocks in this population, daily escapements occur over three days, as shown in table 10.8. Stocks escape only to their own district, and the times shown represent when those fish leave the fishery. (Escapement to the streams occurs some days later.)

In this illustration, both stocks have the same migration matrix Θ . It is assumed that a fish in district 1 on day $t + 1$ has an equal chance of being in either district on the previous day t . A fish in district 2 on day $t + 1$ has a 40% chance of being in district 1 and a 60% chance of being in district 2 on the previous day t . The corresponding migration matrix Θ is shown in table 10.8. Catch data in that table are only available by district; the purpose of the run reconstruction is to estimate the daily proportion of each stock in each district.

The run reconstruction proceeds backward in time from day 10 to day 1. The initial conditions for the back-calculation are the daily escapements on the last day. As shown in table 10.8, the vector of daily population abundances after harvest on day t ($\mathbf{P}_{t,n}^* = \Theta_n \mathbf{P}_{t+1,n} + \mathbf{s}_{t,n}$) is now calculated, given the vector of population abundances on day $t+1$. These estimates are summed over stock to get $P_{t,d}^*$, from which daily harvest rates, $\mu_{t,d}$, are calculated from (10.66). Then the vector of population abundances at the start of the day t is calculated using (10.65), and estimates are combined over districts and stocks. An overall exploitation rate is then calculated by dividing catch by abundance, either daily or over the season.

For this hypothetical population, the overall escapement of stock 1 is about twice as high as for stock 2 (table 10.8). The fish have high movement rates between areas, so each stock becomes rapidly mixed into the two districts as the back-calculation proceeds. The daily catches for the two districts are similar, so the reconstructed population abundance on day 1 (or run size) for stock 1 (847) is about twice as high as for stock 2 (403), a similar result to that for total escapement (350 versus 150). Interday

Table 10.8. Hypothetical example of a returning salmon population.

		Day											
		District	10	9	8	7	6	5	4	3	2	1	Sum
		Daily escapement, <i>s</i>											
	Stock 1	1	100	150	100	0	0	0	0	0	0	0	350
		2	0	0	0	0	0	0	0	0	0	0	0
	Stock 2	1	0	0	0	0	0	0	0	0	0	0	0
		2	75	50	25	0	0	0	0	0	0	0	150
	Catch, <i>C</i>												
	Total	1	25	50	25	100	75	50	25	25	0	0	375
		2	25	25	50	100	50	50	50	25	0	0	375
		Combined	50	75	75	200	125	100	75	50	0	0	750
	<i>P</i> *, Stock 1	1	100	213	256	217	273	310	340	361	377	377	
		2	0	63	170	257	337	385	423	452	471	471	
	<i>P</i> *, Stock 2	1	0	40	74	98	129	147	161	172	179	179	
		2	75	110	125	127	161	183	201	215	224	224	
	<i>P</i> *, Combined	1	100	253	330	316	402	458	501	533	556	556	
		2	75	173	295	384	498	567	624	667	694	694	
	Harvest rate, <i>μ</i>	1	0.200	0.165	0.070	0.241	0.157	0.098	0.048	0.045	0.000	0.000	
		2	0.250	0.127	0.145	0.206	0.091	0.081	0.074	0.036	0.000	0.000	

Catch, c											
Stock 1	1	25	42	19	69	51	34	17	17	0	0
	2	0	9	29	67	34	34	34	17	0	0
Stock 2	1	0	8	6	31	24	16	8	8	0	0
	2	25	16	21	33	16	16	16	8	0	0
Stock 1	Combined	25	51	48	136	85	68	51	34	0	0
Stock 2	Combined	25	24	27	64	40	32	24	16	0	0
Total		50	75	75	200	125	100	75	50	0	0
											750
Population, P											
Stock 1	1	125	255	275	286	324	344	356	378	377	377
	2	0	72	199	324	371	418	457	469	471	471
Stock 2	1	0	48	80	129	153	163	169	180	179	179
	2	100	126	146	161	177	199	217	223	224	224
Combined	1	125	303	355	416	477	508	526	558	556	556
	2	100	198	345	484	548	617	674	692	694	694
Stock 1 Combined		125	326	474	610	695	763	814	847	847	847
Stock 2 Combined		100	174	226	290	330	362	386	403	403	403
Total population		225	500	700	900	1025	1125	1200	1250	1250	1250
											Run, R
Overall exploitation rate, μ											Overall
Stock 1		0.200	0.157	0.102	0.222	0.122	0.089	0.062	0.040	0.000	0.000
Stock 2		0.250	0.137	0.119	0.222	0.122	0.089	0.063	0.040	0.000	0.000
											0.587
											0.627

The migration matrix Θ is the same for each stock and is known. Daily escapements occur over three days and are known. The catches in each district are also known. The run in each district is reconstructed from the latest time to the earliest time using the equations in text.

variability in catches produces variability in exploitation rates for districts and stocks. Although the daily exploitation rates range from 0 to 25%, the cumulative effect is an overall exploitation rate of about 60% for both stocks. ■

Templin et al. (1996) applied the run reconstruction method to pink salmon in Prince William Sound, Alaska. They obtained migration information from a mark-recapture experiment, daily escapement information from aerial surveys, and daily catch information from fish tickets. They were able to reconstruct runs of seven stocks in Prince William Sound and to examine harvest rates, abundances, and return-per-spawner ratios for the stocks. They discovered that stocks that crossed many districts (and hence many fisheries) had higher exploitation rates than others, which shows the difficulty of achieving conservative exploitation rates in mixed-stock fisheries (Hilborn 1976, Hilborn and Walters 1992).

In practice, escapement occurs over a long period of time, so escapement counts must be adjusted for stream life (the average number of days a fish lives in the stream) and for the presence of several daily cohorts surveyed at the same time (Mundy 1985, Templin et al. 1996). If one can construct the area under the curve of escapement over time, then the total area is the number of spawner days. Dividing the number of spawner days by the number of spawners gives the stream life, or vice versa. It is also possible to develop differential equation models for the processes of entry and mortality, which then leads to a model for escapement (Quinn and Gates, 1997).

10.5. GEOGRAPHIC APPORTIONMENT

Given the demanding information requirements for understanding the dynamics of migratory populations, simpler methods of assessment are often sought. One alternative is to analyze the entire population using a single set of population and management parameters and then to apportion or partition the total population to smaller regions based on regional fishery or survey information (Quinn et al. 1982, 1985; Deriso and Quinn 1983; Heifetz et al. 1997). One advantage to combined analysis is that coefficients of variation of information are often lower overall than for individual regions. However, assumptions about the population dynamics (e.g., constant catchability, separability of age selectivity) are more likely to be satisfied on smaller geographic regions than for the entire population. Also, management decisions are often made separately for the different regions to prevent overharvest in any one region, which requires apportioning estimates to regions in any case (Quinn et al. 1985). Geographic apportionment is frequently used for nonmigratory populations as well for these same reasons.

Suppose that an assessment method such as cohort or catch-age analysis is applied to the entire population, resulting in estimates of abundance, \widehat{N}_t , in year t . Further suppose that a direct method of assessment is used to provide relative abundance or density information, \widehat{p}_r , in each region r . Such assessment methods include collection of catch-per-unit-effort (CPUE) information, survey sampling, mark-recapture experiments, and line transect sampling. If it is assumed that the estimate of abundance for the entire population and estimates of relative abundance are unbiased and independent, then an unbiased estimate of abundance for region r is simply

$$\widehat{N}_{t,r} = \widehat{p}_r \widehat{N}_t. \quad (10.67)$$

This procedure can be applied to a single age or many ages (e.g. exploitable population, mature population, female population, total population), as long as the relative

abundance estimate can be obtained for that component. This condition requires an understanding of gear or survey selectivity, as shown in previous chapters. This procedure also applies to abundance in numbers or biomass, as long as relative abundance is measured in the same units or average weight does not differ among regions.

Each source of relative information has its own peculiarities. If CPUE information is used, then relative abundance for a region is estimated from the product of CPUE and habitat area (Quinn et al. 1982, 1985; Deriso and Quinn 1983; see section 1.3.1). When applied to Pacific halibut, the use of CPUE information resulted in inaccurate estimates because catchability among regions varied over time (Quinn et al. 1985). Issues related to combining estimates from individual days or regions are discussed by Mundy (1985) and Quinn et al. (1982). Line transect techniques are applicable to "sightable" species and require much thought to coverage definition (Buckland et al. 1993). Hydroacoustic surveys are available for species that can be detected in the water column but can involve problems with mixed-species aggregations, murky water, and groundfish. Migratory populations that pass a location can frequently be enumerated to estimate abundance, such as gray whales (Reilly 1981), bowhead whales (Zeh et al. 1986), and Pacific salmon (Mundy 1982, 1985). In the latter case, migratory timing curves are examined historically and used to provide in-season escapement estimates.

Once abundance estimates are determined by region, recommended catch levels (total allowable catch, TAC, or acceptable biological catch, ABC) are frequently given. A general principle often applied is to apportion total catch levels across regions in proportion to the distribution of relative biomass. Each region then experiences the same exploitation rate. This principle is used for management of Pacific halibut and groundfish species in the North Pacific. Some other apportionment policies include an equal apportionment among regions, apportionment based on a weighted average of relative biomass estimates over time, and apportionment based on the equilibrium distribution of biomass using an age-structured model from section 10.1 (Heifetz et al. 1997). The equal apportionment policy is equivalent to a biomass-based policy when areas are of equal size and might be used when relative abundance information is highly uncertain or totally lacking. The weighted-average biomass policy adapts to current information but reduces the effects of annual fluctuations caused by measurement error. A variety of weighting schemes have been considered (doubling the weight of the most recent information, exponential weighting). The equilibrium policy anticipates the ultimate progression of the population to an equilibrium distribution among areas.

These four policies were evaluated with a stochastic age-structured simulation model applied to the Gulf of Alaska sablefish population (Heifetz et al. 1997). Total recruitment was simulated from the historical distribution and allocated to regions according to various recruitment hypotheses. A transition matrix from mark-recapture information (section 10.1.3) was an essential component of the population dynamics. The current overall exploitation rate of 10% was used to determine the total catch level, which was then apportioned to regions according to the four policies. Policies were evaluated in terms of expected yield, variation in yield, CPUE, and risk of overfishing (dropping below 30% of unfished spawning biomass). As expected from a model with no stock-dependent effects on recruitment, a policy resulting in lower average yield in a region also produced higher CPUEs and lower risks of overfishing. The equal apportionment policy had the most different results in the regions from the three biomass-based policies due to a much different apportionment: average yield was higher in some re-

gions and lower in others, and the risk of overfishing was much higher in regions where the apportionment was higher than those based on biomass. The highest relative variation in yield occurred with the biomass-based policy using current biomass because of measurement error. Across all areas, the equal apportionment policy had lower average yield, relative variation in yield, and CPUE and higher risk of overfishing than the other policies, which were almost identical. Thus, policies based on biomass distributions appear to be superior to others, and biomass-based policies that reduce measurement error via weighting or by considering equilibrium distributions are desirable. Further study is needed concerning stock-dependent effects and uncertainty in migration rate estimates.

An exponential weighting scheme is appropriate if the ratio of variability due to measurement error and total variability (which also includes variability in natural mortality, recruitment, and movement rates) is known (Meinhold and Singpurwalla 1983). For this scheme, each previous survey estimate is weighted by the variability ratio compared to the next more recent survey.

Example 10.10. Pacific ocean perch in the Gulf of Alaska

Pacific ocean perch (*Sebastodes alutus*) is a rockfish found on the outer continental shelf and slope of the Gulf of Alaska and can live to be up to 100 years old. Assessment of the entire population of Pacific ocean perch in the Gulf of Alaska is made using stock synthesis analysis (section 8.2), which incorporates information on age and length distributions in the commercial fishery, trawl survey estimates of total biomass (across ages and regions) every three years, and annual harvests (Heifetz et al. 1994). Relative biomass estimates are obtained from trawl surveys in the three regions (eastern, central, and western), with projection to the total area in the regions.

The 1995 estimate of exploitable biomass for the Gulf (standard error is not available) and three survey estimates of relative exploitable biomass in 1987, 1990, and 1993 are given in table 10.9. The relative survey estimates are surprisingly variable among years considering that this species is so long lived. The surveys are thought to have large measurement errors because trawl surveys may not accurately sample these rockfish. Estimates based on equal weighting across years are also given in table 10.9, along with the regional biomass estimates from the apportionment using (10.67). Standard errors of relative biomass are calculated from between-survey variability.

Acceptable biological catch for 1995 is determined from the $F_{44\%}$ rate for conservatism (see section 11.4.7), along with some other downward adjustments to prevent overfishing and to provide for rebuilding, resulting in a recommended level of 8232 metric tons. Heifetz et al. (1994) apportioned ABC to regions with the average relative biomasses, which are shown in table 10.9.

In practice, an alternative apportionment scheme is used that weights a previous survey by a factor of 2/3 the next more recent survey. This apportionment results from the assumption that survey error contributes 2/3 of the total variability in estimation of biomass distribution. ■

10.6. MIGRATORY PER-RECRUIT ANALYSES

In chapter 6 per-recruit analyses were given for a single population. Analyses for migratory populations are more complicated. First, the control parameters such as minimum size and fishing mortality could differ by region, which would require evaluation of a

Table 10.9. Geographical apportionment of 1995 Pacific ocean perch exploitable biomass and acceptable biological catch (ABC) using relative exploitable biomass from trawl surveys.

	Overall	Western	Central	Eastern
1995 Exploitable biomass from stock synthesis	142,465			
Relative exploitable biomass from trawl surveys				
1987	27.7%	29.5%	42.8%	
1990	16.3%	22.8%	60.9%	
1993	16.7%	56.2%	27.1%	
Average	20.2%	36.2%	43.6%	
Standard error	3.7%	10.2%	9.8%	
1995 Estimated exploitable biomass by region				
Estimate	142,465	28,797	51,544	62,124
Standard error	0	5,314	14,528	13,895
1995 ABC				
Estimate	8,232	1,664	2,978	3,590
Standard error	0	307	839	803

The standard error of the relative apportionments is calculated from between-year variability. The standard errors of overall exploitable biomass and ABC are unknown, so standard errors reported for apportionments are conditional.

much larger parameter space. This problem could be resolved by considering one of the apportionment methods in section 10.5. Second, specification of relative recruitment by region is required. This may not be a problem if the assessment method produces estimates of relative recruitment. However, if this information is not available, alternatives must frequently be considered (Heifetz et al. 1997).

If the empirical methods in chapter 6 are used, the process of determining per-recruit quantities is straightforward. Let r be the age of first recruitment and $N_{r,i}$ be the given recruitment at age r and region i . For example, the total recruitment across regions could be set at 1000 fish and distributed across regions according to the most recent estimates of recruitment by region. For a given set of control parameters (and biological parameters), exploitation rate, $\mu_{a,i}$, for each age and region can be calculated. Then the population can be projected forward using one of the age-structured models in section 10.1.3, resulting in abundances, $N_{a,i}$, for various ages and regions. Catch for each region and combined over regions for the given recruitment distribution is then

$$C_i = \sum_a \mu_{a,i} N_{a,i} \quad \text{and} \quad C = \sum_i C_i = \sum_i \sum_a \mu_{a,i} N_{a,i}. \quad (10.68)$$

Similarly, yield would be calculated as in (10.68), only with average weight at age included. Given a maturity schedule $\{m_{a,i}\}$ for each region, then spawning abundance by region and across regions for the given recruitment distribution can be calculated as

$$S_{N,i} = \sum_a m_{a,i} N_{a,i} \quad \text{and} \quad S_N = \sum_i S_{N,i} = \sum_i \sum_a m_{a,i} N_{a,i}, \quad (10.69)$$

and analogously for spawning stock biomass by including average weight at age. Similarly, egg production for the given recruitment distribution is obtained by replacing maturity with fecundity, as described in section 4.8. Stochastic terms can be included for any parameter as desired.

Few essays have been published on migratory yield-per-recruit analyses. Polacheck (1990) developed a two-area per-recruit model to examine the efficacy of closed areas (or refuges) for controlling fishing mortality. If movement is not too large and fishing mortality is high, then a closed area can result in a substantial increase in spawning biomass per recruit without a large impact on yield per recruit.

Deriso et al. (1991) used the stochastic model described in section 10.1.2 to examine implications of migration on management. Yield per recruit was determined for a given area of recruitment using (10.20)–(10.22) with movement allowed to be time dependent. First, capture probability, $f_{j,t}$, can be written as

$$f_{j,t} = \mu_{j,t} \sum_{i=1}^R \theta_{i \rightarrow j,t} P_{i,t}.$$

Then yield per recruit is simply

$$Y = \sum_j \sum_t f_{j,t} \bar{W}_{j,t},$$

where $\bar{W}_{j,t}$ is average weight for region j at age t . For a given region, the subsequent residence times for yellowfin tuna in different regions were determined using per-recruit analyses. As mixing rates differed substantially among regions, a minimum size limit would affect yields differently in different zones. This study also pointed out that having accurate migration rates at early ages is critical to evaluate management strategies.

Heifetz et al. (1997) examined yield per recruit for a migratory sablefish population under geographic apportionment of yield based on the distribution of biomass. Thus, there was a single control parameter: the overall exploitation rate. Alternative recruitment distributions were examined because reliable estimates of recruitment by region are not available. Yield-per-recruit results were sensitive to the recruitment distribution. However, no matter what the recruitment scenario, a lower exploitation rate is needed to avoid overharvest (in the sense of fishing beyond the level necessary to obtain maximum yield per recruit) in some regions than that which would maximize yield per recruit overall.

Further study is needed to uncover general principles for harvesting migratory populations. How optimal harvest strategies, goals and objectives, and biological reference points considered in the next chapter are altered under significant movement of fish in the population is essentially unknown.

Optimal Harvesting

Management strategies for exploited fish populations depend on the goals and objectives to be achieved. They are usually defined through a political process, in which stakeholders vie to have their points of view represented. Biological, economic, and social implications result from management action, and frequently formal processes that address these issues are required. Population dynamics and bioeconomic models are often used to derive and evaluate strategies. Two recent proceedings contain several essays related to this topic (Kruse et al. 1993, Smith et al. 1993).

Optimal harvesting has been the most frequently considered topic of management. Fish populations are considered to be renewable resources, so the goal is to provide for optimal harvest while maintaining the biological productivity, or sustainability, of the population. Conservation (in the sense of “wise use”) concerns suggest that a long-term perspective is necessary, although short-term perspectives often receive paramount attention because the management system frequently receives pressure from stakeholders to address immediate concerns. A world fisheries have matured, increasing capitalization and reductions in some fish stocks have led to increases in user conflicts, bycatch and discard problems, safety problems, desires for direct allocations, and calls for ending overfishing, incorporating ecosystem and habitat concerns, and implementing limited access systems (NRC 1994b).

In this chapter we review and apply the population models from previous chapters in the context of optimal harvesting. In section 11.1, we describe quantitative formulae for harvest policies and their performance under equilibrium conditions. In section 11.2, we broaden the context of harvest policies by presenting goals, objectives, and constraints used in fishery management. In section 11.3, we summarize how optimal policies are found, given a biological model and a set of objectives and constraints. Different methods are used depending on the type of harvest control and whether stochasticity is incorporated. In section 11.4, we describe a series of biological reference points that lead to recommended harvesting levels when full optimization techniques cannot be applied. Finally, in section 11.5 we present a view to the future by considering how risk and uncertainty can be better incorporated into harvesting policies and other evaluations of fishery management.

11.1. HARVEST POLICIES AND EQUILIBRIUM CONCEPTS

General principles were derived in chapter 2 regarding the average productivity of a fish population. Under average conditions, the population produces surplus production each year, which can be taken as equilibrium yield without changing the population's size (biomass, B). The relationship between equilibrium yield (Y_*) and biomass is generally dome shaped: equilibrium yield increases as a function of biomass to a maximum level and then decreases (figure 11.1). Equilibrium yield can also be expressed as the product of fishing mortality and equilibrium biomass, or $Y_* = F_* B_*$. Implicit in this description is a negative relationship between equilibrium fishing mortality and biomass, so that a dome-shaped yield curve as a function of either one results. The maximum level of equilibrium harvest is called maximum sustainable yield (MSY) and is equal to a population's maximum productivity (m). The population size at which MSY occurs is denoted B_m , and the fishing mortality that produces MSY is

$$F_m \equiv F_{\text{msy}} = m/B_m.$$

One strategy for managing fish populations is a surplus production policy (e.g., Chapman et al. 1962, Ricker 1975a). One calculates the surplus production in a given year and then sets a harvest below, equal to, or above this level, depending on whether one wishes to rebuild, keep stable, or reduce the current population size. This type of policy was successfully used to rebuild the Pacific halibut population (Quinn et al. 1984). Its major limitation is that estimates of surplus production can be quite variable due to limited data and changing conditions in the population and its fisheries. This policy would require fish to be put back into the population rather than be harvested if the surplus production estimate is negative.

Other frequently discussed policies for managing fish populations include constant harvest (also called constant catch or constant yield) and constant harvest rate (or constant fishing mortality) policies. A constant harvest policy takes the same harvest ($Y = \text{constant}$) year after year and is shown in figure 11.1 as a straight horizontal line as a function of biomass for three different values of harvest. In the first case (Y_1), the harvest level is set above the equilibrium yield for population levels, so the popula-

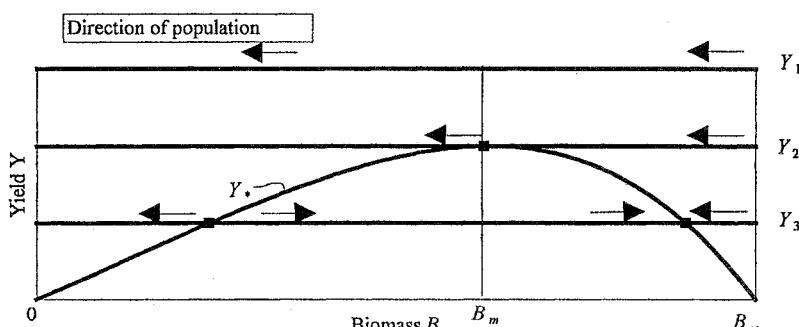


Figure 11.1. The relationship between equilibrium yield, Y_* (equivalent to surplus production) and biomass, B , along with three levels of constant yield, $Y_1 > m$, $Y_2 = m$, and $Y_3 < m$, where m is maximum sustainable yield. Arrows show the direction of population change; squares show equilibrium points.

tion will decline toward extinction. In the second case (Y_2), harvest is set equal to MSY. The population is sustainable only when it is at level B_m . At other levels, the population declines. When harvest (Y_3) is set below equilibrium yield (case 3), there are a variety of population levels that are sustainable, although the population is not sustainable at the lowest or highest levels.

Under a constant harvest rate policy, the harvest is set proportional to biomass, or $Y = FB$, for a selected fishing mortality, F . This policy is shown in figure 11.2 as a straight line with increasing slope for different values of F . Associated with each value of F is an equilibrium biomass level B_* , which is found from the intersection of the equilibrium yield and harvest curves. When the population is below B_* , it will increase toward B_* and vice versa. In the first case (with fishing mortality F_1), $B_* = 0$, so that the population tends toward extinction. Maximum sustainable yield results from setting F to F_m (fishing mortality F_2 in figure 11.2), where the population tends toward B_m . For a lower F (fishing mortality F_3 in figure 11.2), the equilibrium population size is higher than that which produces MSY, but yield from the population is necessarily lower. For an age-structured population, constant harvest rate and constant fishing mortality policies produce slightly different harvests, in that the fraction of the population exploited (harvest rate) may differ from the constant fishing mortality due to changes in age structure.

Another type of policy is a threshold policy (Quinn et al. 1990b), wherein no harvest is permitted below a threshold level, T , and a constant fishing mortality is used above T , or

$$Y = \begin{cases} 0, & B < T \\ FB, & B \geq T \end{cases}. \quad (11.1)$$

This policy is illustrated in figure 11.3 for three threshold levels. An alternative, shown by dotted lines, is to increase fishing mortality linearly beyond the threshold. Note that if a threshold is set above B_m (threshold level T_3 in figure 11.3), then the MSY cannot be obtained. A further variation is used for limits on catches of marine mammals where piecewise linear fishing mortality rates increase for abundances above a given stock's lower threshold abundance, but catches are further capped at a maximum level above

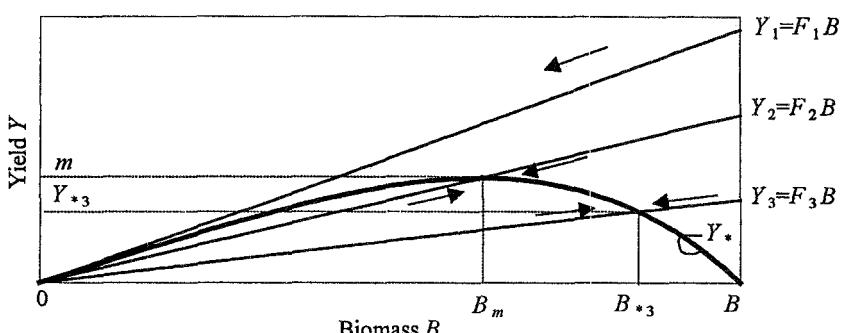


Figure 11.2. The relationship between equilibrium yield, Y_* , and biomass, B , along with three levels of yield, $Y_i = F_i B$, corresponding to a constant harvest rate $F_1 > F_m$, $F_2 = F_m$, and $F_3 < F_m$, where F_m is the harvest rate at MSY. Arrows show the direction of population change.

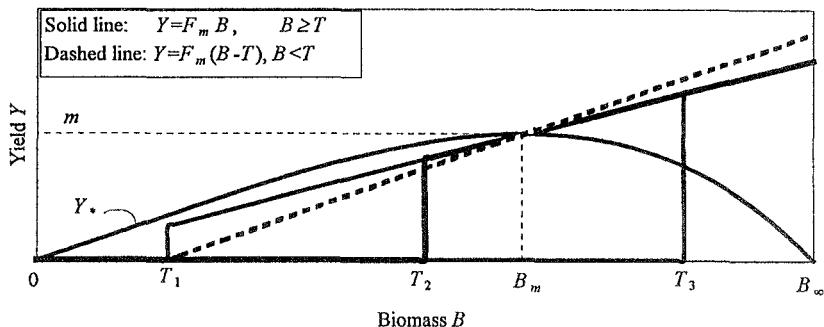


Figure 11.3. The relationship between equilibrium yield, Y^* , and biomass, B , along with three levels of yield, Y_i (solid lines), corresponding to the first threshold policy with $T_1 < B_m$, $T_2 < B_m$, and $T_3 > B_m$, where B_m is the biomass at maximum sustainable yield, and one level of yield, Y_1 (dotted line), corresponding to the second threshold policy with $T_1 < B_m$.

an upper threshold abundance (Punt and Butterworth 1989). Thresholds are further discussed in section 11.4.9.

A special case of this policy is frequently considered for semelparous (once-breeding) populations, as described in section 3.3. Called a *fixed escapement policy*, it allows no harvest when the number of fish is below escapement level T and allows the harvest of all fish beyond that level. Analysis of spawner-recruit relationships allows the determination of optimal escapement. Fixed escapement policies are frequently used in Pacific salmon management; these policies are discussed further in section 11.3.

A fourth type of policy, called the biomass-based or adjustable rate policy, is to scale fishing mortality downward when the population is below some specified level such as the MSY level (Leaman 1993, Sigler and Fujioka 1993). The adjustment is typically proportional to population size, so that $\tilde{F} = (B/B_m) F$ and

$$Y = \begin{cases} \tilde{F} B = (F/B_m) B^2, & B < B_m \\ FB, & B \geq B_m \end{cases}. \quad (11.2)$$

This policy is illustrated in figure 11.4 for the same three values of F used in figure 11.2. Other biological reference points could be used in place of F_m and B_m , such as those based on preserving spawning biomass per recruit (section 11.4.6). Fujioka et al. (1997) showed that a biomass-based policy can provide a greater proportion of maximum yield with less risk of overfishing than a constant harvest rate policy.

Figure 11.5 compares the different policies in terms of fishing mortality as a function of biomass. For the surplus production policy, F is a concave-downward, decreasing function of biomass for most surplus production models (e.g., $n \geq 1$ in the Pella-Tomlinson model). These values of F would keep the population at equilibrium under average conditions. For the constant harvest policy with yield equal to MSY, F is a concave-upward, decreasing function of biomass. The values of F are higher at all biomass levels except the MSY level than those which would remove only the surplus production. The constant F policy with $F = F_m$ provides lower F values at low population sizes than required to keep the population at equilibrium. At high levels,

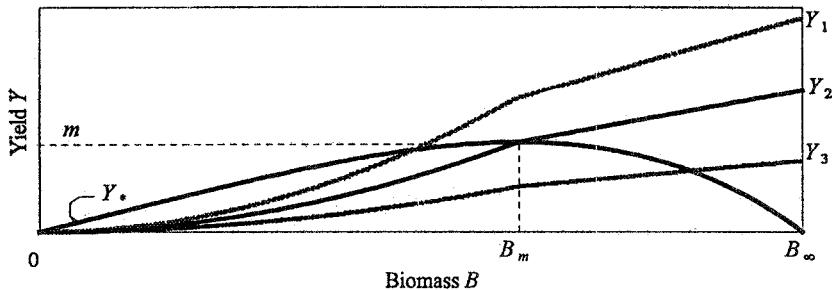


Figure 11.4. The relationship between equilibrium yield, Y_* , and biomass, B , along with three levels of yield, Y_i (solid lines), corresponding to the biomass-based policy with harvest rate parameter $F_1 > F_m$, $F_2 = F_m$, and $F_3 < F_m$.

the population would decline toward the MSY level. For the threshold (with $T < B_m$) and biomass-based (with $F = F_m$) policies, F values are even lower at low population sizes than required to keep the population at equilibrium. Consequently, these policies provide for faster rebuilding of a population that is at low levels. At high levels, they coincide with the constant F policy.

These policies can be synthesized into a three-parameter policy function

$$Y = \begin{cases} 0 & B < T \\ \alpha B^\beta [\text{or } \alpha(B - T)^\beta] & B \geq T \end{cases} \quad (11.3)$$

(Ruppert et al. 1985, Getz and Haight 1989). The constant harvest policy is a special case of (11.3) with $T = 0$ and $\beta = 0$, where parameter α is equivalent to the constant harvest. The constant harvest rate policy is a special case of (11.3) with $T = 0$ and $\beta = 1$, where parameter α is equivalent to fishing mortality, F . The threshold policy uses the

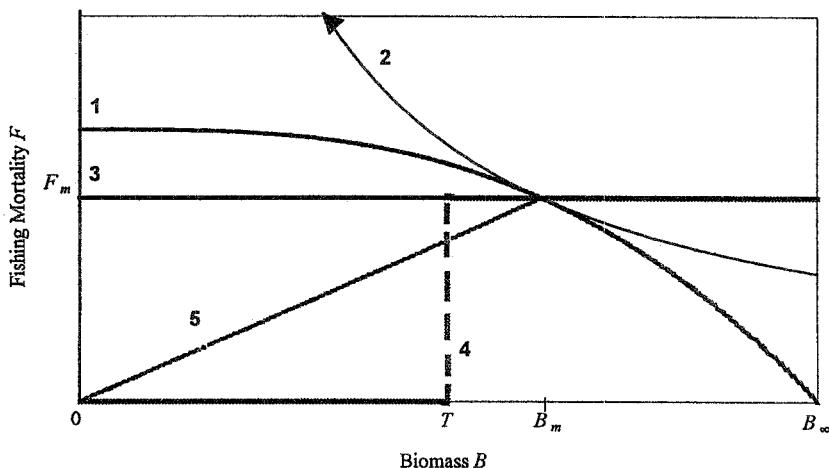


Figure 11.5. The relationship between fishing mortality, F_* , and biomass, B , for five policies: policy 1—surplus production; policy 2—constant harvest $Y = m$; policy 3—constant harvest rate $F = F_m$; policy 4—threshold with $T < B_m$ and $F = F_m$; policy 5—biomass-based with $F = F_m$.

left equation in (11.3) and has $\beta = 1$ and α equivalent to F . The constant escapement policy uses the right equation in (11.3) and is a special case of the threshold policy with $\alpha = 1$ and $\beta = 1$. The biomass-based policy is a special case of (11.3) with $T = 0$ and $\beta = 2$, where α is equivalent to F/B_m [with the adjustment $Y = \alpha_2 B$ to (11.3) when $B > B_m$].

While the equilibrium analysis above contrasts some of the features found in different policies, it is too limited to be of much use in determining management policies. In practice, stochasticity affects the relationship between yield and biomass, particularly due to variability and lag time in recruitment, and uncertainty affects our understanding of the relationship. Larkin (1977, p. 9–10) proposed an end to the notion of managing for MSY:

The foregoing has demonstrated, I hope, that MSY is not attainable for single species and must be compromised: (1) to reduce the risk of catastrophic decline and reduction of genetic variability; and (2) to accommodate the interactions among the species of organisms that comprise aquatic communities. Moreover, MSY is not necessarily desirable from an economic point of view, and is certainly not so in the circumstances of unlimited entry. . . . But now it's time for MSY to ride off into the sunset.

About the same time, Gulland (1978, p. 1) commented: “The age of simplicity is over, whether in the use of simple objectives like maximum sustainable yield or of simple single-species, constant-environment population models.” Nevertheless, Barber (1988) in a survey of 142 essays published from 1977 through 1985 showed that MSY is still frequently used to estimate long-term yield, evaluate stock condition, and analyze policy.

11.2. GOALS, OBJECTIVES, AND CONSTRAINTS

To prescribe appropriate management measures for fisheries, the management system must first define a set of goals and objectives to be achieved. Goals are broad, conceptual statements of what is desired by fisheries management, and objectives are specific elements of a management system, which should allow the goals to be achieved. Often, the objectives are constraints imposed by the biology of the fish species harvested or by the logistics of the fishery.

In the United States, the Magnuson-Stevens Fishery Conservation and Management Act (MSFCMA) of 1996 (earlier versions date back to 1976) governs marine and coastal fisheries management. The goals of fishery management are embodied in national standards:

- (1) Conservation and management measures shall prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery for the United States fishing industry.
- (2) Conservation and management measures shall be based upon the best scientific information available.
- (3) To the extent practicable, an individual stock of fish shall be managed as a unit throughout its range, and interrelated stocks of fish shall be managed as a unit or in close coordination.
- (4) Conservation and management measures shall not discriminate between residents of different States. If it becomes necessary to allocate or assign fishing privileges among various United States fishermen, such allocation shall be (A) fair and equitable to all such fishermen; (B) reasonably calculated to promote conservation; and (C) carried out in such manner that no particular individual, corporation, or other entity acquires an excessive share of such privileges.
- (5) Conservation and management measures shall, where

practicable, consider efficiency in the utilization of fishery resources; except that no such measure shall have economic allocation as its sole purpose. (6) Conservation and management measures shall take into account and allow for variations among, and contingencies in, fisheries, fishery resources, and catches. (7) Conservation and management measures shall, where practicable, minimize costs and avoid unnecessary duplication. (8) Conservation and management measures shall, consistent with the conservation requirements of this Act (including prevention of overfishing and rebuilding of overfished stocks), take into account the importance of fishery resources to fishing communities in order to (A) provide for the sustained participation of such communities, and (B) to the extent practicable, minimize adverse economic impacts on such communities. (9) Conservation and management measures shall, to the extent practicable, (A) minimize bycatch and (B) to the extent bycatch cannot be avoided, minimize the mortality of such bycatch. (10) Conservation and management measures shall, to the extent practicable, promote the safety of human life at sea. (MSFCMA, 1996, pp. 44-45)

To achieve these goals, the U.S. Congress set up a regional system of councils to provide objectives and overall management. The definition of "optimum yield" in the first standard is

the amount of fish (A) which will provide the greatest overall benefit to the Nation, particularly with respect to food production and recreational opportunities, and taking into account the protection of marine ecosystems; (B) is prescribed as such on the basis of the maximum sustainable yield from such fishery, as reduced by any relevant economic, social, or ecological factor; and (C) in the case of an overfished fishery, provides for rebuilding to a level consistent with producing the maximum sustainable yield in such fishery. (MSFCMA, 1996, p. 9)

As another example, the state of Alaska explicitly mandates long-term conservation in its constitution (State of Alaska 1996, Article VIII, Natural Resources, Section 4, Sustained Yield): "Fish, forests, wildlife, grasslands, and all other replenishable resources belonging to the State shall be utilized, developed, and maintained on the sustained yield principle, subject to preferences among beneficial uses." Nowhere in the Alaska constitution is the sustained yield goal explicitly defined, but one may infer that the drafters envisioned proper conservation and management of resources to provide long-term protection and utilization.

For the analyst, the main problem with these goals is how to quantitatively interpret them. The goals may not be mutually compatible and do not explicitly prescribe the objectives to be achieved in terms of population and control parameters, except by reference to sustained, optimal, or maximum sustainable yield. However, as seen in figure 11.1, there is a corresponding sustained yield (equivalent to surplus production) for any biomass level, and the equilibrium analysis in section 11.1 shows that there are many policies that lead to attainment of MSY. Thus, further specification of the management objectives is necessary for quantitative analysis. We describe several quantitative objective functions that have been investigated.

The quantitative framework for evaluating policies is known as control theory, wherein a decision is to be taken based on an objective function (Clark 1976a, 1985). The state variable in the optimal harvesting context is the population dynamics system, whereas the basic decision variable is the fishing mortality or harvest allowed. In more complicated problems, the decision variable may be broadened to consider age-

specific harvests each year and the population dynamics and management system may include stochastic elements. An even more complicated control problem allows for the population dynamics models to be updated each year, which tends to replicate the actual management process; this process is called adaptive management, and the problem is discussed in section 11.3.3.

The most common objective function is to maximize the sum of harvests over a fixed planning horizon of n years. If $\{Y_t, t = 1, \dots, n\}$ is the set of harvests over the planning horizon, then this objective function can be written

$$O_1 = \max \sum_{t=1}^n Y_t. \quad (11.4)$$

A generalization of this objective function is

$$O_2 = \max \sum_{t=1}^n U(Y_t), \quad (11.5)$$

where U is some nonlinear function, called the *utility function*. The utility function maps the harvest into a variable that models the value of the harvest over time according to some biological, economic, or social principle. Utility functions are used frequently in optimal control problems (Ruppert et al. 1984).

Objective function (11.4) is called *risk neutral* because the one-period utility of catch is a linear function of catch and so has a constant first derivative (Reed 1979, Deriso 1985b). The implication is that management is indifferent to a given harvest at a particular point in time. Thus the risk of obtaining lower or higher harvests in the future in relation to the current harvest is considered unimportant.

In contrast, a *risk-averse* policy has a decreasing marginal utility function, so that extreme harvests are to be avoided. With such a policy, managers are more reluctant to increase harvests in the future than with a risk-neutral policy. Thus a unit of biomass in a small harvest is worth more than in a large harvest.

One example of a risk-averse function is the logarithm (Mendelsohn 1982, Deriso 1985b, Ruppert et al. 1985), or

$$O_3 = \max \sum_{t=1}^n \ln Y_t \quad \text{or} \quad \max \sum_{t=1}^n \ln(Y_t + 1). \quad (11.6)$$

The latter choice is appropriate when zero catches are of interest. Solutions for a logarithmic utility function tend to avoid boom-or-bust fisheries by smoothing out the harvests across years. Deriso (1985b) showed that a constant harvest rate policy is the solution to (11.6) for a semelparous population following a Cushing spawner-recruit curve with lognormal error. For a specific Ricker spawner-recruit curve under similar circumstances, an approximate constant escapement policy is the solution to (11.6) when recruitment is high (Mendelsohn 1982). Because the Ricker curve declines sharply at higher spawning levels, it makes sense that unlimited escapement does not provide for optimal harvest.

Another way to avoid boom-and-bust fisheries is to explicitly include variability of harvests into the objective function. As a general rule, a harvest policy that increases average harvest will also increase the variation in harvests over the planning

horizon. Quinn et al. (1990b) suggested an objective function that maximizes a linear combination of average harvest and the negative of the standard deviation of harvests, or

$$\begin{aligned} O_4 &= \max \left[(1 - \lambda) \frac{1}{n} \sum_{t=1}^n Y_t - \lambda \frac{1}{n-1} \sum_{t=1}^n (Y_t - \bar{Y})^2 \right] \\ &= \max [(1 - \lambda) \bar{Y} - \lambda SD(Y_t)], \end{aligned} \quad (11.7)$$

where λ is a weighting term governing the relative influence of average harvest and standard deviation (SD) of harvests. When $\lambda = 0$, the maximum harvest policy (11.4) results. As λ increases in (11.7), an increasing penalty for more variable harvests occurs in the objective function. Quinn et al. found that (11.7) approximates the logarithmic objective function (11.6) well when $\lambda \approx 0.2$.

A different set of policies can be formulated by explicitly considering optimal or target levels for abundance and harvest (Hightower and Grossman 1987). Let Y_* be the optimal or target level for harvest (for example, MSY may be one candidate), which may be found from equilibrium analysis, quantitative evaluation of alternative objectives, or even an arbitrary decision of a management system. The main point is that some target level has been established a priori. Similarly, let B_* be a optimal or target level for population abundance, be it exploitable abundance or biomass, spawning stock abundance or biomass, or some function of abundance or biomass at age. A biological objective might be to minimize the sum of squared deviations of abundance from the optimal level over the planning horizon, or

$$O_5 = \min \sum_{t=1}^n (B_t - B_*)^2. \quad (11.8)$$

An alternative approach combines the maximum harvest objective (11.4) with a biological objective constraint that keeps the population near the optimal level at the end of the planning horizon (Hightower and Grossman 1987). This is accomplished by adding a penalty term to (11.4), which results in

$$O_6 = \max \sum_{t=1}^n Y_t - \delta (B_n - B_*)^2, \quad (11.9)$$

where δ is a penalty weight influencing how close abundance at the end of the planning horizon should be to the target level. As δ increases, the ending abundance is less likely to be away from the target level.

A different harvesting objective is to minimize the sum of squared differences between harvest and optimal harvest, or

$$O_7 = \min \sum_{t=1}^n (Y_t - Y_*)^2. \quad (11.10)$$

Walters (1975) used this objective function for Pacific salmon, arguing that this objective conformed to actual harvest management practices more than harvest maximization. Hightower and Grossman (1987) found two problems with this objective in

a stock rebuilding context. First, two values of fishing mortality (one above F_m , one below) resulted in the same equilibrium harvest, but the use of (11.10) with a low starting population led to the higher fishing mortality and a resultant lower abundance. Second, for an age-structured population, the same harvest could be obtained from more than one age structure in the population. This resulted in increases in harvest to offset decreases in stock size. To alleviate these problems, Hightower and Grossman suggested a modification of (11.10) that includes a penalty term for the deviation of abundance at the end of the planning horizon, as in (11.9), or

$$O_8 = \min \sum_{t=1}^n (Y_t - Y_*)^2 + \delta(B_n - B_*)^2. \quad (11.11)$$

Hightower and Grossman pointed out that the policies given by (11.10) and (11.11) could be inappropriate in some situations because departures from the optimal level are given equal weight regardless of sign. In reality, the management system may wish to penalize harvests and abundances lower than the optimum levels. A simple solution would be to introduce appropriate weighting functions into (11.10) and (11.11).

11.2.1 Stochasticity

The preceding objective functions were constructed under a deterministic setting. Several investigations have incorporated stochastic terms in the equations for abundance and management (e.g., Mendelsohn 1979, Ruppert et al. 1984, Sluzanowski 1984, Deriso 1985b, Hightower and Lenarz 1989, Koslow 1989, Kope 1992), so that future abundance and catch are random variables. The above objective functions can be easily revised to deal with stochasticity by optimizing the expected value of the functions. In addition, objectives and constraints related to risk of over- or underharvesting can also be formulated in terms of probabilities of desirable or undesirable events (Hollowed and Megrey 1993, Lowe and Thompson 1993). We expand on this topic in section 11.3.

11.2.2 Bioeconomic Objectives

Bioeconomic models are frequently constructed to evaluate management strategies, consisting of a biological component for the dynamics of a population and an economic component for the characteristics and possibly dynamics of the harvesting sector (Clark 1976a, 1985; Criddle 1993, Palsson et al. 1993). Economic objectives incorporate price and cost information and may involve a discount rate, as explained below. In the simplest bioeconomic models, (1) gross revenue, R_t , in year t is obtained as the product of price (amount paid per unit of fish) and harvest, or $R_t = p_t Y_t$; (2) fishing effort, E_t , is proportional to fishing mortality, F_t , or $F_t = q E_t$, where q is a catchability coefficient; (3) gross expense is obtained as the product of cost (amount expended per unit of fishing effort) and fishing effort, or $X_t = c_t E_t$; and (4) profit or net revenue (or loss) is the difference of gross revenue and expense, or $P_t = R_t - X_t$. The economic equivalent to the harvest maximization objective is the profit maximization objective, or

$$O_9 = \max \sum_{t=1}^n P_t = \max \sum_{t=1}^n (R_t - X_t) = \max \sum_{t=1}^n (p_t Y_t - c_t E_t). \quad (11.12)$$

Thus, this objective function is a weighted function of yields and fishing efforts (or equivalently, fishing mortalities) over time.

According to economic principles, the future value, FV , of money invested at the present time, say P , increases (inflates) through payment of interest according to the formula $FV = P(1+i)^n$, where i is the annual interest rate and n is the number of years invested (Clark 1976a, 1985; Hilborn and Walters 1992). In terms of an instantaneous annual rate of interest, δ , $FV = P e^{\delta t}$ for any continuous time, t . Accordingly, the value of capital in the future viewed from the current time diminishes due to inflation.

Applying this principle to fisheries, one would view a fish stock as an asset with dividends being paid out annually by selling the harvests $\{Y_t\}$. To find the present value of these future harvests, one would apply the discount formulae. Thus, a modification of (11.12) that incorporates a discount rate is

$$O_{10} = \begin{cases} \max \sum_{t=1}^n \frac{P_t}{(1+i)^t} & \text{for discrete times} \\ \max \int_1^n P(t) e^{-\delta t} dt & \text{for continuous times.} \end{cases} \quad (11.13)$$

Some examples of bioeconomic models that use discount rates are given by Clark (1973, 1976a, 1985), Mendelsohn (1979, 1982), and Sluzanowski (1984).

The use of discount rates in fisheries problems is controversial. Federal law in the United States and Canada mandates the use of a discount rate of 10% in policy analysis (Hilborn and Walters 1992), although discount rates under this level are also frequently used. Some economic models suggest that economic considerations create pressure to overexploit fish stocks in unregulated fisheries because the present value of equivalent harvests made at later times is smaller than earlier harvests under discounting (Clark 1973, 1976a). Some conservation groups have suggested that a negative discount rate might be appropriate to achieve biological conservation objectives. Such a view holds that saving fish stock until a future time provides for long-term preservation of stock abundance.

More complicated economic objective functions have been constructed. Sluzanowski (1984) constructed an objective function that incorporates the fraction of revenues paid to crew, the number and cost of vessels, and the discount rate and that models price as a function of average fish weight. Hilborn and Walters (1992) gave a variety of models for fleet dynamic behavior which include economic considerations.

11.3. OPTIMIZATION METHODS

Several components go into finding an optimal solution to a decision problem. First, a biological component must be specified, which gives the response of the harvested population to a set of controls. Second, the class of controls of interest must be specified, along the lines of section 11.1. The parameters for the controls may be constant in time, such as constant harvest or constant harvest rate parameters, or the controls may be time varying in the sense that a different control value is selected for each year in the future. Third, a set of objectives and constraints must be specified, along the lines of section 11.2. This component also involves the specification of stochasticity in the biological model and decision process and whether economic and social objectives are to be included. Once these choices have been made, the mathematical methodology for finding the optimal solution falls out. For further details on optimization in fisheries, the texts by Clark (1976a, 1985), Mangel (1985), Walters (1986), and Hilborn and Walters (1992) offer many additional insights beyond those presented here.

11.3.1. Biological Models

We have already considered the two general classes of biological models that are used in evaluating optimal harvesting strategies: one for semelparous (once-breeding) populations (section 3.3), the other for iteroparous (age-structured, multiple-breeding) populations (chapters 5 and 7). For a semelparous population, population size is dependent exclusively on the population at some lag time representing the generation length, say, r . A general model for the dynamics of a semelparous population can be written

$$N_{t+r} = \mathcal{F}(S_t, \{T_{t+x}\}, \epsilon_t) \quad (11.14)$$

$$S_t = N_t - C_t, \quad (11.15)$$

where \mathcal{F} is a generalized spawner-recruit function; N_t = the number of recruits R (or returns) at time t ; S_t = spawning abundance; $\{T_{t+x}\}$ = environmental variables affecting recruitment ($0 \leq x \leq r$); ϵ_t = a random variable with mean 0 and variance σ^2 ; and C_t = catch. The random variable ϵ_t represents unexplained variability (also known as “white noise”) and is modeled as a lognormal variable, which can be represented by the multiplicative term $\exp(\epsilon_t)$. To determine optimal policies, it suffices to follow the succeeding generations of the population every r years. If the goal is to examine average future behavior, then the expected value of recruitment with lognormal variability can be used, which is $\mathcal{F}(S, \{\mathcal{T}\}) e^{\sigma^2/2}$, where S is treated as a variable and $\{\mathcal{T}\}$ is either average environmental conditions or some function or model for the environment.

For an age-structured population (see chapter 7), additional dynamic equations are needed because part of the population survives to the next year. Let $N_{a,t}$ be the abundance at age a and year t ; $S_{a,t}$ be the survival at age a and year t ; f_a be the average net fecundity of a female at age a ; m_a be the proportion mature at age a ;

$$\mathcal{E}_t \equiv N_{0,t} = \sum_{a=r}^A f_a N_{a,t} = \text{egg production in year } t; \quad (11.16)$$

and

$$S_t = \sum_{a=r}^A m_a N_{a,t} = \text{spawning abundance in year } t. \quad (11.17)$$

The general recursive equation for abundance is then

$$N_{a+1,t+1} = N_{a,t} S_{a,t}, \quad (11.18)$$

where $S_{a,t}$ is a survival function incorporating natural mortality, $M_{a,t}$, and fishing mortality, $F_{a,t}$ (or exploitation fraction, $\mu_{a,t}$). Catch is then given by

$$C_{a,t} = \mu_{a,t} N_{a,t}. \quad (11.19)$$

The connection between recruitment in the future and the spawning population for this age-structured population must be made, as was done for the semelparous population in (11.14). By analogy, assume that the relationship between recruitment and egg production can be written

$$N_{r,t+r} = \mathcal{F}(\mathcal{E}_t, \{\mathcal{T}_{t+x}\}, \epsilon). \quad (11.20)$$

Sometimes spawning abundance, S_t , is used in place of egg production. Special cases of this recruitment function include the deterministic spawner-recruit model (omit $\{\mathcal{T}_{t+x}\}$, ϵ), the stochastic spawner-recruit model (omit $\{\mathcal{T}_{t+x}\}$), the random recruitment model [set $\mathcal{F}() = f(\epsilon)$], and the constant recruitment model [set $\mathcal{F}() = \text{constant}$].

Koslow (1989) and Collie and Spencer (1993) handled environmental variability by including “red noise,” which is sinusoidal variation, in the recruitment function in place of environmental variables. This introduces autocorrelation into the recruitment time series, so that good years are followed by good years, bad years by bad.

Simpler versions of this general model can be used. If parameters do not vary with age and no lag between egg production and recruitment is used, a simple surplus production model results, such as in chapter 2 and section 11.1. If simplifying assumptions are made about average weight and selectivity, then a simple delay-difference model (chapter 5) in terms of biomass, B , and yield, Y , results.

Collie and Spencer (1993) incorporated multispecies considerations by exploring a simple surplus production model with a Holling type III predation equation of the form

$$\frac{dB}{dt} = rB \left(1 - \frac{B}{K}\right) - \frac{CB^2}{D^2 + B^2} - FB,$$

where r is the intrinsic rate of population growth, K is carrying capacity, C is a consumption rate, and D relates to prey density at which predator satiation occurs. For some combinations of parameters, this model exhibits compensatory behavior with two stable and one unstable equilibrium points. After including red noise to represent environmental variability, they found that harvesting makes the chances of a stock collapse more likely and prolongs the time to recovery. Constant harvest rate and threshold policies performed similarly; a fixed escapement policy had slightly higher average yield but nearly twice the SD of yields.

11.3.2. Fixed-Parameter Harvest Control

The first type of harvest control is fixed in the sense that the parameters for the controls are constant in time. The policies described in section 11.1, such as the constant harvest or constant harvest rate policies, all are described by parameters constant in time. The generalized policy (11.3) has three fixed parameters for harvest control: a threshold level for biomass, a base fishing mortality parameter, α , and a shape parameter, β , controlling magnitude of fishing mortality as a function of biomass.

In addition to controls on fishing mortality, some control may be exerted on the size and/or age distribution of fish. Minimum, maximum, and slot size limits fall into this category (chapter 6). A more general approach is to specify the pattern of age selectivity as a function of age for different types of controls.

Finally, time/area closures, individual quotas, trip limits, bag limits, gear restrictions and limits, and fishing regulations and management actions may all have effects on the selectivity and fishing mortality exerted on a fish stock. It is often quite difficult to quantify these effects, except through experimentation and comparative study.

After a set of objectives and constraints is specified, as in section 11.2, optimal solutions are sought within a class of policies. It is possible to derive the optimal solution for a simple model and a simple objective function. For more complicated

problems, the solution is found numerically. Walters (1986) refers to this approach as “policy space optimization.” One caveat to restricting the search to a particular class of policies is that a suboptimal solution may result if the class is not broad enough.

If stochastic elements are not present, the population is projected from an initial population into the future, with appropriate calculation of biological and harvest quantities being made under initial parameter values specified for the harvest control. Numerical methods of optimization (e.g., R. Fletcher 1987) are then used to obtain the optimal policy value(s). For some simple problems, a simple grid search technique is sufficient.

Example 11.1. Hypothetical semelparous population

Suppose that a population follows the system (11.14)–(11.15) with the deterministic Ricker spawner-recruit model [$\mathcal{F} = \alpha S \exp(-\beta S)$]. The values for the parameters α and β are e and 0.001, respectively. The maximum recruitment of 1000 fish occurs from 1000 spawners. It can be shown that recruitment, spawning abundance, and catch corresponding to MSY are 763, 433 and 330, respectively. Hence, fishing mortality at MSY is 0.433.

Three policies are evaluated (constant harvest, constant harvest rate, and fixed escapement) under a planning horizon of 20 years. Two objective functions are examined: harvest maximization function (11.4) and the weighted function (11.7) with $\lambda = 0.2$, which approximates a log utility function. Two initial values are used: $S_0 = 100$ and $S_0 = 1000$. The objective functions are optimized under the constraints that catch, recruitment, and escapement are all non-negative. Solutions are found by using spreadsheet software.

Values for each policy parameter and the objective function that produce the optimal solution are shown in table 11.1. The time trajectories for catch, escapement, and recruitment are shown in figure 11.6 for the optimal solutions under harvest maximization. For harvest maximization, the best policy for the high starting population of 1000 is the constant catch policy, although average catch is close for the three policies. The constant catch of 343 is larger than MSY, with a result that the population is driven to a very low level at the end. Had an objective or constraint been imposed to keep the population above a critical level, this policy would not have been the best. The next best policy is the harvest rate policy. Results for the weighted average objective are nearly identical to harvest maximization.

For the low population size of 100, the harvest maximization objective is best achieved under a fixed escapement policy, although average catch for the constant harvest rate policy is within 10% of the maximum, and its standard deviation is smaller. The constant catch policy is clearly inferior because the small population at the start restricts the value for constant catch. As a result, the abundance at the end of the period is much higher than that producing MSY. Similar results are obtained once again for the weighted average objective function.

In figure 11.6, the constant harvest rate and fixed escapement policies both result in stable parameters near their MSY levels after a few time periods. The fixed escapement policy is at MSY in no more than two time units, whereas the harvest rate policy attains MSY levels more gradually. The constant catch policy does not result in levels near MSY. With this policy, the low starting population ends up at a high level, while the high population ends up at a low level, because the low starting level essentially constrains

Table 11.1. Harvest policy and objective function values for a hypothetical semelparous population.

		$S_0 = 1000$			$S_0 = 100$			MSY
		Constant harvest rate	Fixed escapement	Constant catch	Constant harvest rate	Fixed escapement	Constant catch	
Objective function 1								
Average catch	Harvest rate	0.451	—	—	0.421	—	—	0.433
	Escapement	—	414.1	—	—	413.1	—	432.9
	Catch	—	—	343.3	—	—	145.9	330.4
	\bar{C}	341.8	342.7	343.3	287.7	302.3	145.9	
	SD(C)	29.7	57.2	0.0	69.5	86.5	0.0	
	Wt. avg .	267.5	262.7	274.6	216.2	224.6	116.7	
Objective function 2								
Weighted average	Harvest rate	0.442	—	—	0.421	—	—	0.433
	Escapement	—	435.0	—	—	399.6	—	432.9
	Catch	—	—	343.3	—	—	145.9	330.4
	\bar{C}	341.6	342.1	343.3	287.7	302.1	145.9	
	SD(C)	27.1	52.5	0.0	69.5	84.6	0.0	
	Wt. avg .	267.8	263.2	274.6	216.2	224.7	116.7	

The three harvest policies are constant F (or harvest rate), fixed escapement, and constant harvest (or catch) with a planning horizon of 20 years. The two objective functions are to maximize total catch and to maximize a weighted average of average catch and standard deviation of catches (weighting parameter $\lambda = 0.2$). For each objective function, optimal policy parameters are given for a high starting population (1000) and a low one (100). Also given are values of average catch \bar{C} , standard deviation of catches $SD(C)$, and the weighted average and values corresponding to maximum sustainable yield (MSY). The values optimizing the objective function among the three policies are highlighted in bold.

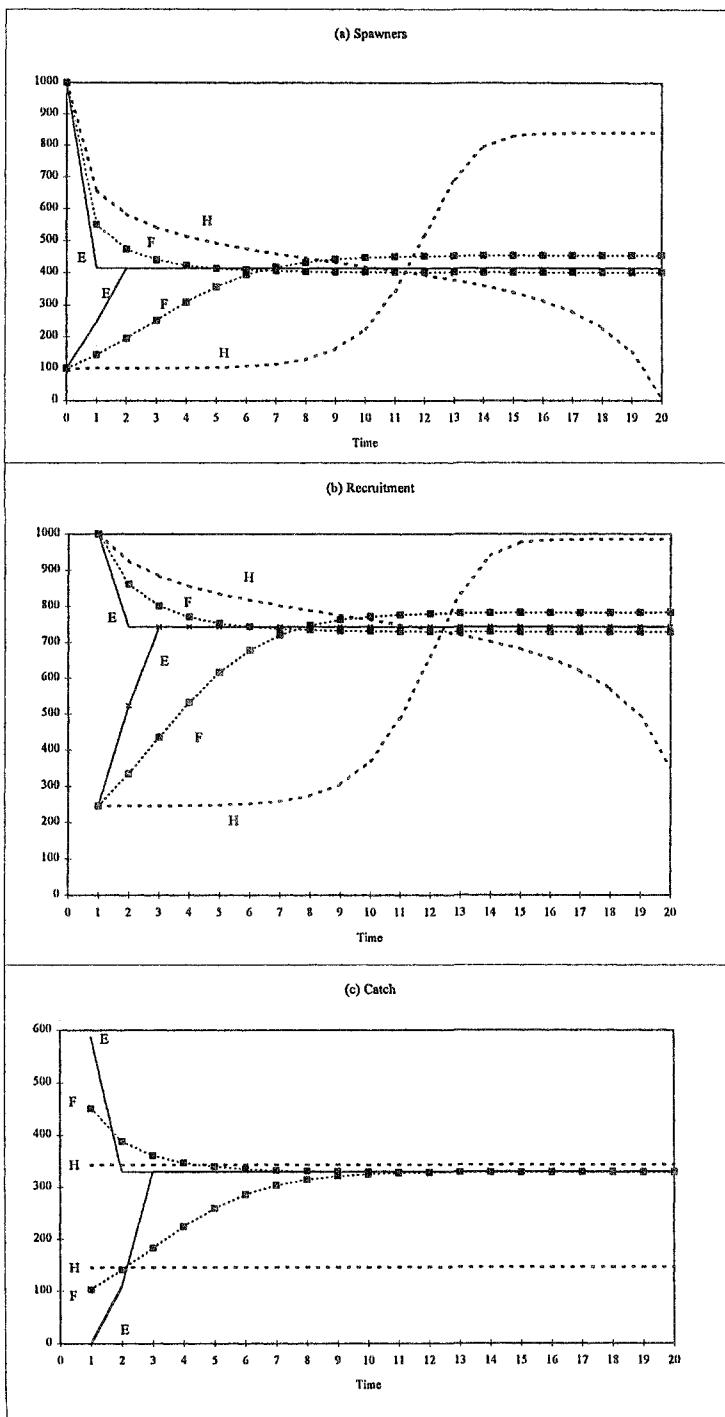


Figure 11.6. Temporal dynamics for a semelparous population with two starting levels of abundance, S_0 , of 100 and 1000 under the constant harvest (H), constant harvest rate (F), and fixed escapement (E) policies using solutions to objective 1: (a) spawners, (b) recruitment, (c) catch.

the catch to be low. Therefore, the inconsistency of the constant catch policy suggests that it should be avoided unless sufficient constraints are added to keep the population near optimal levels. ■

If stochasticity in the biological model and decision process is present, then Monte Carlo methods of computer simulation are needed. Several replications of the process are made and summary statistics of interest (such as mean and standard deviation) are compared among policy choices. Examples of this approach include Hightower and Lenarz (1989), Quinn et al. (1990b), and Sigler and Fujioka (1993). The first two papers deal with the issue of stock rebuilding for an age-structured population. Hightower and Lenarz compared constant F and the general policy (11.3) in terms of average yield, SD of yield, and stability of parameter estimates for the harvest maximization and log harvest maximization policies. They used a replication-deletion approach where only values from the last half of the planning horizon were used. The constant F policy generally provided comparable results to the more general policy. Only when strong density-dependence was present was the more complicated policy (11.3) warranted.

Quinn et al. (1990b) evaluated the threshold policy (11.1) for an age-structured population with stochastic recruitment and the trade-off objective function (11.7). They found that average yield and SD of yield increased as higher threshold levels were used (up to some point). As greater weight was given to variability in harvest, the objective function favored lower levels of the threshold. Simultaneous optimization by threshold level and fishing mortality resulted in an intermediate threshold level and a fishing mortality slightly greater than F_m that produces MSY; this result was obtained for all reasonable values of λ , the weighting term.

Using an age-structured model with autocorrelated but density-independent recruitment, Sigler and Fujioka (1993) evaluated constant F , threshold, and biomass-based F policies for sablefish in the Gulf of Alaska. They found that catch variability was lowest and average catch was highest for the constant F policy. However, if the goal is to minimize risk of falling below a particular biomass level, either the threshold or biomass-based policies would be favored. The decrease in average catch was slight with either policy compared to the constant F policy.

Ruppert et al. (1984) applied the method of stochastic approximation of Robbins and Monro (1951) to optimize the utility function (11.5) under the general policy (11.3). This method is an iterative method for finding the optimum of a random function. The advantage to using stochastic approximation is that the solution is found more efficiently than with a grid search. In application to the Atlantic menhaden population, Ruppert et al. found that the general policy (11.3) with $\beta = \frac{1}{2}$ and B replaced with potential egg production was better than a constant F policy in terms of optimizing the objective function, which in turn was better than a constant catch policy. Hightower and Lenarz (1989) used stochastic approximation to determine optimal values for the general policy (11.3).

Parma (1993) performed a retrospective analysis for Pacific halibut of the catch-age method. Due to probable trends in catchability and selectivity over time that were not incorporated into the model, there would have been a long period of time in which abundance was overestimated. The International Pacific Halibut Commission had recently inaugurated a constant harvest rate policy, taking 35% of exploitable biomass each year. Had that strategy been in place earlier, the population would have reached

historically low levels. Thus, a seemingly conservative strategy may turn out not to be conservative when there is failure of the model to handle important aspects of error and variability. Retrospective analysis is one tool for avoiding such problems. Further consideration of retrospective analysis is found in NRC (1998a).

11.3.3. Time-varying Harvest Control

Harvest control may be time varying in the sense that a different harvest control value is selected for each year in the future. Harvest controls can vary over time for a number of reasons. First, harvest controls often have time dependence near the beginning and end of the time horizon chosen for optimization (fishing-up and terminal-year effects). In the middle years they are often “state-dependent” harvest controls, such as harvest controls that are a function of the current biomass of the population like those discussed in section 11.3.2. Second, there are harvest controls that depend on year due to nonstationarity in the dynamics or environment, such as harvest controls linked to time dependent environmental cycles (Parma 1990), or harvest controls such as “pulse-fishing” rules that are linked to changes in age or size composition of the population (Clark 1976a, Botsford 1981b); more generally, controls vary because they are part of an adaptive management scheme (Smith and Walters 1981, Walters 1986). In either case, optimal harvest is calculated as the series of harvests $\{Y_t\}$, or, equivalently, fishing mortalities $\{F_t\}$, that optimize an objective function, possibly subject to constraints.

If the problem is not too complicated, analytical methods can be used to find the optimal solution. Analytical solutions have often been obtained with semelparous populations for a variety of objectives. For a linear utility function (e.g., harvest maximization) and no constraints under fairly general conditions, the optimal policy is derived to be a fixed escapement policy (Mendelsohn 1982, Clark 1985, Walters 1986). Such a policy is often called a “bang-bang” solution, in that no fishing occurs until a threshold level is reached and then maximal fishing effort is applied as long as the population stays high. However, Walters (1986) warned that such a simple solution is obtained only if the control function is linear.

If stochasticity is present, the optimal policy is still the same, but the fixed escapement level must be larger to counteract the uncertainty in the form of lognormal recruitment variability. However, the adjustment depends on details of the underlying spawner-recruit model; for example, Clark (1985) found that the two levels differed by no more than 5%, even if the coefficient of variation on recruitment was 100%, and that the loss in expected value was less than 1%.

The fixed escapement policy has as its principal advantages low biological risk because harvest rates are set to zero below an “optimal” escapement level and, under broad conditions, maximum discounted economic value (Mendelsohn 1979, Clark 1985). However, such policies trade off a lower variability in abundance of the stock for a higher variability in catches. For example, with an objective that emphasizes a smoother time sequence of catches, such as maximization of long-term geometric mean catch, the optimal policy for some models is a constant harvest rate policy (Deriso 1985b). Constant harvest rate policies have been shown to perform well in many simulation studies including some complex situations, such as when population dynamics change over time, called “nonstationary” production (Parma 1990, Walters and Parma 1996), or when there are multiple hypotheses about stock dynamics (Parma and Deriso 1990); other studies are discussed in other sections of this chapter.

For a discrete-time, deterministic, age-structured population model with density dependence, the maximum harvest objective is achieved by harvesting all members of one age class and possibly some of the previous class (Reed 1980, Getz and Haight 1989). In practice, this strategy cannot be used because the pattern of harvest by age is controlled by selectivity properties of the gear, availability of fish to the gear, fishing patterns, and perhaps regulation (Horwood and Whittle 1986b). It is still possible to derive maximum sustainable yield and related quantities for this age-structured population (Getz and Haight 1989). Given a fixed selectivity pattern, a sustainable fishing mortality that keeps the population at equilibrium can be derived (Lawson and Hilborn 1985, Quinn and Szarzi 1993). For stochastic age-structured populations, the usual result is a bang-bang control: do not fish at low population levels, fish hard at high population levels (Mendelsohn 1978, Reed 1979, Horwood and Whittle 1986b).

For a finite-time horizon, static optimization techniques, as in section 11.3.2, can often be used to find the optimal controls (Horwood 1987). For realistic solutions, some constraints are usually necessary; otherwise, the entire population will be harvested at the last time interval (Mendelsohn 1979, Sluzanowski 1984, Horwood 1987). Some possible constraints are restricting the ratio of fishing mortalities in successive years (e.g., $r_1 \leq F_{t+1}/F_t \leq r_2$), restricting fishing mortality to some maximum level, F_c (e.g., $0 \leq F_t \leq F_c$), and ensuring that biomass at the end of the planning horizon exceeds some critical level, B_c (e.g., $B_{n+1} \geq B_c$). Horwood (1987) applied this approach to a deterministic, age-structured population. The economic objective function (11.13) was used, along with the above constraints. The results depended on the discount rate and the planning horizon. The optimal solution consisted of three stages: a move toward a particular biomass level, an intermediate period which had either oscillatory or stable behavior, and a move downward at the end toward the minimum biomass constraint. This result is in line with the typical bang-bang solution: do not fish until biomass is at a suitable level and then fish hard if the abundance is high to take advantage of strong recruitment.

The method of dynamic programming has frequently been used to find optimal policies in many fields; a review directed toward fisheries problems is given by Cohen (1987). Applications in fisheries include those by Hilborn (1976), Mendelsohn (1979), Ludwig and Walters (1981, 1982), Walters (1981, 1986), Clark (1985), Deriso (1985b), Getz (1985), Mangel (1985), Horwood and Whittle (1986a,b), Hightower and Grossman (1987), Kope (1992), Criddle (1993), and Horwood (1993). The objective is to find the management policy that maximizes J_t , the total value function from current time t forward to an end time T , which is written as

$$\max_{\pi_t} J_t(\mathbf{x}_t | \pi_t) = \sum_{j=t}^T \beta^{j-t} U(\mathbf{x}_j | \pi_t), \quad (11.21)$$

where \mathbf{x}_t is the state vector at time t , π_t is the policy to be followed from time t to T , β is related to the discount factor [$\beta = \exp(-\delta)$], and U is the utility function (e.g., harvest, log harvest, profit, etc.). The policy $\pi_t = \{\mathbf{u}_t, \dots, \mathbf{u}_T\}$ is a sequence of controls, such as harvest rate functions, that are applied to the stock (or stocks) each year. As written in (11.21), J is a real-valued function that depends on the current state of the system, \mathbf{x} , and management policy, π . The state of the system, \mathbf{x} , could include multiple species and time-lagged abundances. All of the previous objective functions are subsumed in this equation. The planning horizon may be infinite ($T = \infty$).

The utility function U for year t depends only on current state of the system and current harvest control; thus, the maximum value of J_t , denoted by an asterisk, can be written as a function of current state, \mathbf{x}_t , in a recursive formula:

$$J_t^*(\mathbf{x}_t) = \max_{\mathbf{u}_t} [U(\mathbf{x}_t, \mathbf{u}_t) + \beta \max_{\pi_{t+1}} J_{t+1}(\mathbf{x}_{t+1} | \pi_{t+1})].$$

The state dynamics are governed by the general vector equation

$$\mathbf{x}_{t+1} = g(\mathbf{x}_t, \mathbf{u}_t). \quad (11.22)$$

Substitute (11.22) above to obtain the Bellman equation of dynamic programming:

$$J_t^*(\mathbf{x}_t) = \max_{\mathbf{u}_t} \{U(\mathbf{x}_t, \mathbf{u}_t) + \beta J_{t+1}^*[g(\mathbf{x}_t, \mathbf{u}_t)]\}. \quad (11.23a)$$

Stochastic elements, denoted ϵ_t , can be included in the state equations (11.22) by writing $g = g(\mathbf{x}_t, \mathbf{u}_t, \epsilon_t)$. The objective function is altered slightly to include an expected value operator, so that the resultant Bellman equation is given by

$$J_t^*(\mathbf{x}_t) = \max_{\mathbf{u}_t} \{U(\mathbf{x}_t, \mathbf{u}_t) + \beta E[J_{t+1}^*(g(\mathbf{x}_t, \mathbf{u}_t, \epsilon_t))]\}, \quad (11.23b)$$

where the expectation operator is taken across the stochastic elements in (11.22). For example, suppose the dynamic equation is a single-species model that has a scaled multiplicative lognormal element $\epsilon \sim N(0, 1)$, then

$$x_{t+1} = g(x_t, u_t, \epsilon_t) = \bar{g}(x_t, u_t) \exp(\epsilon_t \sigma). \quad (11.24)$$

We can then write (11.23b) as

$$J_t^*(x_t) = \max_{u_t} \left\{ U(x_t, u_t) + \frac{\beta}{\sqrt{2\pi}} \int_{-\infty}^{\infty} J_{t+1}^*[g(x_t, u_t, \epsilon \sigma)] \exp(-\epsilon^2/2) d\epsilon \right\}.$$

Operationally, dynamic programming proceeds starting at the last time, n , and working backward to time 0 (Clark 1985, Walters 1986). At each time, an optimal solution is found as a function of the state variables at that time. One problem with dynamic programming is the “curse of dimensionality,” in that the number of searches increases multiplicatively as the number of time values and the number of possible levels of the state variables increases. This problem is resolved by limiting the number of levels examined that the state variables are allowed to take. This set of values is called a grid. By searching over the grid of state variables and working backward in time, the optimal solution is found. The planning horizon n should be large enough to result in a stationary policy. Hightower and Grossman (1987) suggested that n should be 2–3 times the life span of the species.

A convenient numerical method for calculating (11.23b) is described by Ludwig and Walters (1982), which appears reliable for a number of related problems (such as in Parma 1990, Parma and Deriso 1990). The basic idea is to obtain a numerical approximation for the expectation by breaking up the integral into a finite number of

pieces with end points on a grid, $\epsilon(i)$, $i = 1, \dots, I$. The generic problem for the single-species model (11.24) is to evaluate the integral

$$E(x) = 1/\sqrt{2\pi} \int_{-\infty}^{\infty} J[g(x, u, \epsilon\sigma)] \exp(-\epsilon^2/2) d\epsilon$$

for a given state x and control u as a sum

$$E(x) = \sum_{i=1}^{I-1} E_i,$$

where

$$E_i = \int_{\epsilon(i)}^{\epsilon(i+1)} J[g(x, u, \epsilon\sigma)] \exp(-\epsilon^2/2) d\epsilon$$

and $J[g(x, u, \epsilon)]$ is approximated by an interpolation linear equation

$$J[g(x, u, \epsilon)] \approx a + b\tilde{g}(x, u) \exp(\epsilon_t \sigma).$$

The interpolation constants a, b are chosen so that J matches to previously calculated values at grid points $\epsilon(i)$ and $\epsilon(i+1)$. The grid on the state variable is chosen first, usually logarithmically spaced values are consistent with lognormal stochasticity. Then for each given x and u , the $\epsilon(i)$ grid point is chosen so that $x_i = g[x, u, \epsilon(i)\sigma]$, except for end points that are taken to be $\pm\infty$ to ensure complete integral coverage. Only 30–40 grid points are usually necessary for satisfactory approximation. Substitution of the interpolation equation into the formula for E_i produces a solution involving the standard cumulative normal density function.

The Bellman equation can be further generalized to allow for optimization under alternative hypotheses about dynamics governing future states of the system (Walters 1986, Parma and Deriso 1990). The resultant Bellman equation looks similar to (11.23b) for the important special case of Bayesian updating of odds of alternative hypotheses. For example, suppose there are H alternative hypotheses about the dynamics of the system—label them as alternative models $g_1 \dots g_H$. Bayes theorem can be used to update the current probability, $P_{t+1}(i)$, that model i is the correct model given a new observation x_{t+1} , as follows:

$$P_{t+1}(i) = \frac{P_t(i)p(x_{t+1}|\text{model } i \text{ is correct})}{\sum_j P_t(j)p(x_{t+1}|\text{model } j \text{ is correct})}, \quad (11.25)$$

where $p(x_{t+1}|\text{model } i \text{ is correct})$ is the probability of observing state x_{t+1} with model g_i . The Bellman equation (11.23b) generalizes to

$$\begin{aligned} J_t^*(\mathbf{x}_t, P_t) &= \max_{\mathbf{u}_t} \left\{ U(\mathbf{x}_t, \mathbf{u}_t) + \beta \sum_{j=1}^H P_t(j) E [J_{t+1}^*[g_j(\mathbf{x}_t, \mathbf{u}_t, \epsilon_t), P_{t+1}]] \right\} \\ &= \max_{\mathbf{u}_t} \left\{ U(\mathbf{x}_t, \mathbf{u}_t) + \beta E [J_{t+1}^*[g_j(\mathbf{x}_t, \mathbf{u}_t, \epsilon_t), P_{t+1}]] \right\}. \end{aligned} \quad (11.26)$$

This equation looks like (11.23b) except that the current odds of each of the alternative hypotheses is an argument of the J^* value function and the expectation operator \mathbf{E} is taken across both the PDF of the alternative hypotheses and the PDF of the stochasticity in the dynamics.

The Bellman equation (11.26) can be used to describe the primary classification of adaptive management strategies into two groups—namely, active adaptive management and passive adaptive management (Walters 1986, Walters and Ludwig 1987). In both, an optimal course of action is selected after evaluating the value J^* under the alternative models $g_1 \cdots g_H$. They differ in that the effect of current decisions on future learning is taken into account in the case of active adaptation, whereas it is neglected in the case of passive adaptation. Active learning takes place by choosing management actions that purposively attempt to alter the sequence $P_t \cdots P_T$, the probabilities of the alternative hypotheses from time t forward. Such alterations are explicitly incorporated into the decision analysis by the structure of (11.26) where the P_t is updated each year via Bayes theorem. To eliminate this active learning, we still apply (11.26), except we assume $P_{t+1} = P_t$ and replace P_{t+1} on the right side of (11.26) with P_t . These passive adaptive policies have been referred to as either “Bayes equivalent” (Mendelsohn 1980, Walters 1981) or “myopic Bayes” (Ludwig and Walters 1982). Although future learning is ignored in the calculations, the P_t will change as new data become available.

Several applications of numerical dynamic programming solutions have been undertaken. For example, Hilborn (1976), Walters (1981), and Kope (1992) determined optimal escapement solutions for Pacific salmon populations. Hightower and Grossman (1987) found optimal stock rebuilding solutions for a deterministic, age-structured population. They used a first-order gradient procedure and assumed that the initial state was known. Their optimal stock rebuilding solutions were thresholdlike: no fishing until the population rebuilt, followed by a period of varying constant fishing mortality. Their conclusion is consistent with the fixed-parameter search results of Quinn et al. (1990b). Sluzanowski (1984) determined maximum economic yield for an age-structured population with constant recruitment. Consistent with other studies, the optimal solution was bang-bang (no fishing when the population was below some level, maximum effort if the population was above that level).

An approximate solution to the dynamic programming problem may be obtained by using a perturbation technique (Horwood and Whittle 1986a,b, Horwood 1993). First, an optimal equilibrium solution is found. Then an approximation is made that is linear in the state variable and quadratic in the cost function, called the LQ approximation (Whittle 1982). The LQ optimal solution is linear in the state variable. The approach is easily generalized to include stochastic noise with nonzero covariance. Horwood and Whittle (1986a) applied the technique to a logistic surplus production model with constant yield, constant effort, and changing costs, to the Beverton-Holt yield-per-recruit model, and to the semelparous population model. Horwood and Whittle (1986b) also applied the perturbation technique to an age-structured population. The equilibrium age vector is found in two stages: first, the equilibrium proportionate age structure of the population is found for a particular fishing mortality and then the optimal equilibrium fishing mortality is found. The controls by age are linear functions of the population age vector. Horwood and Whittle suggested that the problems of dealing with multicohort optimization noted by Clark (1985) are partially resolved by this technique. In both papers, this approach does not work in some cases, suggesting that the optimal control

solution is extreme or oscillatory in these cases. Horwood (1993) applied the technique to a population with logistic dynamics, a multicohort fish population, and a predator-prey-pest complex. A variety of other solution techniques are given in texts on optimal control (see, e.g., techniques and bibliography in Mangel 1985).

Criddle (1993) combined structural models with time series models for use in solving multispecies, multiage-structured dynamic control problems. The structure of the model permits reasonable parameter estimates with small sample sizes, which is a major problem with time series models.

When multiple objectives exist, there must be some means of balancing the various objectives. Mendelsohn (1979) suggested limiting the class of policies to those that are "Pareto" optimal; that is, there is no other feasible policy that does better in one objective and at least as well in the others. He solved for the optimal solution with linear programming for the objective of obtaining a large expected, discounted value of the harvest and a small long-term risk of reducing the population.

11.4. BIOLOGICAL REFERENCE POINTS

For many fish populations, there is insufficient information available to determine optimal harvesting policies. Much attention has therefore been given in the literature to determining biological reference points (BRPs) that can be readily calculated from available information. As described below, these BRPs are usually fishing mortalities (F_m , $F_{0.1}$, $F_{35\%}$, $F = M$, etc.) or abundance levels (thresholds) and may be specified either as a target for optimal harvesting or a danger zone to be avoided (Leaman 1993).

11.4.1. Yield-Effort Parameters F_m and F_{ey}

A ubiquitous BRP is F_m , the fishing mortality that produces MSY. We have derived this parameter from a surplus production model (chapter 2), from a spawner-recruit relationship for a semelparous population (chapter 3), from a delay-difference model (chapter 5), and from an age-structured model (chapter 7). For age-structured populations, information on the spawner-recruit relationship, growth, and mortality must be available. If this information is available, then the dome-shaped equilibrium yield-fishing mortality curve can be constructed (figure 11.7), from which F_m and MSY can be obtained. For any of the population models in this book, harvesting at this rate leads in most cases to the population moving toward its most productive level, B_m , and to relatively high yields and low variation in yield compared to most other strategies. However, relatively few fish populations have sufficiently accurate estimates of MSY and F_m for these values to be used for management.

An alternative fishing mortality drawn from this curve, called F_{ey} for "efficient yield" (Deriso 1987), is analogous to $F_{0.1}$ described in chapter 6 and in section 11.4.3. It corresponds to the fishing mortality that results in a marginal increase of 10% in equilibrium yield compared to that at $F = 0$. It is found that taking 10% of the slope at the origin and finding where on the curve this value occurs (figure 11.7). Deriso (1987) derived relationships between F_{ey} , $F_{0.1}$, and F_m and defined the generalized efficient yield fishing mortality, $F_{0.x}$, at equilibrium for a slope value $0.x$ as

$$\left. \frac{dY}{dF} \right|_{F=F_{0.x}} = 0.x \left. \frac{dY}{dF} \right|_{F=0} \quad (11.27)$$

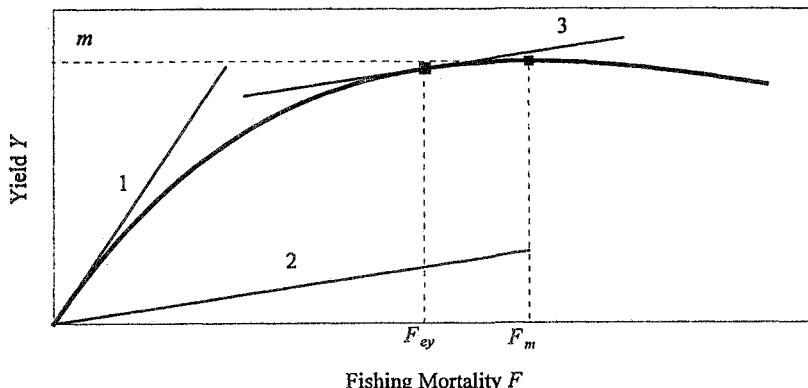


Figure 11.7. Biological reference points F_m ($m \equiv \text{MSY}$) and F_{ey} from the equilibrium yield–fishing mortality relationship. 1, Slope of curve at origin, 2, 10% of slope at origin, 3, point on curve where slope is 10% of origin.

A similar concept is presented by Andrew and Butterworth (1987), where they argued that the x to choose in $F_{0,x}$ should differ for different hake stocks of the Benguela region of South Africa.

11.4.2. Natural Mortality Parameter M

Being able to determine F_m requires substantial information about the population, particularly the spawner-recruit relationship. As there is usually great uncertainty in this relationship, researchers have long sought surrogates for F_m . In the 1960s and early 1970s, Alverson and Pereyra (1969) and Gulland (1970, 1971) suggested the use of natural mortality, M , because the rate of production should be directly related to natural mortality. By appeal to the Graham-Schaefer production model in chapter 2, one could then determine MSY and equilibrium biomass level, B_m , at MSY as

$$\text{MSY} = 0.5MB_\infty = MB_m \quad \text{and} \quad B_m = 0.5B_\infty,$$

given a value for pristine biomass, B_∞ . Although natural mortality is subject to great uncertainty, several methods are available for its estimation (section 8.3). Francis (1993a) used $F_{0.1}$ in place of M in the MSY equation, under the assumption that $F_{0.1}$ is a surrogate for F_m , an approximation which is discussed in later sections. Garcia et al. (1989) investigated similar simple relationships to estimate MSY.

The equivalence between F_m and M is false under most conditions in the Graham-Schaefer production model (Francis 1974). Deriso (1982) further explored the relationship between F_m , M , and growth parameter ρ by using a delay-difference model. Use of the delay-difference model (5.12) with a logistic spawner-recruit model produced more conservative results than the production model, the main difference between them being the separation of fishing and natural mortality in the former. The spawner-recruit model is written

$$\mathcal{F}_B(S) = S(\alpha - \beta S),$$

which has zero recruitment at $S = 0$ and $S = \alpha/\beta$ and maximum recruitment at $S = \alpha/2\beta$. Pristine biomass from (5.13) under no fishing ($S = B$) occurs when

$$R_r(\alpha - \beta S_\infty) = 1,$$

where $R_r = [(1 - \rho\ell)(1 - \ell)]^{-1}$ is reproductive value of an age r fish under no fishing. The solution can be written as $S_\infty = c\alpha/\beta$, where $\alpha = [R_r(1 - c)]^{-1}$. Parameter c is a measure of density dependence; as c nears 1, recruitment nears 0.

When fishing occurs, the annual exploitation fraction can be written $\mu = 1 - \exp(-F)$, and equilibrium occurs when

$$R_r^*(\alpha - \beta S_*) = 1,$$

where reproductive value of an age r fish under exploitation is given by

$$R_r^* = (1 - \mu)\{[(1 - \rho\ell(1 - \mu))[1 - \ell(1 - \mu)]]\}^{-1}.$$

The general equilibrium solution for the delay-difference model in terms of μ_* from Deriso (1980, 1982) is

$$R_r \mathcal{F}'(S_*) = 1 - \rho\ell^2 R_r \mu_*^2.$$

[This is just (5.13) for any equilibrium level.] Combining these two relationships (noting that $\mathcal{F}'(S_*) = \alpha - 2\beta S_*$) leads to a relationship between natural mortality, ℓ , exploitation rate, μ_* , growth, ρ , and density dependence parameter c :

$$2 \frac{R_r}{R_r^*} - \frac{1}{1 - c} = 1 - \rho\ell^2 R_r \mu_*^2.$$

Evaluating this equation at μ_m gives relationships at the MSY level.

Comparing values of $\mu = 1 - \exp(-F)$ and $1 - \ell = 1 - \exp(-M)$ for various values of ρ and c is equivalent to comparing values of F and M . As shown by Deriso (1982, table 2), reproduced here as table 11.2, MSY exploitation fraction, μ_m , is less than annual natural mortality, $1 - \ell$, in almost all cases for values of ρ between 0.1 and 1.0 and values of c between $\frac{1}{2}$ and $\frac{3}{4}$. The exception is when growth and natural mortality are low and density dependence parameter c is high, the latter condition imposing severe depression of recruits in the unfished population. Therefore, M can be viewed as an upper bound for F_m rather than a surrogate in most cases.

Further support for the view of M as an upper bound comes from Thompson (1993). By application of a dynamic pool model, Thompson showed that a fishing mortality under $0.8M$ should keep spawning stock biomass per recruit (SPR) above 30% of the SPR when no fishing occurs. Thompson further argued that the 30% level would keep a stock from collapsing in a model containing a depensatory spawner-recruit relationship. Thus,

Table 11.2. Range of exploitation fractions, μ , corresponding to a range of growth values ($\rho = 0.1$ –1.0) and specified natural mortality ($1 - \ell$) and constant c (from Deriso 1982, table 2).

Natural mortality	$c = 1/2$	$c = 2/3$	$c = 3/4$
0.2	0.05 – 0.09	0.08 – 0.16	0.11 – 0.22
0.4	0.10 – 0.26	0.18 – 0.28	0.24 – 0.36
0.6	0.17 – 0.23	0.29 – 0.37	0.37 – 0.47
0.8	0.25 – 0.28	0.39 – 0.44	0.49 – 0.54

fishing at $F = M$ may not be sustainable for some populations. Further discussion of SPR relationships is given below (section 11.4.7).

11.4.3. Yield-per-Recruit Parameter F_{\max}

In chapter 6, the year-class or dynamic pool model was presented. Under the assumption of knife-edge selectivity, the two control parameters in this model are fishing mortality, F , and age of entry, t_c . The most common objective has been to maximize yield per recruit, Y/R , with respect to the control parameters. In chapter 6, it was shown that the maximum yield per recruit, Y/R , is obtained by applying infinite fishing mortality at the critical size, t^* , where maximum cohort biomass occurs. More useful finite-value solutions can be found for three conditional objectives, after Fletcher (1987): (1) given F , maximize Y/R with respect to age of entry t_c (finding $t_{c \max}$), (2) given t_c , maximize Y/R with respect to F (finding F_{\max}), (3) given Y/R , minimize F with respect to t_c (finding $t_{c \min}$).

We write recruitment, R , as N_r to show the reference age, r . To solve problem 1, (6.7) is rewritten as

$$Y = FN_r e^{Mt_r + Ft_c} \int_{t_c}^{t_\infty} e^{-Zt} W(t) dt = FN_c e^{Zt_c} I, \quad (11.28)$$

where I is the integral in (11.28). The maximum yield per recruit is found by taking the derivative with respect to t_c and setting to 0:

$$\begin{aligned} \frac{\partial Y}{\partial t_c} &= FN_r e^{Mt_r + Ft_c} (FI - e^{-Zt_c} W_c) = 0 \\ \Rightarrow \max Y/N_c &= FI e^{Zt_c} = W_c. \end{aligned} \quad (11.29)$$

Thus, the solution to problem 1 is to adjust t_c so that the maximum yield per recruit is equal to the entry weight of an individual. Examination of (11.29) also indicates that total maximum yield can be as great as cohort biomass at entry.

Further insight can be gained by considering the average weight of an individual in the harvest, or

$$\bar{W} = \frac{Y}{C} = \frac{\int FN W dt}{\int FN dt} = \frac{I}{\int e^{-Zt} dt} = \frac{I}{(E/F)e^{-Zt_c}},$$

where E is the exploitation fraction, $(F/Z)[1 - e^{-Z(t_\infty - t_c)}]$. Rearranging and substituting for I in (11.29) results in the condition

$$\bar{W}E = W_c \quad \Rightarrow \quad E = W_c/\bar{W}. \quad (11.30)$$

This condition states that to maximize yield per recruit given F , exploitation rate must be equal to the ratio of entry weight to average weight of the catch. Note that the right-hand side of (11.30) is calculable given a growth curve. As $t_\infty \rightarrow \infty$, $E \rightarrow F/Z$. The approximation $F/Z \approx W_c/\bar{W}$ from (11.30) is known as Allen's condition. Fletcher (1987) performed an error analysis to explore the sensitivity of the approximation.

To solve problem 2, the maximum yield per recruit is found by taking the derivative of the rightmost expression in (11.28) with respect to F and setting to 0:

$$\begin{aligned} \frac{1}{N_c} \frac{\partial Y}{\partial F} &= e^{Zt_c} I + F \left[t_c e^{Zt_c} I - e^{Zt_c} J \right] = 0 \\ \Rightarrow I + F t_c I - F J &= 0, \end{aligned} \quad (11.31)$$

where

$$J = \int_{t_c}^{t_\infty} t e^{-Zt} W(t) dt.$$

Solving for F in (11.31) results in the condition

$$F_{\max} = \frac{1}{(J/I) - t_c} = \frac{1}{\bar{t}_w - t_c}, \quad (11.32)$$

where \bar{t}_w is the mean age of year-class biomass in the harvest (J/I). Thus, the inverse of the difference between mean age and age of entry is the fishing mortality that maximizes Y/R for fixed t_c .

The solution to problem 3 is obtained by taking the derivative of (11.28) with respect to t_c for fixed Y and setting $\partial F/\partial t_c$ to 0. As shown by Fletcher (1987), the solution $t_{c,\min}$ is identical to that for problem 1. Thus the problems of maximizing Y/R given F and minimizing F given Y/R with respect to t_c have the same solution, although they clearly involve different objectives.

Example 11.2. Sablefish in the Gulf of Alaska

This example illustrates the use of F_{\max} using the LVB isometric model described in chapter 6 (see examples 6.1 and 6.2). The values E_{\max} and F_{\max} were determined by trial and error at various values of E (table 11.3) using a table similar to table 6.2. For larger values of l_c , exploitation rates near 1 are obtained. The optimal $E_{\max} = 1$ occurs at a critical size of 67 cm. For no minimum size limit ($l_r = l_c = 37$ cm), the value of E_{\max} is 0.62, and its location on a yield-per-recruit plot is shown in figure 11.8. If fishing was at the rate F_{\max} , then imposition of a minimum size limit ($L_c > 37$ cm) would improve yield per recruit. But the recommended sablefish exploitation rate is usually much lower than E_{\max} ($E \approx 0.1$), so a minimum size limit would not lead to an increase in yield per recruit. ■

Table 11.3. Exploitation fraction, fishing mortality, and yield per recruit for the F_{\max} and $F_{0.1}$ criteria for Gulf of Alaska sablefish, along with the value obtained from making the sides of (11.45) equal.

	L_c								
	37	47	57	60	62	67	72	77	81
E_{\max}	0.617	0.704	0.823	0.868	0.901	1.000	1.000	1.000	1.000
F_{\max}	0.161	0.237	0.465	0.656	0.907	∞	∞	∞	∞
Y/R_{\max}	1.202	1.364	1.531	1.573	1.597	1.627	1.541	1.187	0.473
(11.45)	0.188	0.254	0.360	0.404	0.436	0.535	0.656	0.809	0.959
$E_{0.1}$	0.465	0.510	0.560	0.575	0.586	0.612	0.637	0.661	0.679
$F_{0.1}$	0.087	0.104	0.127	0.135	0.141	0.158	0.175	0.195	0.212
$Y/R_{0.1}$	1.110	1.228	1.314	1.322	1.319	1.271	1.136	0.838	0.325

Values for the optimal F_{\max} and $F_{0.1}$ criteria are highlighted in bold.

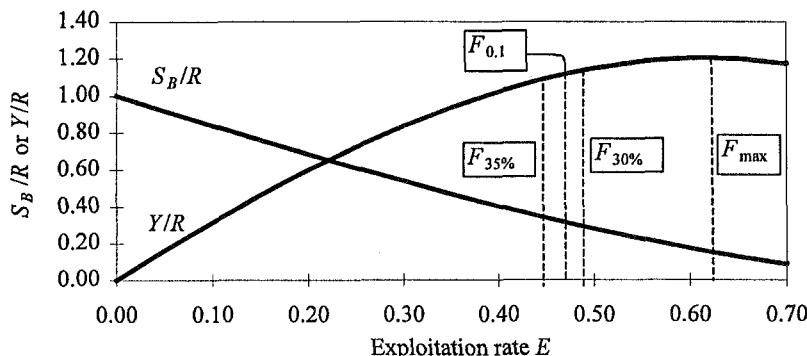


Figure 11.8. A plot of yield per recruit, Y/R , and spawning biomass per recruit, S_B/R (standardized to 1 at $E = 0$), as a function of exploitation rate, E , with no minimum size limit ($t_r = t_c$) for the sablefish example. Corresponding biological reference points are also shown.

Example 11.3. Rainbow trout in Blue Lake, Sitka, Alaska

This example illustrates the generic approach (section 6.3) for calculating per-recruit statistics related to F_{\max} using the rainbow trout example from chapter 6 (see example 6.4). One generic BRP was the fishing mortality, $F_{\max,5+}$, that maximized catch of mostly mature fish of ages 5+. The other generic BRP was the fishing mortality, $F_{Y\max}$, that maximized yield of all fish. Solutions were found by trial and error.

Age-specific values for fishing mortality, abundance, and exploitation fraction per 100 recruits are given in table 11.4. Corresponding catch and yield per 100 recruits are given in table 11.5. Presentation of the results by age allows determination of the effect of fishing mortality on the population.

Catch per recruit increases asymptotically as F increases (table 11.5, figure 11.9). The maximum catch occurs by applying infinite fishing pressure at the age of recruitment. As F increases, the age composition of the population shifts to lower ages (table 11.4), with resultant decreases in catch and yield of older ages. As suggested by Quinn and Szarzi (1993), an alternative management strategy to maximizing yield per recruit is to maximize catch or yield of older ages—say, those ages with essentially fully mature fish (ages 5+). Maximum catch of these older ages occurs at $F_{C\max,5+} = 0.43$. Maximum yield per recruit occurs at $F_{Y\max} = 0.94$, which is much higher. ■

11.4.4. Relationships among F_m , F_{\max} , and F_p

By examining the slopes of the yield-effort, yield per recruit, and spawner-recruit curves, certain relationships among their fishing mortality parameters emerge at equilibrium for a simple population model. Following Deriso (1982, 1987), suppose that the following system of equations describes a population at equilibrium:

$$\text{Spawner-recruit relationship } R = \mathcal{F}(S) \quad (11.33a)$$

$$\text{Relationship between yield and YPR } Y = (Y/R)R \quad (11.33b)$$

$$\text{Relationship between yield and spawning stock } Y = FS \quad (11.33c)$$

Age of entry, t_c , is implicitly defined by the definition of the population; i.e., knife-edge selectivity applies to the entire population defined by (11.33). Taking the derivative

Table 11.4. Calculations of fishing mortality, abundance, and exploitation fraction for selected biological reference points for Blue Lake rainbow trout.

F	Age					Avg.
	3	4	5	6	7	
Fishing mortality, F_a						
Unfished	0.00	0.00	0.00	0.00	0.00	0.00
$F_{0.2}$	0.39	0.24	0.36	0.39	0.23	0.29
$F_{Cmax,5+}$	0.43	0.26	0.40	0.43	0.26	0.32
$F_{0.1}$	0.53	0.32	0.49	0.53	0.32	0.40
$F_{SN50\%}$	0.55	0.34	0.51	0.55	0.33	0.41
$F_{SB35\%}$	0.64	0.39	0.59	0.64	0.38	0.48
$F_{0.05}$	0.66	0.40	0.61	0.66	0.40	0.49
$F_{SB30\%}$	0.76	0.46	0.70	0.76	0.46	0.57
F_{Ymax}	0.94	0.57	0.86	0.94	0.56	0.70
$F_{SN35\%}$	0.99	0.60	0.91	0.99	0.59	0.74
Abundance, N_a, per 100 recruits						
						<u>Sum 3+</u> <u>Sum 5+</u>
0.00	100	77	59	46	35	318 141
0.39	100	61	33	17	10	221 60
0.43	100	59	31	15	9	215 55
0.53	100	56	26	12	7	201 45
0.55	100	55	26	11	6	198 43
0.64	100	52	22	9	5	188 36
0.66	100	52	22	9	4	186 35
0.76	100	49	19	7	3	177 29
0.94	100	43	14	4	2	164 20
0.99	100	42	13	4	2	161 18
Exploitation Fraction, μ_a						
	F	3	4	5	6	7
0.00	0.00	0.00	0.00	0.00	0.00	0.00
0.39	0.19	0.27	0.29	0.18	0.18	0.22
0.43	0.20	0.29	0.31	0.20	0.20	0.24
0.53	0.24	0.34	0.37	0.24	0.24	0.29
0.55	0.25	0.35	0.38	0.25	0.25	0.30
0.64	0.29	0.40	0.42	0.28	0.28	0.33
0.66	0.29	0.41	0.43	0.29	0.29	0.34
0.76	0.33	0.45	0.48	0.33	0.33	0.38
0.94	0.39	0.52	0.55	0.38	0.38	0.44
0.99	0.40	0.54	0.57	0.40	0.40	0.45

C, catch; N, abundance; B, biomass; F, fishing mortality; μ , exploitation fraction; S, spawning; 5+, ages 5 and older.

of (11.33b) with respect to F and using the chain rule $dR/dF = \mathcal{F}'(S)dS/dF$ results in

$$\frac{dY}{dF} = R \frac{d(Y/R)}{dF} + (Y/R)\mathcal{F}'(S) \frac{dS}{dF}. \quad (11.34)$$

Taking the derivative of (11.33c) and rearranging results in

$$\frac{dS}{dF} = \left(\frac{dY}{dF} - S \right) / F. \quad (11.35)$$

Table 11.5. Calculations of catch and yield for selected biological reference points for Blue Lake rainbow trout.

F	Age					Sum 3+	Sum 5+
	3	4	5	6	7		
Catch, C_a, per 100 Recruits							
Unfished	0.00	0	0	0	0	0	0
$F_{0.2}$	0.39	19	16	9	3	2	49
$F_{C_{max},5+}$	0.43	20	17	10	3	2	52
$F_{0.1}$	0.53	24	19	10	3	2	58
$F_{SN50\%}$	0.55	25	19	10	3	2	59
$F_{SB35\%}$	0.64	29	21	9	3	1	63
$F_{0.05}$	0.66	29	21	9	3	1	64
$F_{SB30\%}$	0.76	33	22	9	2	1	67
$F_{Y_{max}}$	0.94	39	23	8	2	1	72
$F_{SN35\%}$	0.99	40	23	7	1	1	73
Yield, Y_a, per 100 Recruits (kg)							
	0.00	0.0	0.0	0.0	0.0	0.0	0.0
	0.39	2.9	4.4	3.8	1.7	1.3	14.1
	0.43	3.2	4.7	3.9	1.7	1.2	14.6
	0.53	3.8	5.2	3.9	1.6	1.1	15.6
	0.55	3.9	5.3	3.9	1.5	1.0	15.7
	0.64	4.5	5.6	3.8	1.4	0.9	16.2
	0.66	4.6	5.7	3.8	1.3	0.9	16.3
	0.76	5.1	5.9	3.6	1.2	0.7	16.5
	0.94	6.1	6.1	3.1	0.9	0.5	16.7
	0.99	6.3	6.2	3.0	0.8	0.4	16.7

Substituting (11.35) into (11.34) and noting that $F = Y/S$ from (11.33c) results in (after several steps)

$$\frac{dY}{dF} = \frac{R \frac{d(Y/R)}{dF} - S(S/R)\mathcal{F}'(S)}{1 - (S/R)\mathcal{F}'(S)}, \quad (11.36)$$

which shows that the slopes of the yield-effort, yield per recruit-effort, and recruit-spawner curves are all interrelated.

We use subscripts m for MSY, p for maximum recruitment, and “max” for maximum yield per recruit. At MSY from (11.36),

$$\frac{dY}{dF} = 0 \quad \Rightarrow \quad \left. \frac{d(Y/R)}{dF} \right|_{F=F_m} = (S/R)_m^2 \mathcal{F}'(S_m), \quad (11.37)$$

showing that the slope of the yield-per-recruit curve at MSY is a function of spawners per recruit (SPR) and the slope of the spawner-recruit curve at MSY. Thus, if $\mathcal{F}'(S_m) \geq 0$, then $d(Y/R)/dF \geq 0$, and for typically unimodal yield per recruit curves, this implies that $F_{max} \geq F_m$. Most spawner-recruit curves will have positive slope at MSY; it is always true for semelparous populations and monotonic spawner-recruit curves and usually true for dome-shaped curves except in cases of strong overcompensation. Thus, one would expect F_{max} to be greater than F_m in most situations.

At maximum recruitment from (11.36),

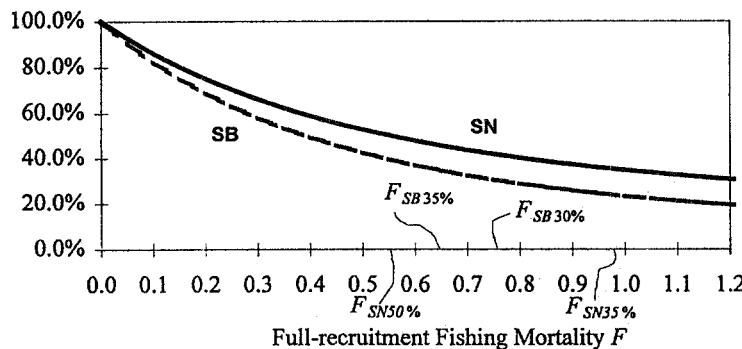
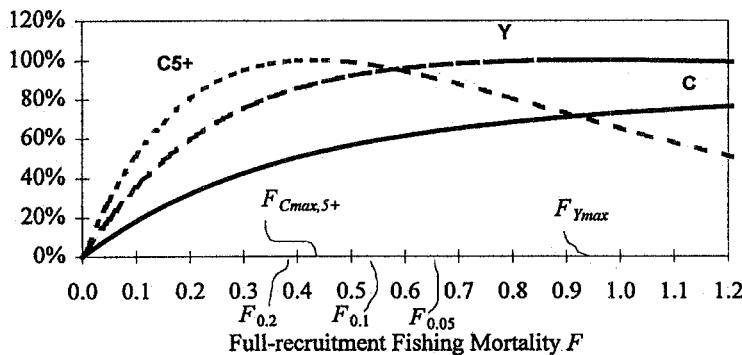


Figure 11.9. Per-recruit curves for the Blue Lake rainbow trout example of yield, Y , catch, C , catch of older fish, C_{5+} , spawning abundance, S_N , and spawning biomass, S_B , as a function of full-recruitment fishing mortality control parameter F . Corresponding BRPs are also shown.

$$\mathcal{F}'(\mathcal{S}_p) = 0 \quad \Rightarrow \quad \left. \frac{dY}{dF} \right|_{F=F_p} = R_p \left. \frac{d(Y/R)}{dF} \right|_{F=F_p}, \quad (11.38)$$

showing that the slopes of the yield and yield per recruit curves are proportional. Indeed, if there is no relationship between recruits and spawners, then R can be considered constant and the slope of the spawner-recruit curve is 0 everywhere. In (11.38), $d(Y/R)/dF = (1/R)(dY/dF)$, so that (11.38) is a tautology. This result is not surprising because at equilibrium, the yield from a cohort over its lifetime should be the same as the yield of several cohorts in the same year if there is no spawner-recruit relationship (i.e., the synthetic cohort and the true cohort are equivalent).

At maximum yield per recruit from (11.36),

$$\begin{aligned} & \left. \frac{d(Y/R)}{dF} \right|_{F=F_{\max}} = 0 \\ & \Rightarrow \left. \frac{dY}{dF} \right|_{F=F_{\max}} = \frac{-\mathcal{S}_{\max}(\mathcal{S}/R)_{\max} \mathcal{F}'(\mathcal{S}_{\max})}{1 - (\mathcal{S}/R)_{\max} \mathcal{F}'(\mathcal{S}_{\max})}. \end{aligned} \quad (11.39)$$

As (R/\mathcal{S}) is the slope of the chord connecting $(0, 0)$ to the point (R, \mathcal{S}) on a spawner-recruit curve, that slope must be less than the tangent of the curve at that point for

nondecreasing curves. Thus, $\mathcal{F}'(\mathcal{S}) \leq R/\mathcal{S}$, so that the denominator of (11.39) is non-negative. Therefore, the slope of the yield-effort curve at the maximum yield-per-recruit point is negative if the slope of the spawner-recruit curve at that point is positive. For a unimodal yield-effort curve, this condition implies that $F_m < F_{\max}$.

11.4.5. Yield-per-Recruit Parameter $F_{0.1}$

Experience with using F_{\max} suggested that it led to harvests that were too high (Anthony 1982). As shown in section 11.4.4, F_{\max} is frequently greater than F_m , which backs up this experience. In the 1970s and 1980s, an alternative to F_{\max} was sought which would be lower but yet still use the yield-per-recruit formulation with its modest data requirements (Gulland and Boerema 1973, Anthony 1982, Doubleday et al. 1984). The argument was that the relative gain in yield per recruit diminished as fishing mortality approached F_{\max} and that the last marginal increment of fishing effort was economically inefficient.

Thus, it was recommended that the optimal fishing mortality, called $F_{0.1}$, might be the point at which the marginal gain in yield per recruit decreased to an arbitrary 10% from that at $F = 0$. Mathematically, this can be written for a desired marginal gain 0.x as

$$\frac{dY}{dF} \Big|_{F=F_{0.1}} = (0.x) \frac{dY}{dF} \Big|_{F=0}, \quad (11.40)$$

where Y is the yield from a cohort and usually expressed on a per-recruit basis. Graphically, $F_{0.1}$ is the point on the yield-per-recruit curve (as a function of fishing mortality) where the slope of the curve is 10% of the slope at the origin (figure 11.10). Experience with $F_{0.1}$ suggested that it was usually a conservative rate, and it rapidly became the most used BRP in the 1980s (e.g., Hollowed and Megrey 1993, Leaman 1993, Rivard and Maguire 1993).

Deriso (1987) derived theoretical principles associated with $F_{0.1}$. The general yield-per-recruit formulation with knife-edge selectivity from chapter 6 and section 11.4.3 can be written

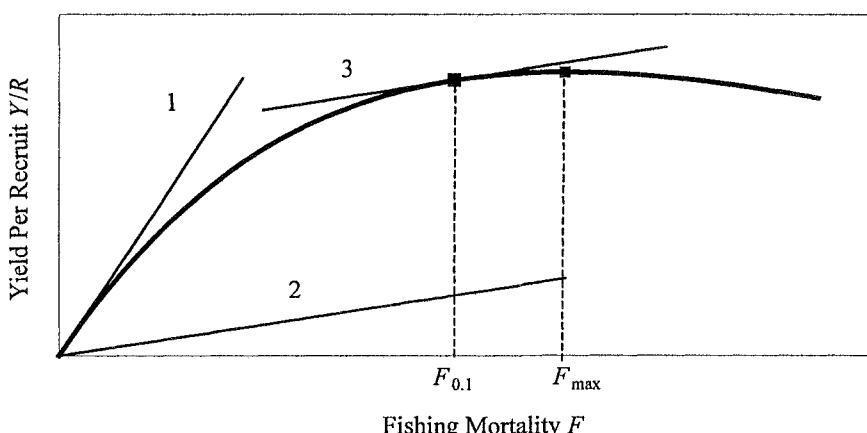


Figure 11.10. Biological reference points F_{\max} and $F_{0.1}$ from the yield per recruit–fishing mortality relationship (after Deriso 1987). 1, Slope of curve at origin, 2, 10% of slope at origin, 3, point on curve where slope is 10% of origin.

$$Y = \int_{t_c}^{t_\infty} FN(t)W(t)dt = FN_c \int_{t_c}^{t_\infty} e^{-(F+M)(t-t_c)} W(t)dt. \quad (11.41)$$

The derivative of yield with respect to F is then

$$\begin{aligned} \frac{dY}{dF} &= N_c \int_{t_c}^{t_\infty} e^{-(F+M)(t-t_c)} W(t)dt \\ &\quad - FN_c \int_{t_c}^{t_\infty} (t - t_c) e^{-(F+M)(t-t_c)} W(t)dt. \end{aligned} \quad (11.42)$$

Substituting (11.42) into the criterion (11.40) and eliminating N_c produces

$$\begin{aligned} \int_{t_c}^{t_\infty} e^{-(F_{0.1}+M)(t-t_c)} W(t)dt - F_{0.1} \int_{t_c}^{t_\infty} (t - t_c) e^{-(F_{0.1}+M)(t-t_c)} W(t)dt \\ = (0.1) \int_{t_c}^{t_\infty} e^{-M(t-t_c)} W(t)dt \\ \Rightarrow (B/\tilde{R})_{F=F_{0.1}} - F_{0.1}(\bar{t}_w - t_c)(B/\tilde{R})_{F=F_{0.1}} = (0.1)(B/\tilde{R})_{F=0}, \end{aligned} \quad (11.43)$$

where (B/\tilde{R}) is biomass per age- t_c recruit \tilde{R} ($\int NW dt/N_c$) and \bar{t}_w is average age of cohort biomass, defined in section 11.4.3. Solving for $F_{0.1}$ in (11.43) gives

$$F_{0.1} = \frac{1 - (0.1)(B/\tilde{R})_{F=0}/(B/\tilde{R})_{F=F_{0.1}}}{\bar{t}_w - t_c} < \frac{0.9}{\bar{t}_w - t_c},$$

because (B/\tilde{R}) is highest at $F = 0$. In contrast, $F_{\max} = 1/(\bar{t}_w - t_c)$ from (11.32), showing that $F_{0.1}$ is at least 10% less than F_{\max} . Analogously, $F_{0.x}$ is at least $x\%$ less than F_{\max} .

A closed-form solution for calculating $F_{0.1}$ can be found for the LVB isometric model (6.12) described in chapter 6. As that model is parameterized in terms of exploitation fraction, $E = F/(F + M)$, instead of F , the $F_{0.1}$ criterion (11.40) (with $x = 1$) must first be reexpressed. From the chain rule,

$$\frac{dY}{dF} = \frac{dY}{dE} \left(\frac{dE}{dF} \right) = \frac{dY}{dE} \left[\frac{M}{(F+M)^2} \right] = \frac{dY}{dE} \left[\frac{(1-E)^2}{M} \right].$$

Substituting into the $F_{0.1}$ criterion,

$$\begin{aligned} \frac{dY}{dE} \Big|_{E=E_{0.1}} \frac{(1-E_{0.1})^2}{M} &= \frac{(0.1)}{M} \frac{dY}{dE} \Big|_{E=0} \\ \Rightarrow \frac{dY}{dE} \Big|_{E=E_{0.1}} &= \frac{(0.1)}{(1-E_{0.1})^2} \frac{dY}{dE} \Big|_{E=0}. \end{aligned} \quad (11.44)$$

Note that $E_{0.1}$ is the exploitation rate corresponding to $F_{0.1}$; it is *not* the point where the slope is 10% of that at the origin on a yield-exploitation rate curve.

As the criterion (11.44) applies to any proportionate quantity of yield per recruit, we carry on in terms of percentage lifetime yield

$$y = E \sum_{n=0}^3 \frac{U_n(1-c)^{n+m}}{1+n(1-E)/m}$$

from (6.12). Its derivative can be derived as

$$\frac{dY}{dE} = \sum_{n=0}^3 \frac{U_n(1-c)^{n+m}}{[1+n(1-E)/m]^2} (1+n/m).$$

Substituting into (11.44),

$$\begin{aligned} & \sum_{n=0}^3 \frac{U_n(1-c)^n}{[1+n(1-E_{0.1})/m]^2} (1+n/m) \\ &= \frac{0.1}{(1-E_{0.1})^2} \sum_{n=0}^3 \frac{U_n(1-c)^n}{[1+n/m]}. \end{aligned} \quad (11.45)$$

With this implicit solution, the numerical value of $E_{0.1}$ can be obtained using trial and error or numerical methods. The corresponding value of $F_{0.1}$ is obtained from the relationship $F = EM/(1-E)$. Likewise, E_{\max} can be found by setting the left hand side of (11.45) to 0.

Because $F_{0.1}$ is implicitly a function of t_c , it is not uniquely defined unless t_c is set. Unlike F_{\max} , however, yield per recruit peaks as a function of t_c when fishing at $F = F_{0.1}$. The policy of constraining fishing mortality to $F_{0.1}$ and then maximizing yield per recruit as a function of t_c is called the *optimal* $F_{0.1}$ criterion. The optimal $F_{0.1}$ level is a function of $m = M/\kappa$ and is approximately equal to M over the range $1 < m < 4$ (Deriso 1987). More generally, Deriso (1987) gave the optimal policy parameters by approximation to exponential cubic polynomials, which are reproduced in table 11.6. The calculations of the optimal $F_{0.1}$ policy for three stocks are shown in the Deriso (1987) essay.

Deriso (1987) also explored the relationships among $F_{0.1}$ and absolute yield parameters F_m and F_{ey} described in section 11.4.1. For the Ricker spawner-recruit model, there is one value of productivity parameter α for which $F_m = F_{0.1}$; for a more pro-

Table 11.6. Polynomial coefficients used to approximate the optimal $F_{0.1}$ criteria parameters listed in the table (c_{opt} , optimal relative size; c^* , the relative size at critical age t^*).

Policy parameter	A_0	A_1	A_2	A_3
c_{opt}	-0.072	-0.392	0.063	-0.006
$E_{0.1}$	-0.400	-0.263	0.079	-0.009
$F_{0.1}/M$	0.699	-0.698	0.236	-0.029
c_{opt}/c^*	-0.070	-0.068	0.022	-0.003

Approximation is based on the function $f(m) = \exp(A_0 + A_1m + A_2m^2 + A_3m^3)$ where $m = M/\kappa$ is in the range $0.1 < m < 4$ (from Deriso 1987, table 1).

ductive population, $F_m > F_{0.1}$ and vice versa. Similarly, there is a higher value of α for which $F_{ey} = F_{0.1}$. Deriso suggested that the optimal $F_{0.1}$ criterion can be adapted to a multispecies setting and a changing environment by letting M and κ change slowly over time. Thus, m and consequently optimal $F_{0.1}$ would also change slowly over time.

Example 11.4. Sablefish in the Gulf of Alaska

This example illustrating the Beverton-Holt approach follows from example 11.2. In table 11.3, the $E_{0.1}$ values that solve (11.45) and the corresponding values of $F_{0.1}$ and yield per recruit are given for several values of l_c . The $F_{0.1}$ value for no minimum size limit shown in figure 11.8 is smaller than F_{\max} as expected. The optimal $F_{0.1}$ criterion leads to a recommended minimum size limit of 60 cm, a finite fishing mortality of 0.13, and Y/R of 1.30 kg (table 11.5). For this size limit of 60 cm, the corresponding value of F_{\max} is much larger but the gain in Y/R is small ($Y/R = 1.40$ kg). ■

Example 11.5. Rainbow trout in Blue Lake, Sitka, Alaska

This example illustrating the generic approach follows from example 11.3. The slope at the origin of the Y/R versus F curve is approximated numerically from the Y/R values at $F = 0$ and $F = 0.01$ (0 and 0.70, respectively), which gives a slope of 70. The slope is calculated analogously at other points on the curve, from which $F_{0.1} = 0.53$ can be found as the point where the slope is 0.1 of that at the origin. Per-recruit calculations corresponding to this F are given in tables 11.4 and 11.5. Also given are the calculations for $F_{0.05} = 0.66$ and $F_{0.2} = 0.39$, which were found analogously. These points are indicated on the Y/R curve (figure 11.9). ■

Brody-LVB weight-age model

Useful closed-form results are also obtained with the Brody-LVB model of section 6.1.3. The derivative of the lifetime percentage yield equation (6.19) is

$$\frac{\partial y}{\partial E} \Big|_{E=0} = (1 - c')^{m'} \left(\frac{1 + m'c'}{1 + m'} \right),$$

the *marginal* yield at $E = 0$. Because it is also the maximum marginal yield (for any $E \geq 0$), it is a convenient benchmark against which we can compare the marginal yield at any other fixed $E > 0$. In particular, we can find the value of E , say E'_p , where

$$\frac{\partial y}{\partial E} \Big|_{E=E'_p} = p \frac{\partial y}{\partial E} \Big|_{E=0}$$

As $p \rightarrow 0$, E'_p approaches the exploitation rate at the maximum of the y curve (where $F = F_{\max}$); for values of $p > 0$, E'_p will lie to the left of the maximum. After quite a bit of algebra, we find that

$$E'_p = 1 - m' \left(1 - \sqrt{\frac{(1 - c')(1 + 1/m')}{1 - p[(1 + m'c')/(1 + m')]} } \right). \quad (11.46)$$

One important feature of (11.46) is that it gives an explicit formula for E'_p . One disadvantage is that p does not equal 0.1 when $F = F_{0.1}$; that is, $E'_{0.1} \neq E_{0.1}$ where the latter is the corresponding exploitation rate for $F_{0.1}$. Deriso (1987) showed that

$p = 0.1/(1 - E'_p)^2$ at the $F_{0.1}$ reference point. Therefore, if $F_{0.1} \approx M$, for example, then $E'_p = 0.5$ and thus $p = 0.4$.

11.4.6. Spawning Population per Recruit Parameters $F_x\%$

One of the major limitations of BRPs based on yield per recruit such as F_{\max} and $F_{0.1}$ is that the effects on the spawning population are essentially ignored. As a worst case scenario, suppose that infinite fishing pressure were applied at critical age t^* but that fish matured at ages older than t^* . The maximum yield per recruit would be taken, but at the expense of rendering the population extinct.

Since the early 1980s, spawning stock or egg production on a per-recruit basis has received much attention as a means to preserve reproductive potential of the population (e.g., Shepherd 1982, Campbell 1985, Sissenwine and Shepherd 1987, Gabriel et al. 1989, Clark 1991, Lowe et al. 1991, McShane 1992, Nash 1992). Data requirements for calculating reproductive variables per recruit are fairly modest: growth, mortality, and maturity and/or fecundity parameters.

No BRP results from maximization of these reproductive variables because they decline monotonically as a function of F . A related problem is solvable—namely, the maximization of yield per recruit subject to a constraint on amount of egg production per recruit (Botsford and Hobbs 1986). The question is, how much spawning biomass is enough (Mace and Sissenwine 1993)? The approach that has been used to address this question is to construct lightly parameterized population models with components for the spawner-recruit, mortality, and growth processes (e.g., Clark 1991, Mace and Sissenwine 1993, Thompson 1993). The delay-difference model (chapter 5) is an excellent candidate in this regard. The class of BRPs coming out of this approach is denoted $F_x\%$, where x is generally in the range of 20–40. Reference fishing mortality, $F_x\%$, results in a spawning stock biomass or egg production per recruit that is $x\%$ of that with no fishing.

Beddington and Cooke (1983) determined values of $F_{20\%}$ but chose the level arbitrarily. Shepherd (1982) explored the relationship between spawning biomass per recruit and the spawner-recruit relationship, noting that too high of a fishing mortality would reduce spawning biomass per recruit below a level where a stock would be maintained. Sissenwine and Shepherd (1987) also showed the relationship between BRPs based on spawning biomass per recruit and other BRPs (see the next section). Gabriel et al. (1989) applied the Sissenwine and Shepherd approach and suggested that $F_{30\%}$ was the highest level of F that would maintain the Georges Bank haddock stock.

Clark (1991) showed that $F_{35\%}$ was frequently near F_m for a variety of life-history parameters. The reference point F_{mmy} was obtained in Clark's study by considering the “maximin yield,” which is the maximum of the minimum yields obtained at each level of spawning biomass per recruit across a variety of spawner-recruit relationships. For what Clark calls a “typical life history,” this F was $F_{36\%}$ and was almost identical to $F_{0.1}$ and near M as well. For other life histories, F_{mmy} changed only slightly. Clark (1993) continued the same study with the addition of recruitment variability. This addition changed the typical F_{mmy} value to 40%, although a range from $F_{35\%}$ to $F_{45\%}$ would provide only slightly less yield. He further found that the $F = M$ strategy was close to $F_{42\%}$ and the $F_{0.1}$ strategy was near $F_{35\%}$, although these approximations depend on a similar selectivity and maturity schedule. In U.S. commercial fisheries, levels between $F_{35\%}$ and $F_{45\%}$ are frequently used to define acceptable biological catch levels. The

North Pacific Fishery Management Council recently accepted $F_{40\%}$ as an upper bound for groundfish target harvest levels.

Thompson (1993) showed for a depensatory model that harvesting with an upper bound of $F_{30\%}$ would make a stock collapse unlikely. Mace and Sissenwine (1993) suggested that a conservative strategy is to maintain spawning biomass per recruit above the 30% level (see next section). In U.S. commercial fisheries, the percentages used to define overfishing have usually been in the range of 20–35% (Mace and Sissenwine 1993); Goodyear (1993) suggested that this range should avoid stock depletion.

Quinn and Szarzi (1993) suggested that fishing mortalities between $F_{30\%}$ and $F_{45\%}$ in terms of spawning abundance instead of spawning biomass would result in sustainable harvests, but example 11.7 suggests that a minimum spawning abundance criterion should be 50% or greater. Because spawning abundance declines less rapidly than spawning biomass, one would expect that an abundance criterion would involve a higher percentage of the unfished population than a biomass criterion.

Example 11.6. Sablefish in the Gulf of Alaska

Spawning biomass per recruit statistics were calculated in example 6.5 (table 6.5). Corresponding values for various BRPs are shown in table 11.7. The $F_{35\%}$ value of 0.07 is slightly lower than the $F_{0.1}$ value of 0.09, which is slightly lower than $F_{30\%}$. All three are much lower than the value for F_{\max} of 0.16, which reduces spawning biomass per recruit to 16% of the unfished amount. A plot of yield per recruit and spawning biomass per recruit (figure 11.8) allows for comparison of trade-offs between yield and spawning biomass. The first three BRPs provide for about 90% of maximum yield per recruit, while keeping spawning biomass per recruit almost twice as high. Goodyear (1993) used three-dimensional graphs of yield per recruit with spawning biomass-per-recruit contours to examine the same trade-offs as a function of age of entry as well.

■

Example 11.7. Rainbow trout in Blue Lake, Sitka, Alaska

This example illustrates the generic approach for calculating spawning abundance and biomass per recruit for selected BRPs. These are simply obtained in table 11.8 by multiplying abundance at age from table 11.4 by maturity and by maturity and average weight (from table 6.4), respectively. The resulting curves for abundance and biomass are shown in figure 11.9.

Spawning abundance per recruit is reduced the least by $F_{0.2}$ (to 60% of unfished)

Table 11.7. For the sablefish example, calculations of spawning biomass per recruit for selected biological reference points (BRPs) ($t_r = t_c = 1$ and $t_s = 5$, so that $s = 0.699$).

BRP	E	F	y_s	SB/N_s	SB/R	% SB/R
Unfished	0.000	0.000	0.000	43.5	29.2	100.0
$F_{35\%}$	0.441	0.079	0.119	20.9	10.2	35.0
$F_{0.1}$	0.465	0.087	0.124	19.8	9.4	32.1
$F_{30\%}$	0.482	0.093	0.128	19.0	8.8	30.0
F_{\max}	0.617	0.161	0.150	12.9	4.5	15.6
F_{med}	0.737	0.280	0.163	8.0	1.8	6.0
F_{rep}	0.750	0.300	0.164	7.5	1.5	5.2

Table 11.8. Spawning abundance and biomass for different reference points for Blue Lake rainbow trout.

F	Age					Sum	% of F=0	
	3	4	5	6	7			
Spawning abundance, SN_a, per 100 recruits								
Unfished	0.00	29	59	57	46	35	227	100.0
$F_{0.2}$	0.39	29	47	31	17	10	135	59.5
$F_{Cmax,5+}$	0.43	29	46	30	15	9	129	56.9
$F_{0.1}$	0.53	29	43	25	12	7	116	51.2
$F_{SN50\%}$	0.55	29	42	25	11	6	114	50.2
$F_{SB35\%}$	0.64	29	40	21	9	5	104	46.1
$F_{0.05}$	0.66	29	40	21	9	4	103	45.3
$F_{SB30\%}$	0.76	29	37	18	7	3	94	41.5
F_{Ymax}	0.94	29	33	14	4	2	82	36.2
$F_{SN35\%}$	0.99	29	32	13	4	2	79	35.0
Spawning biomass, SB_a, per 100 recruits								
	0.00	4.5	16.1	23.1	24.7	23.3	91.7	100.0
	0.39	4.5	12.7	12.7	9.2	6.9	46.0	50.2
	0.43	4.5	12.4	12.0	8.3	6.1	43.3	47.2
	0.53	4.5	11.7	10.3	6.5	4.4	37.4	40.7
	0.55	4.5	11.5	10.0	6.1	4.2	36.3	39.6
	0.64	4.5	10.9	8.7	4.9	3.1	32.2	35.1
	0.66	4.5	10.8	8.4	4.6	2.9	31.3	34.2
	0.76	4.5	10.2	7.2	3.6	2.2	27.7	30.2
	0.94	4.5	9.1	5.5	2.3	1.2	22.6	24.7
	0.99	4.5	8.8	5.1	2.0	1.0	21.5	23.4

and the most by F_{Ymax} and $F_{SN35\%}$ (to about 35%) (table 11.8). Based on this example, a prudent level to recommend for a BRP based on spawning abundance is around 50–60% based on the values obtained for commonly used BRPs thought to be conservative in that table.

Spawning biomass per recruit is reduced the least by $F_{0.2}$ (to 50% of unfished) and the most by F_{Ymax} and $F_{SN35\%}$ (to about 24%) (table 11.8). A prudent level to recommend for a BRP based on spawning biomass is around 35–50%. ■

11.4.7. Spawning Population Parameters F_{rep} , F_{med} , F_{low} , and F_{high}

Sissenwine and Shepherd (1987) graphically showed the interrelationships between the yield–fishing mortality curve (production model), the spawning biomass and yield per recruit–fishing mortality curves (dynamic pool model), and the spawner-recruit curve. One connection among them is a replacement line that has a slope equal to the inverse of spawning biomass per recruit at a particular fishing mortality. Thus, knowledge of the spawner-recruit relationship permits the deduction of the production model from the dynamic pool model.

We can show this interrelationship mathematically as well. Let

$$\text{Spawner-recruit relationship} \quad R \equiv S\psi(S) \quad (11.47a)$$

$$\text{Spawners per recruit relationship} \quad S/R \equiv g(F) \quad (11.47b)$$

$$\text{Yield per recruit relationship} \quad Y/R \equiv h(F) \quad (11.47c)$$

for arbitrary functions ψ , g , and h . At equilibrium, recruits from (11.47a) and (11.47b) must be the same, so that

$$R = \mathcal{S}\psi(\mathcal{S}) = \frac{\mathcal{S}}{g(F)} \Rightarrow \psi(\mathcal{S}) = 1/g(F). \quad (11.47d)$$

This equation can be solved for equilibrium \mathcal{S} if ψ^{-1} exists:

$$\mathcal{S}_* = \psi^{-1}[1/g(F)], \quad (11.48)$$

which is the equilibrium relationship between the absolute spawner level and fishing mortality. Corresponding equilibrium recruitment is then

$$R_* = \mathcal{S}_*\psi(\mathcal{S}_*) = [1/g(F)]\psi^{-1}[1/g(F)] \equiv k(F), \quad (11.49)$$

showing that equilibrium recruitment can also be written solely as a function of fishing mortality. The production model can then easily be found from

$$Y_* = (Y/R)_*R_* = h(F)k(F), \quad (11.50)$$

which is solely a function of fishing mortality.

Example 11.8. Hypothetical population

Consider a hypothetical population that follows a Ricker spawner-recruit relationship $R = \alpha\mathcal{S} \exp(-\beta\mathcal{S})$, so that $\psi(\mathcal{S}) = \alpha \exp(-\beta\mathcal{S})$. The inverse function for ψ is $\psi^{-1}(x) = (\ln \alpha - \ln x)/\beta$. Suppose that the per-recruit dynamics can be approximated by

$$\begin{aligned} S/R &= g(F) = \gamma_1 \exp(-\gamma_2 F) && \text{(exponential decline)} \\ \text{and} \quad Y/R &= h(F) = \delta_1 F \exp(-\delta_2 F) && \text{(dome-shaped curve).} \end{aligned}$$

Then from (11.48) and (11.49), the equilibrium spawner and recruit functions are

$$\begin{aligned} \mathcal{S}_* &= (\ln \alpha + \ln \gamma_1 - \gamma_2 F)/\beta \\ \text{and} \quad R_* &= \mathcal{S}_* \exp(\gamma_2 F)/\gamma_1 = k(F). \end{aligned}$$

The production model from (11.50) is then just the product of $h(F)$ and $k(F)$.

For selected values of the parameters ($\alpha = 10$, $\beta = 0.001$, $\gamma_1 = 0.9$, $\gamma_2 = 8$, $\delta_1 = 13.6$, and $\delta_2 = 5$), the resultant curves are shown in figure 11.11. The yield-per-recruit curve is scaled to have a maximum of 1. The spawner-per-recruit curve starts arbitrarily at 0.9. Maximum recruitment occurs at 1000 spawners. For this example, the values of various BRPs are $F_{35\%} = 0.13$, $F_{30\%} = 0.15$, $F_{\max} = 0.20$, $F_{0.1} = 0.12$, and $F_m = 0.16$.

This example demonstrates the interrelationships between models using simple functions. Similar examples can be constructed for more commonly used curves. ■

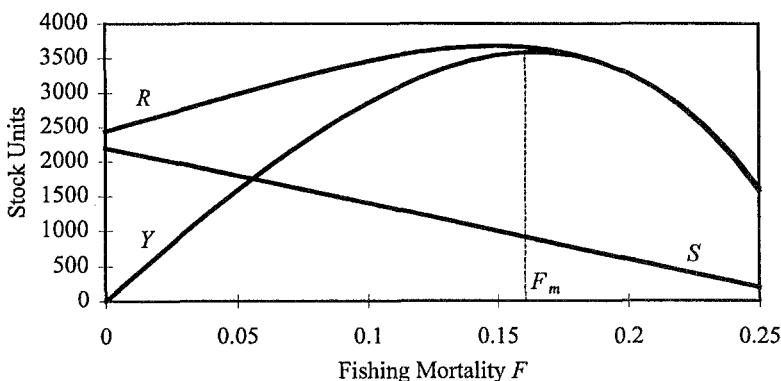
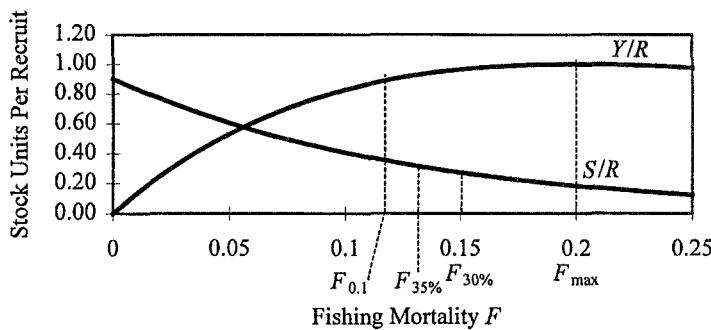
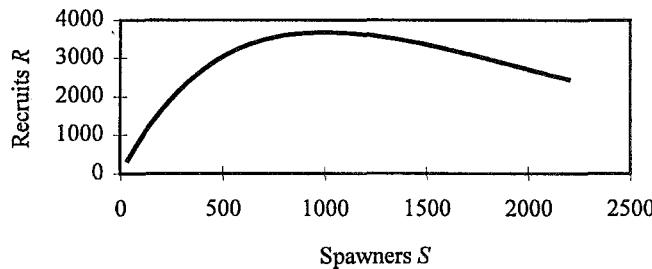


Figure 11.11. The spawner-recruit relationship and the yield and spawning biomass per recruit relationships for the hypothetical population example and the corresponding relationships for recruits, absolute spawners, and absolute yield as a function of fishing mortality.

Sissenwine and Shepherd (1987) defined a BRP called F_{ro} (for recruitment overfishing) as a level of fishing mortality that results in a sharp decrease in recruitment at equilibrium; this level would be at some arbitrary point beyond F_m . One possibility they suggested is where the spawner-recruit curve has a slope of 10% of that at the origin. For each value of F_{ro} , a corresponding spawning biomass level, S_{ro} , can be found.

When there is no apparent spawner-recruit relationship, Sissenwine and Shepherd

(1987) suggested an alternative approach. They assumed that the recruitment process is stationary through time and that compensation and depensation do not occur. A time series of spawner and recruit data is plotted and a straight line through the origin is drawn which is the replacement line. This line gives the equilibrium recruitment that replaces spawning biomass. The area above the line corresponds to values of recruitment exceeding that needed for replacement, and vice versa. The corresponding fishing mortality, F_{rep} (for replacement), can be found by inverting the slope, which gives the value $(R/S)^{-1} = S/R$, and finding the corresponding fishing mortality from the spawning biomass-per-recruit curve. For a population at equilibrium, fishing at a rate greater than F_{rep} will cause the population to decline. As different choices of the replacement line will lead to different equilibrium population levels, further specification of the objective is necessary.

Sissenwine and Shepherd (1987) proposed to estimate F_{rep} from the median line, as pointed out by Maguire and Mace (1993). That line has 50% of the recruit values above and 50% below; the corresponding fishing mortality has come to be known as F_{med} . Their argument seems to be based on the idea that the current population level is a function of its history and, hence, to keep the population stable at that level, the median line is the one to use. According to Jakobsen (1993a, p. 324), " F_{med} corresponds to the level of fishing mortality where accessions to the stock by recruitment in half of the observed years have been more than sufficient to balance out losses due to mortality."

Sissenwine and Shepherd (1987) noted that F_{med} should be conservative if compensation is operative (but obscured by a fluctuating environment), particularly when the data set is a small one from a developing fishery. Clearly, it is not conservative from a time series of a greatly overexploited population; one would not want to keep the population at a low level. If depensation exists, then F_{med} is also not conservative because the population might be driven near the depensation point, which would lead to stock collapse.

Two other BRPs have been derived from this approach: F_{low} and F_{high} , corresponding to replacement lines with 90% and 10% of the recruitment values being above the line (Shepherd 1982, ICES 1984, Jakobsen 1992, 1993a,b). In Jakobsen's terms, the balance between recruitment and mortality is achieved in 9 out of 10 years with F_{low} and 1 out of 10 with F_{high} . Jakobsen (1992, 1993a) showed that all three BRPs are more robust to variations in parameters used to estimate them than is F_{max} .

Mace and Sissenwine (1993) collected information on life-history parameters from 91 stocks around the world. They calculated percentage spawning biomass per recruit (%SPR) levels that allowed for replacement of spawning biomass. They found that F_{med} (which they called F_{rep}) resulted in an average %SPR of 19% with a large range from 2% to 65%. They suggested using the 80th percentile to estimate the threshold replacement level of about 30% for use in defining overfishing. On average, F_{med} was 1.4 times F_{max} but both had similar %SPRs (21% for F_{max}). They found that F_{med} was on average 2.4 times $F_{0.1}$, which had a such higher average %SPR of 38%. However, in about 13% of the cases, $F_{0.1}$ was higher than F_{med} , suggesting that $F_{0.1}$ is not always conservative. They recommended not using F_{med} if it is larger than F_{max} because there is no need to sacrifice yield per recruit. However, when F_{med} is less than F_{max} or $F_{0.1}$, they recommended its use to fish conservatively. For depleted stocks, they recommended fishing below F_{med} to promote rebuilding.

In single-species studies, Hollowed and Megrey (1993) found that the values of

$F_{35\%}$, F_m , and F_{med} were all similar and lower than $F_{30\%}$ and $F_{0.1}$ for walleye pollock. They noted that problems may occur with F_m and F_{med} if the recruitment series is not stationary (i.e., that there is a change in the distribution of recruitment due to environmental changes). Lowe and Thompson (1993) considered several BRPs for Atka mackerel. They found the following ordering: $F_{0.1} \approx F_{40\%} < F_{35\%} < F_{30\%} < F_{max}$. The values of F_m varied across the range of these previous BRPs depending on the nature of the spawner-recruit relationship. Maguire and Mace (1993), in a survey of several Canadian stocks, found that $F_{med} > F_{0.1}$ and suggested that the corresponding stock size, S_{med} , might be a useful threshold for dealing with overfishing.

Example 11.9. Sablefish simulation

A simulation based on the sablefish example illustrates the calculation of F_{med} . Population parameters are as in table 6.3. Recruitment was generated from a lognormal distribution with mean 300,000 and coefficient of variation 0.5; values were chosen to mimic the Gulf of Alaska sablefish population, as in Sigler (1993). These estimates were then combined with the per-recruit models to get a time series of recruitment and spawning biomass. The simulation covered 26 years, which produced 25 spawner-recruit observations. For this simulation the mean and median observed recruitments were 355,000 and 330,000, respectively. Figure 11.12 shows the spawner-recruit graph of the resultant data.

To calculate F_{med} according to the Sissenwine and Shepherd procedure, the straight line that bisected the data was found. Its slope (R/S) was 0.57 and its inverse (S/R) was 1.8. From inspection of the S_B/N_r column in table 11.7, the value of $F_{med} = 0.28$. This value is slightly lower than that which generated the population, suggesting a slight bias. For $F = 0.3$, the corresponding S_B/N_r value is 1.5 (table 11.7). In contrast, the mean and median S_B/N_r value from the observations were 1.9 and 1.7, respectively, with the straight line procedure producing a value closer to the median. The overestimation of the actual S_B/N_r and the resulting underestimation of F_{med} is likely a consequence of recruitment having a skewed distribution. While higher recruitment produces higher spawning biomass later in time, a given year's spawning biomass is made up of several cohorts. Thus, dividing spawning biomass by recruitment even at the proper lag is likely to result in a skewed distribution when there is no relationship between recruitment and spawning biomass. ■

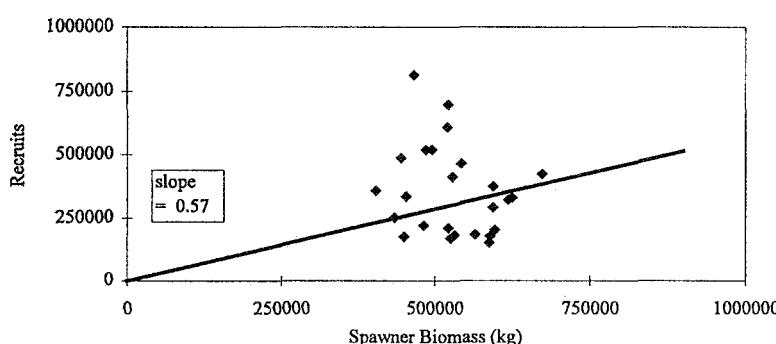


Figure 11.12. Simulated spawner-recruit data for the sablefish example for $F_{rep} = 0.3$ and the median straight line that separates the points into two equal groups.

11.4.8. Age-structured Population Parameter F_{st}

Quinn and Szarzi (1993) used a generic age-structured model from Getz and Haight (1989) to determine a BRP called F_{st} (for steady), similar in philosophy to F_{rep} . Essentially, an estimate of early life survival is used to find the corresponding fishing mortality level that keeps the population at equilibrium. The population model is a Leslie matrix model with density-independent survival. The equations describing the population model are given in chapter 7 and section 11.3.1.

The needed parameters for calculating F_{st} are natural mortality, M , net fecundity $\{f_a\}$, selectivity $\{s_a, a \geq r\}$, and early life survival, ℓ_r , from age 0 to age r , the age of recruitment. The age of recruitment, r , is assumed to be young enough so that no younger fish are mature ($f_a = 0$ for $a < r$). The control parameter is full-recruitment fishing mortality, F . Given F , survival at age is given by $S_a = \exp[-(M + s_a F)]$. The cumulative survival from age r to age a is then $\mathcal{L}_a = \prod_{x=r}^{a-1} S_x$. The expected lifetime egg production of an r year old is

$$P_r = \sum_{a=r}^A f_a \mathcal{L}_a. \quad (11.51)$$

The net reproductive value, R_0 , is defined as the expected number of progeny that survive to age r produced by an individual at age r . It is determined from the expected lifetime egg production of an r year old multiplied by early life survival, so that

$$R_0 = \ell_r P_r = \ell_r \sum_{a=r}^A f_a \mathcal{L}_a. \quad (11.52)$$

Suppose that a time series of abundance $N_{a,t}$ and egg production $N_{0,t}$ estimates are available (say, from cohort or catch-age analysis). Empirical estimates of early life survival from age 0 to age r for each year, t , can be obtained from

$$\hat{\ell}_{r,t} = N_{r,t+r}/N_{0,t}.$$

The fishing mortality that keeps the population stable, denoted F_{st} , can be found for each estimate or some measure of central tendency of these estimates. The procedure is to solve the equation $R_0 = 1$ for F using (11.52), or equivalently to solve the equation $P_r = 1/\hat{\ell}_{r,t}$ from (11.51), treating all other quantities as fixed. Fishing mortalities less than F_{st} will increase the population over the long term and vice versa. Thus, F_{st} provides an estimate of sustained yield. It can essentially be viewed as the mathematical representation of F_{rep} for an age-structured population. Quinn and Szarzi (1993) suggested that F_{st} is advantageous in that it is not data hungry and makes use of data often collected in studies for recreational fisheries.

Example 11.10. Razor clams at Clam Gulch, Alaska

A large recreational fishery for razor clams in Alaska occurs at Clam Gulch. Abundance, selectivity, and fishing mortality are estimated from catch-age analysis (Quinn and Szarzi 1993). Basic population parameters from their paper are reproduced in table 11.9.

The basic calculations of mortality, survival, and lifetime egg production in table 11.9 are made using the median early life survival, $\bar{\ell}_r$, and a trial value for

Table 11.9. Population information about razor clams at Clam Gulch (net fecundity, f_a ; selectivity, s_a ; and natural mortality, M_a , at age a) and illustration of the calculations involved in finding F_{st} , the fishing mortality that results in net reproductive value, R_0 , being equal to 1 (the median early life survival is used).

a	4	5	6	7	8	9	10	11+	Sum
$f_a (\times 10^6)$	4.1	10.7	17.3	21.5	25.2	27.8	29.4	35.8	
s_a	0.07	0.25	0.42	1	1	1	1	1	
M_a	0.125	0.125	0.125	0.125	0.125	0.125	0.125	0.125	
$\ell_r (\times 10^{-8})$	3.41								
F_{st}	1.308								
F_a	0.092	0.327	0.549	1.308	1.308	1.308	1.308	1.308	
Z_a	0.217	0.452	0.674	1.433	1.433	1.433	1.433	1.433	
S_a	0.805	0.636	0.510	0.239	0.239	0.239	0.239	0.239	
\mathcal{L}_a	1.000	0.805	0.512	0.261	0.062	0.015	0.004	0.001	
$\ell_r f_a \mathcal{L}_a$	0.141	0.293	0.302	0.192	0.053	0.014	0.004	0.001	(R_0) 1.000

full-recruitment fishing mortality, F . Using a nonlinear search procedure, the value $F_{st} = 1.027$ solves the equation $R_0 = 1$, which corresponds to equilibrium (table 11.9). The corresponding values of F_{st} as a function of early life survival are shown in figure 11.13: as ℓ_r increases, the fishing mortality at equilibrium increases because more clams survive at early ages. When early life survival is below about 1×10^{-8} , no sustainable fishery is possible. ■

11.4.9. Threshold Reference Points

Until recently, little attention has been given to threshold reference points, which are abundance or biomass levels below which fishing is curtailed or other management actions are taken. This could be due to the difficulty in establishing standards based on an absolute biomass level, the usually satisfactory behavior of fixed harvest rate or fishing mortality policies, or lack of confidence in estimates of absolute abundance or biomass. With the advent of more sophisticated catch-age or catch-length analyses

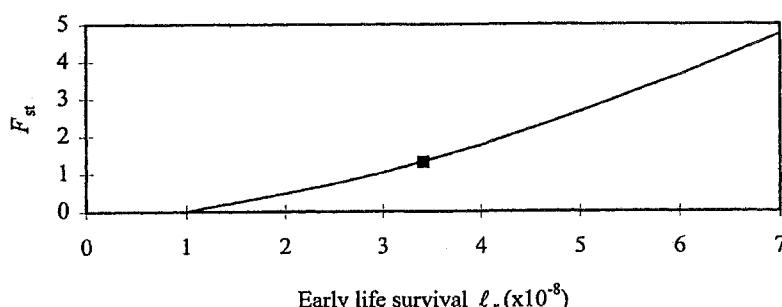


Figure 11.13. Steady fishing mortality, F_{st} , as a function of early life survival, ℓ_r (after Quinn and Szerzi 1993). The square shows the point corresponding to median early life survival ($\bar{\ell}_r = 3.41 \times 10^{-8}$, $F_{st} = 1.308$).

(chapters 8 and 9), more confidence in abundance estimates has occurred. Also, concern over populations falling to low levels due to overfishing has increased, so strategies that curtail fishing at low levels are receiving more attention.

The first approach to threshold reference points is empirical: define a reference point based on a time series of abundance information. Sigler and Fujioka (1993) used the minimum observed spawning biomass as a threshold level for sablefish. Overholtz et al. (1993) used current spawning biomass as a reference point for New England groundfish and considered strategies that increase biomass beyond that point. Though not conceived as a point to stop fishing, that step has recently occurred. Thresholds for Pacific herring were set at 20–25% of average observed spawning biomass to protect stocks at low levels. Jakobsen (1993) determined a minimum safe threshold level by examining a plot of recruits versus spawners and noting a point below which the chance of obtaining a low level of recruitment appeared larger.

The second approach has been to consider threshold levels based on spawning biomass-per-recruit (S/R) levels. As mentioned in section 11.4.6, $F_{35\%}$ reduces S/R to 35% of the unfished level and may be a reasonable surrogate for MSY fishing mortality, F_m . This relative level can be converted to an absolute level, $S_{35\%}$, by multiplying by average recruitment, if there is no apparent spawner-recruit relationship. If there is a relationship, then the relationships in section 11.4.7 can be used to perform the conversion. This reference level would likely be considered a target rather than a threshold. If an overfishing limit is based on the 20–30% levels (Mace and Sissenwine 1993), the corresponding spawning levels could be used as thresholds.

If there is compensation in the population, other approaches are possible. As shown in section 2.1.5, a surplus production model can be shifted to the right and the left x -intercept (where surplus production is zero) used as the threshold level. This approach can be generalized to a depensatory surplus production model by inclusion of a cubic term (Zheng et al. 1993b):

$$Y_* = r B_* (B_*/T - 1)(1 - B_*/B_\infty),$$

where intrinsic rate of increase, r , threshold, T , and pristine biomass, B_∞ , are the parameters. If there is a spawner-recruit relationship, a population model can be constructed (as in chapters 5 and 7), which results in the relationship between absolute spawning level and fishing mortality. The value of S_m corresponding to MSY would be a target and some level below that might be used for the threshold. Such levels are often expressed in terms of some percentage of pristine biomass. If the spawner-recruit curve is depensatory, then the inflection point (where the second derivative is maximum) is a candidate for a threshold level (Thompson 1993).

Francis (1993) recommended that the threshold level should be part of an objective function that seeks to keep the probability of a population falling below the threshold below a specified level; he used 10%. With this objective, he showed that the acceptability of a harvest policy depends on the steepness of the spawner-recruit curve. As a consequence, he recommended that harvest strategies be evaluated with simulation exercises instead of with BRPs. A similar conclusion was reached by Lowe and Thompson (1993). They evaluated several BRPs and showed that error in assessments leads to lower fishing mortalities than suggested by the BRPs.

The value of 20% has often been recommended as a threshold level (Beddington

and Cooke 1983, Goodyear 1993, Hollowed and Megrey 1993, Thompson 1993). Thompson's rationale comes from the compensatory generalized Beverton-Holt spawner-recruit model

$$R = \frac{\alpha S}{1 + \beta S^{-\gamma}},$$

combined with an equilibrium spawner-per-recruit model that is a function of fishing mortality alone. He showed for a particular functional form of the inflection point that the inflection point is usually less than 20% of pristine biomass. The value of 25% has also been common (Quinn et al. 1990b, Francis 1993, Leaman 1993, Schweigert 1993) and is (arbitrarily) intuitive, being halfway to MSY in the simple Graham-Schaefer surplus production model (section 2.1.1). The threshold level that optimizes the weighted objective function (11.7) tends to increase as fishing mortality increases (Quinn et al. 1990b, Zheng et al. 1993a), so these two controls should probably not be considered independently. When density-dependent natural mortality is present, Haist et al. (1993) found that a threshold level was necessary to prevent stock collapse, even when exploitation rate was low.

Zheng et al. (1993b) presented two methods based on life-history parameters referred to as Fowler's method and May's method based on studies cited by Zheng et al. In Fowler's method, the inflection point of population growth curves is estimated from production/biomass ratios with a linear regression equation. The inflection point is then a candidate for a threshold level; the equation for fishes is

$$T = 0.11 + 0.074 \ln(B_m/\text{MSY}) = 0.11 + 0.074 \ln(1/F_m),$$

where threshold level T is a percentage of pristine biomass, and B_m is biomass at MSY. For example, an MSY exploitation rate $F_m = 0.2$ translates to an inflection point that is 16% of pristine biomass.

In May's method, a resource-consumer approach is used to find a critical stock size, $T = B_m$ (as a percentage of pristine biomass), below which a stock collapse is likely, which leads to the equations:

$$T = \sqrt{1 + \tau} / \tau \quad \text{and} \quad \tau = (1 - v)/(v + M/r),$$

where M is natural mortality, r is intrinsic rate of increase, and v is a coupling coefficient representing the effective coupling strength between the resource and the consumer. This latter parameter is difficult to estimate; Zheng et al. (1993b) arbitrarily chose 0.45 for walleye pollock and 0.28 for herring. In passively adaptive simulations, they found that a fixed level near 25% of pristine biomass was near optimal and that Fowler's method was fairly robust if the estimation of pristine biomass was precise. However, both Fowler's and May's methods were greatly influenced by measurement error.

11.5. RISK, UNCERTAINTY, AND DECISION ANALYSIS

A key feature of fisheries stock assessment is uncertainty, which arises from an inability to precisely measure the system due to a lack of complete knowledge about factors influencing population dynamics and about natural stochasticity of the system. Recognition of the importance of inclusion of uncertainty into assessment analyses has been emphasized throughout this book.

One source of uncertainty is the continuing discovery of contradictory data when conducting assessments of fish populations (e.g., Richards 1991, Schnute and Hilborn 1993). Although it is straightforward to construct the composite likelihood for different data sets and to look for discrepancies among data sets (through hypothesis testing or analysis of residuals), it is less clear how to deal with the uncertainty once found. We believe that it is more likely that one of the data sets is providing incorrect information than that all data sets are subject to random error. As a consequence, taking intermediate values of parameters or averaging across data sets is probably the wrong thing to do (Richards 1991, Schnute and Hilborn 1993). For example, using a biased index of abundance along with an unbiased index in age-structured assessment is usually worse than just using the unbiased index (NRC, 1998a). Yet without prior information on which data sets are accurate and precise, the only solutions to the problems induced by contradictory data involve further experimentation, adaptive management, and highlighting the contradiction within a decision-making framework.

Previous sections of this chapter have shown various attempts to integrate uncertainties directly into the calculations of optimal harvesting controls. Formal methods of decision making under uncertainty are well developed (Lindley 1983, Berger 1985), with several applications in fisheries. As described in the review by Punt and Hilborn (1997), Walters and Hilborn (1976) were the first to suggest that Bayesian analysis could be used to evaluate alternative fisheries policies. Bergh and Butterworth (1987) and Sainsbury (1988) provided the first major applications to stock assessment models. An explosion of interest has occurred in the 1990s with essays on Bayesian methods applied to a broad range of stock assessment issues (Collie and Walters 1991, Geiger and Koenings 1991, Hilborn and Walters 1992, Thompson 1992, Givens et al. 1993, Hilborn et al. 1993, 1994; Kinas 1993, 1996; Hoenig et al. 1994, McAllister et al. 1994, Punt et al. 1994, Walters and Ludwig 1994, Walters and Punt 1994, Adkison and Peterman 1996, McAllister and Ianelli 1997, McAllister and Pikitch 1997). These essays deal with one or both of two primary objectives. The first is with Bayesian estimation, in which the goal is to estimate the statistical posterior distributions for key population quantities, given prior distributions for some population parameters and a likelihood function for the data. The second is decision making, as we now describe.

Bayesian decision analysis consists of four steps:

1. Identify alternative hypotheses, H_i , about population abundance, productivity, and dynamics (sometimes referred to as “states of nature”). Contemporary problems typically consider an infinite number of alternative hypotheses when model parameters are treated as random variables, such as in calculations of posterior probability distributions. Nevertheless, a finite number of groups of such hypotheses can often be postulated as, for example, the environment versus density-dependence hypothesis treated in Parma and Deriso (1990).
2. Determine the probability, $P(H_i)$, of each alternative hypothesis. Bayes theorem can be used to calculate such probabilities, as in (11.25).
3. Identify alternative management actions or controls, u_j , which could be infinite in number considering the broad range of catch quotas that could be implemented in any given year. Actions can often be classified into a finite number of alternative management-action decision rules.
4. In traditional decision analysis, one evaluates the distribution and expected

value of each performance measure, I_k , given the management actions and the hypotheses. Performance measures can include measures of risk (both to the fishery and to the fish population), measures of amount of catch, and variation in catch. For a large number of actions and hypotheses, evaluations of I_k for each hypothesis are not practical, and alternative summaries are needed such as expectation across all hypotheses for a given management-action decision rule. Performance measures of risk can be summarized simply as a probability. An advantage of separate evaluations of I_k for each hypothesis is that it simplifies sensitivity analysis of changes in performance to changes in $P(H_i)$.

Results can be summarized as a type of decision table, as illustrated in table 11.10. In the simple case, a separate table is made for each information measure, I_k , and for a set of discrete alternative hypotheses and management actions. Such a table contains columns for each hypothesis. The second row contains $P(H_i)$ for each hypothesis. Rows below contain the calculated performance measure I_{kij} for each hypothesis, H_i , and each alternative management action, u_j . The rightmost column lists the expected value of I_k for each management action. Decision tables are sometimes too cumbersome for complex decision problems, as, for example, with an infinite number of alternative hypotheses and management actions that are “rule”-driven.

Alternative non-Bayesian approaches have also been used to deal with uncertainty and risk. A simple approach is to use decision trees to examine the impact of management actions under alternative states of nature (Brown and Patil 1986). Approaches based on Monte Carlo and bootstrap methods are also used to quantify risk (e.g., Francis 1992, 1993a, Restrepo et al. 1992, Cordue and Francis 1994). There is often disagreement on the proper approach to be used (Francis 1993b, Walters 1993). An approach using fuzzy arithmetic is espoused by Ferson (1993), whereby measurement error is treated as subjective uncertainty, which requires an alternative arithmetic system. The consideration of risk has led some managers to perform uncertainty adjustments (e.g., to lower a harvest limit by an amount related to the imprecision in the data). A method for rigorously determining an uncertainty adjustment in an age-structured model is given by Frederick and Peterman (1995). Francis and Shotton (1997), in a comprehensive review of risk and uncertainty, concluded that more formal procedures are needed to strengthen the effectiveness and credibility of fisheries management.

A number of applications of decision analysis in the fisheries literature illustrate the

Table 11.10. A simple decision table to evaluate the consequences, in terms of the ratio of the stock size at the end of the management period to the virgin biomass, of a variety of alternative future annual total allowable catches (TACs) (from Hilborn et al. 1994).

	Alternative hypothesis (virgin biomass)						Expectation
	750	950	1150	1350	1550	1750	
Probability	0.099	0.465	0.317	0.096	0.020	0.003	
TAC (1000 tons)							
100	0.51	0.63	0.70	0.75	0.78	0.81	0.66
150	0.26	0.45	0.56	0.63	0.69	0.72	0.49
200	0.22	0.26	0.42	0.52	0.59	0.64	0.34

diversity of approaches that can be followed (Walters and Hilborn 1976, Walters 1981, Bergh and Butterworth 1987, Sainsbury 1988, Collie et al. 1990, Hilborn and Walters 1992, Pelletier and Laurec 1992, Kruse et al. 1993, A. Smith 1993, S. Smith et al. 1993, Hilborn et al. 1994, Punt et al. 1994, Ianelli and Heifetz 1995a,b, Punt and Hilborn 1997). Particular emphasis has been given in recent literature to risk as a performance measure (Francis 1992, Restrepo et al. 1992, Hilborn et al. 1993, Walters and Punt 1994, Walters and Ludwig 1994). As shown in section 11.3.3, risk can sometimes be incorporated directly into the maximization objective by using a utility function which is either concave (a risk-averse utility) or convex (a risk-prone utility). Concave utility functions, such as the logarithm of catch (equation 11.6), when maximized produce policies that are extremely averse to complete collapse of a population, yet maximize the geometric mean of catch; modifications to a logarithmic utility, such as $\ln(C - k)$ where k is a positive constant would, when maximized, produce policies averse to partial collapse of a population [that is, $P(N < k) \rightarrow 0$]. An advantage of incorporating risk directly into the management objective is that the stochastic dynamic programming equation (11.26) can be applied to optimize policy under alternative hypotheses about the states of nature. No matter what approach is taken, explicit treatment of uncertainty and risk in population modeling and fishery management is now attainable.

References

- Adkison, M.D., and R.M. Peterman. 1996. Results of Bayesian methods depend on details of implementation: an example of estimating salmon escapement goals. *Fisheries Res.* 25: 155–170.
- Adkison, M.D., R.M. Peterman, M.F. LaPointe, D.M. Gillis, and J. Korman. 1996. Alternative models of climatic effects on sockeye salmon, *Oncorhynchus nerka*, productivity in Bristol Bay, Alaska, and the Fraser River, British Columbia. *Fisheries Oceanogr.* 5: 137–152.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in (B.N. Petran and F. Csaaki, eds.) *International Symposium on Information Theory*, 2nd ed., Academiai Kiadó, Budapest, Hungary.
- Akamine, T. 1993. A new standard formula for seasonal growth of fish in population dynamics. *Nippon Suisan Gakkaishi* 59: 1857–1863.
- Aldenberg, T. 1975. Virtual population analysis and migration, a theoretical treatment. International Council for Exploration of the Sea C.M. 1975/F: 32, Copenhagen, Denmark. Mimeo.
- Allen, K.R. 1963. Analysis of stock-recruitment relations in Antarctic fin whales. *Cons. Int. Explor. Mer, Rapp. et Proc.–Verb.* 164: 132–137.
- Allen, K.R. 1971. Relation between production and biomass. *J. Fish. Res. Board Can.* 28: 1573–1581.
- Allen, R. L. 1976. Method for comparing fish growth curves. *New Zealand J. Marine Freshw. Res.* 10: 687–692.
- Allen, R. L., and P. Basasibwaki. 1974. Properties of age structure models for fish populations. *J. Fish. Res. Board Can.* 31:1119–1125.
- Allen, R., and R. Punsky. 1984. Catch rates as indices of abundance of yellowfin tuna *Thunnus albacares* in the eastern Pacific Ocean. *Int.-Amer. Trop. Tuna Comm. Bull.* 18: 301–379.
- Alverson, D.L., and M.J. Carney. 1975. A graphic review of the growth and decay of population cohorts. *J. Cons. Int. Explor. Mer* 36: 133–143.
- Alverson, D.L., and W.T. Pereyra. 1969. Demersal fish exploitation in the Northeastern Pacific Ocean: an evaluation of exploratory fishing methods and analytical approaches to stock sizes and yield forecasts. *J. Fish. Res. Board Can.* 26: 1985–2001.
- Anderson, B.D.O., and J.B. Moore. 1979. Optimal Filtering. Prentice-Hall, Englewood Cliffs, New Jersey.
- Anderson, J.L., and J.E. Wilen. 1985. Estimating the population dynamics of coho salmon (*Oncorhynchus kisutch*) using pooled time-series and cross-sectional data. *Can. J. Fish. Aquat. Sci.* 42: 459–467.

- Anderson, K.P., and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorous circulation and primary productivity. *Meddelelser* 7: 319–435.
- Andrew, P.A., and D.S. Butterworth. 1987. Is $f_{0.1}$ an appropriate harvesting strategy for the Cape hakes? *S. Afr. J. Mar. Sci.* 5: 925–935.
- Anganuzzi, A., R. Hilborn, and J.R. Skalski. 1994. Estimation of size selectivity and movement rates from mark-recovery data. *Can. J. Fish. Aquat. Sci.* 51: 734–742.
- Angelsen, K.K., and S. Olsen. 1987. Impact of fish density and effort level on catching efficiency of fishing gear. *Fisheries Res.* 5: 271–278.
- Anon., Forschungszentrum Jülich. 1992. Techniques for biological assessment in fisheries management; report of the workshop Jülich, July 17–24, 1991. Berichte aus der Ökologischen Forschung, Band 9.
- Anthony, V. 1982. The calculation of $F_{0.1}$: a plea for standardization. *NAFO Ser. Doc. SCR* 82/VI/64.
- Appeldoorn, R. S. 1982. Variation in the growth rate of *Mya arenaria* and its relationship to the environment as analyzed through principal components analysis and the omega parameter of the von Bertalanffy equation. *U.S. Fish. Bull.* 81: 75–84.
- Appeldoorn, R. S. 1987. Modification of a seasonally oscillating growth function for use with mark-recapture data. *J. Cons. Int. Explor. Mer* 43: 194–198.
- ABM (Applied Biomathematics, Inc.). 1983. Relative sensitivity of Hudson River striped bass to competing sources of mortality and the implications for monitoring programs. Prepared for the New York Power Authority. Setauket, New York.
- Armstrong, M.J., and P.A. Shelton. 1988. Bias in estimation of stock-recruit function parameters caused by nonrandom environmental variability. *Can. J. Fish. Aquat. Sci.* 45: 554–557.
- Arnason, A.N. 1972. Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Res. Pop. Ecol. (Kyoto)* 13: 97–113.
- Arnason, A.N. 1973. The estimation of population size, migration rates, and survival in a stratified population. *Res. Pop. Ecol. (Kyoto)* 15: 1–8.
- Baelde, P. 1991. Assessment of the Australian deep-water royal red prawn stock using commercial catch and effort data. *Fisheries Res.* 12: 243–258.
- Baird, J.W., and S.C. Stevenson. 1983. Levels of precision—sea versus shore sampling. *Can. Spec. Pub. Fish. Aquat. Sci.* 66: 185–188.
- Baker, T.T., R. Lafferty, and T.J. Quinn II. 1991. A general growth model for mark-recapture data. *Fisheries Res.* 11: 257–281.
- Bannerot, S.P., and C.B. Austin. 1983. Using frequency distributions of catch per unit effort to measure fish stock abundance. *Trans. Amer. Fish. Soc.* 112: 608–617.
- Barber, W.E. 1988. Maximum sustainable yield lives on. *N. Amer. J. Fish. Manage.* 8: 153–157.
- Bartlett, M.S. 1970. Age distributions. *Biometrics* 26: 377–385.
- Bartoo, N. W., and K. R. Parker. 1983. Stochastic age-frequency estimation using the von Bertalanffy growth equation. *U.S. Fish. Bull.* 81: 91–96.
- Basson, M., A.A. Rosenberg, and J.R. Beddington. 1988. The accuracy and reliability of two new methods for estimating growth parameters from length-frequency data. *J. Cons. Int. Explor. Mer* 44: 277–285.
- Bates, D.M., and D.G. Watts. 1988. *Nonlinear Regression Analysis and Its Applications*. Wiley, New York.
- Bayley, P.B. 1993. Quasi-likelihood estimation of marked fish recapture. *Can. J. Fish. Aquat. Sci.* 50: 2077–2085.
- Bayliff, W.H. 1971. Estimates of the rates of mortality of yellowfin tuna in the eastern Pacific Ocean derived from tagging experiments. *Inter.-Amer. Trop. Tuna Comm. Bull.* 15: 381–436.
- Beamish, R.J., and G.A. McFarlane. 1987. Current trends in age determination methodology.

- Pages 15–42 in R.C. Summerfelt and G.E. Hall, eds., Age and Growth of Fish. Iowa State Univ. Press, Ames.
- Beddington, J. R. 1974. Age distribution and the stability of simple discrete time population models. *J. Theor. Biol.* 47:65–74.
- Beddington, J.R., and J.G. Cooke. 1981. Development of an assessment technique for male sperm whales based on the use of length data from the catches, with special reference to the Northwest Pacific stock. *Rep. Int. Whal. Comm.* 31: 747–760.
- Beddington, J., and J.G. Cooke. 1983. The potential yield of fish stocks. U.N. FAO Fisheries Tech. Paper 242, Rome, Italy.
- Beinissen, K.H.H., and D. Powell. 1979. Measurement of natural mortality in a population of blacklip abalone, *Notohaliotis ruber*. *Cons. Int. Explor. Mer, Rapp. et Proc.–Verb.* 175: 23–26.
- Berger, O.J. 1985. Statistical Decision Theory and Bayesian Analysis. Springer-Verlag, New York.
- Bergh, M.O., and D.S. Butterworth. 1987. Towards rational harvesting of the South African anchovy considering survey imprecision and recruitment variability. *S. Afr. J. Mar. Sci.* 5: 937–951.
- Bergh, M.O., and W.M. Getz. 1988. Stability of discrete age-structured and aggregated delay-difference population models. *J. Math. Biol.* 26: 551–581.
- Bernard, D. F. 1981. Multivariate analysis as a means of comparing growth in fish. *Can. J. Fish. Aquat. Sci.* 38: 233–236.
- Bernardelli, H. 1941. Population waves. *J. Burma Res. Soc.* 31: 1–18.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (Inquiries on growth laws II). *Human Biol.* 10: 181–213.
- Beverton, R.J.H., and S.J. Holt. 1957. On the Dynamics of Exploited Fish Populations. Chapman and Hall, London. Facsimile reprint, 1993.
- Beverton, R.J.H. and S.J. Holt. 1964. Tables of yield functions for fishery assessment. FAO Fish. Tech. Pap. 38. 49p.
- Beyer, J. 1989. Recruitment stability and survival—simple size-specific theory with examples from the early life dynamics of marine fish. *Dana* 7: 45–147.
- Blyth, P.J., R.A. Watson, and D.J. Sterling. 1990. Spawning, recruitment, and life history studies of [tiger prawns] in Torres Strait. Pages 38–50 in J.E. Mellors, ed., Torres Strait prawn project: a review of research 1985–1987. Queensland Dept. Primary Indust. Info. Series QI90018, Brisbane, Australia.
- Boehlert, G.W. 1985. Using objective criteria and multiple regression models for age determination in fishes. *U.S. Fish. Bull.* 82: 103–117.
- Bosch, D.E. 1995. Population dynamics and stock assessment of Arctic grayling (*Thymallus arcticus*) in the Gulkana River drainage, Alaska. M.S. Thesis, Univ. of Alaska Fairbanks, Juneau, AK.
- Botsford, L.W. 1981a. The effects of increased individual growth rates on depressed population size. *Amer. Nat.* 117: 38–63.
- Botsford, L.W. 1981b. Optimal fishery policy for size-specific, density-dependent models. *J. Math. Biol.* 12: 265–293.
- Botsford, L.W., and R.C. Hobbs. 1986. Static optimization of yield per recruit with reproduction and fishing costs. *Fisheries Res.* 4: 181–189.
- Box, G.E.P., and G.M. Jenkins. 1976. Time Series Analysis: Forecasting and Control, revised edition. Holden-Day, Oakland, California.
- Bradford, M.J., and R. M. Peterman. 1989. Incorrect parameter values used in virtual population analysis (VPA) generate spurious time trends in reconstructed abundances. *Can. Sp. Pub. Fish. Aquat. Sci.* 108: 87–99.

- Braun, M. 1983. Differential Equations and Their Applications, 3rd ed. Springer-Verlag, New York.
- Brock, V.E., and R.H. Riffenburgh. 1960. Fish schooling: a possible factor in reducing predation. *J. Cons. Int. Explor. Mer* 25: 307–317.
- Brody, S. 1927. Growth rates. *Univ. Missouri Agri. Exp. Sta. Bull.* 97.
- Brody, S. 1945. Bioenergetics and Growth. Reinhold, New York. [Reprinted 1964 by Hafner Publishing.]
- Brown, B.E., and G.P. Patil. 1986. Risk analysis in the Georges Bank haddock fishery—a pragmatic example of dealing with uncertainty. *N. Amer. J. Fish. Manage.* 6: 183–191.
- Brownie, C., D.R. Anderson, K.P. Burnham, and D.S. Robson. 1985. Statistical Inference from Band-Recovery Data: A Handbook, 2nd edition. U.S. Fish. Wildl. Serv., Resource Pub. 156, Washington, D.C.
- Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock, and J.B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* 49: 1173–1187.
- Buckland, S.T., D.R. Anderson, K.P. Burnham, and J.L. Laake. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London.
- Burnham, K.P., D.R. Anderson, G.C. White, C. Brownie, and K.H. Pollock. 1987. Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture. Amer. Fish. Soc. Monograph 5.
- Butler, J.L., P.E. Smith, and N.C. Lo. 1993. The effect of natural variability of life history parameters on anchovy and sardine population growth. CalCOFI Rep. 34.
- Butterworth, D.S., and A.E. Punt. 1993. The robustness of estimates of stock status for the western North Atlantic bluefin tuna population to violations of the assumptions underlying the associated models. ICCAT Working Document SCRS 93/68.
- Caddy, J. In press. Modeling natural mortality with age in short-lived invertebrate populations: definition of a strategy of gnomonic time division. *Aquatic Living Resources*.
- Campana, S.E. 1987. Comparison of two length-based indices of abundance in adjacent haddock stocks (*Melanogrammus aeglefinus*) on the Scotian shelf. *J. Cons. Int. Explor. Mer* 44: 43–55.
- Campana, S.E. 1990. How reliable are growth back-calculations based on otoliths? *Can. J. Fish. Aquat. Sci.* 47: 2219–2227.
- Campbell, A. 1985. Application of a yield and egg-per-recruit model to the lobster fishery in the Bay of Fundy. *N. Amer. J. Fish. Manage.* 5: 91–104.
- Caputi, N. 1988. Factors affecting the time series bias in stock-recruitment relationships and the interaction between time series and measurement error bias. *Can. J. Fish. Aquat. Sci.* 45: 178–184.
- Carlander, K.D. 1981. Caution on the use of the regression method of back-calculating length from scale measurements. *Fisheries* 6: 2–4. [See also Corrections. *Fisheries* 8: 25.]
- Carlander, K.D. 1987. A history of scale age and growth studies of North American freshwater fish. Pages 3–14 in R.C. Summerfelt and G.E. Hall, eds., *The Age and Growth of Fish*. Iowa State University Press, Ames.
- Carroll, R.J., and D. Ruppert. 1984. Power transformations when fitting theoretical models to data. *J. Amer. Stat. Assoc.* 79: 321–328.
- Casella, G., and E.I. George. 1992. Explaining the Gibbs sampler. *American Statistician* 46: 167–174.
- Casselman, J.M. 1990. Growth and relative size of calcified structures of fish. *Trans. Amer. Fish. Soc.* 119: 673–688.
- Caswell, H. 1989. Matrix Population Models. Sinauer Associates, Sunderland, Massachusetts.
- Caughley, G. 1967. Parameters for seasonally breeding populations. *Ecology* 48: 834–839.
- Cerrato, R.M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* 47: 1416–1426.

- Chapman, D.G. 1961. Statistical problems in dynamics of exploited fisheries populations. Proc. 4th Berkeley Symp. Math. Stat. Prob. Contr. Biol. Probl. Med. 4: 153–168.
- Chapman, D.G. 1973. Spawner-recruit models and estimation of the level of maximum sustainable catch. Cons. Int. Explor. Mer Rapp. et Proc.-Verb. 164: 325–332.
- Chapman, D.G., R.J. Myhre, and G.M. Southward. 1962. Utilization of Pacific halibut stocks: estimation of maximum sustainable yield, 1960. Int. Pac. Halibut Comm., Rep. 31, Seattle, Washington.
- Chapman, D.G., and D.S. Robson. 1960. The analysis of a catch curve. Biometrics 16: 354–368.
- Chiang, C.L. 1968. Introduction to Stochastic Processes in Biostatistics. Wiley, New York.
- Chilton, D.E., and R.J. Beamish. 1982. Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. Can. Spec. Pub. Fish. Aquat. Sci. 60.
- Clark, C.W. 1973. The economics of overexploitation. Science 181: 630–634.
- Clark, C.W. 1974. Possible effects of schooling on the dynamics of exploited fish populations. J. Cons. Int. Explor. Mer 36: 7–14.
- Clark, C.W. 1976a. Mathematical Bioeconomics. Wiley, New York.
- Clark, C.W. 1976b. A delayed recruitment model of population dynamics, with an application to baleen whale populations. J. Math. Biol. 3: 381–391.
- Clark, C.W. 1985. Bioeconomic Modelling and Fisheries Management. Wiley-Interscience, New York.
- Clark, C.W., and M. Mangel. 1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. U.S. Fish. Bull. 77: 317–337.
- Clark, W.G. 1975. A study of the virtual population of the Peruvian anchoveta in the years 1962–1972. Ph.D. Dissertation, University of Washington, Seattle.
- Clark, W.G. 1981. Restricted least-squares estimates of age composition from length composition. Can. J. Fish. Aquat. Sci. 38: 297–307.
- Clark, W.G. 1991. Groundfish exploitation rates based on life history parameters. Can. J. Fish. Aquat. Sci. 48: 734–750.
- Clark, W.G. 1993. The effect of recruitment variability on the choice of a target level of spawning biomass per recruit. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 233–246.
- Clifford, P. 1994. Discussion of the paper by Newton and Raftery. J. R. Statist. Soc. B 56: 34–35.
- Cloern, J.E., and F.H. Nichols. 1978. A von Bertalanffy growth model with seasonally varying coefficient. J. Fish. Res. Board Can. 35: 1479–1482.
- Cochran, W.G. 1977. Sampling Techniques, 2nd Edition. Wiley, New York.
- Cohen, J. E., S. W. Christensen, and C. P. Goodey. 1983. A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. Can. J. Fish. Aquat. Sci. 40: 2170–2183.
- Cohen, M.-D., and G. S. Fishman. 1980. Modeling growth-time and weight-length relationships in a single year-class fishery with examples for North Carolina pink and brown shrimp. Can. J. Fish. Aquat. Sci. 37: 1000–1011.
- Cohen, Y. 1987. A review of harvest theory and applications of optimal control theory in fisheries management. Can. J. Fish. Aquat. Sci. 44 (Suppl. 2): 75–83.
- Collie, J.S., R.M. Peterman, and C.J. Walters. 1990. Experimental harvest policies for a mixed-stock fishery: Fraser River sockeye salmon, *Oncorhynchus nerka*. Can. J. Fish. Aquat. Sci. 47: 145–155.
- Collie, J.S., and M.P. Sissenwine. 1983. Estimating population size from relative abundance data measured with error. Can. J. Fish. Aquat. Sci. 40: 1871–1879.
- Collie, J.S., and P.D. Spencer. 1993. Management strategies for fish populations subject to long-term environmental variability and depensatory predation. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 629–650.
- Collie, J.S., and C.J. Walters. 1991. Adaptive management of spatially replicated groundfish populations. Can. J. Fish. Aquat. Sci. 48: 1273–1284.

- Conser, R. 1993. A brief history of ADAPT. *Northw. Atl. Fish. Org., Sci. Council Studies* 17: 83–87. Dartmouth, Nova Scotia.
- Conser, R., and J.E. Powers. 1989. Extensions of the ADAPT VPA tuning method designed to facilitate assessment work on tuna and swordfish stocks. *Int. Comm. Conserv. Atlantic Tunas (ICCAT)*, Madrid, Spain Working Document SCRS/89/43.
- Cordue, P.L. 1993. MIAEL estimation of biomass and fishery indicators for the 1993 hoki assessment. *New Zealand Min. Agri. Fisheries, Fish. Assess. Res. Doc.* 93/15.
- Cordue, P.L., and R.I.C.C. Francis. 1994. Accuracy and choice in risk estimation for fisheries assessment. *Can. J. Fish. Aquat. Sci.* 51: 817–829.
- Cormack, R.M., and J.R. Skalski. 1992. Analysis of coded wire tag returns from commercial catches. *Can. J. Fish. Aquat. Sci.* 49: 1816–1825.
- Criddle, K.R. 1993. Optimal control of dynamic multispecies fisheries. *Univ. Alaska Sea Grant College Program, Rep. No. 93-02:* 609–628.
- Crone, P.R. 1995. Sampling design and statistical considerations for the commercial groundfish fishery of Oregon. *Can. J. Fish. Aquat. Sci.* 52: 716–732.
- Cushing, D.H. 1971. Dependence of recruitment on parent stock in different groups of fishes. *J. Cons. Int. Explor. Mer* 33: 340–362.
- Cushing, D.H. 1973. Dependence of recruitment on parent stock. *J. Fish. Res. Board Can.* 30: 1965–1976.
- Cushing, D.H., and J.W. Horwood. 1977. Development of a model of stock and recruitment. Pages 21–35 in J.H. Steele, ed., *Fisheries Mathematics*. Academic Press, London.
- Darroch, J.N. 1961. The two-sample capture-recapture census when tagging and sampling are stratified. *Biometrika* 48: 241–260.
- Davies, N., C. Walsh, and B. Hartill. 1993. Estimating catch at age of snapper from west coast and Hauraki Gulf fisheries, 1992–93. *MAF Fisheries North Region, Auckland, New Zealand, Internal Rep.* 17.
- Day, R.W. 1992. The determinants and measurement of abalone growth. Pages 141–168 in S.A. Shepherd, M.J. Tegner, and S.A. Guzman del Proo, eds., *Abalone of the World: Biology, Fisheries, and Culture*. Blackwell Scientific, Oxford.
- DeAngelis, D.L., L.J. Svoboda, S.W. Christensen, and D.S. Vaughan. 1980. Stability and return times of Leslie matrices with density-dependent survival: applications to fish populations. *Ecol. Model.* 8: 149–163.
- Dempson, J.B., and D.E. Stansbury. 1991. Using partial counting fences and a two-sample stratified design for mark-recapture estimation of an Atlantic smolt population. *N. Amer. J. Fish. Manage.* 11: 27–37.
- Dempster, A.P., N.M. Laird, and D.B. Rubin. 1977. Maximum likelihood estimation from incomplete data via the EM algorithm (with Discussion). *J. Royal Stat. Soc. B* 39: 1–38.
- Der Hovanessian, J.A. 1994. Stock assessment of rainbow trout in a Southeast Alaska impoundment. *M.S. Thesis, University of Alaska Fairbanks, Juneau.*
- Deriso, R.B. 1978. Nonlinear age-structured models for seasonally breeding populations. *Ph.D. Dissertation, University of Washington, Seattle.*
- Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age-structured model. *Can. J. Fish. Aquat. Sci.* 37: 268–282.
- Deriso, R.B. 1982. Relationship of fishing mortality and growth and the level of maximum sustainable yield. *Can. J. Fish. Aquat. Sci.* 39: 1054–1058.
- Deriso, R.B. 1985a. Management of the North Pacific Halibut Fishery, II. Stock assessment and new evidence of density-dependence. In *Real-time Fishery Management*. Washington Sea Grant Tech. Rep. WSG-85-1: 49–60.
- Deriso, R.B. 1985b. Risk adverse harvesting strategies. Pages 65–73 in *Proc. Second Ralf Yorque Conference. Lecture Notes in Biomathematics*. Springer-Verlag, Berlin.

- Deriso, R.B. 1987. Optimal $F_{0.1}$ criteria and their relationship to maximum sustainable yield. *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2): 339–348.
- Deriso, R.B., P.R. Neal, and T.J. Quinn II. 1989. Further aspects of catch-age analysis with auxiliary information. *Can. Spec. Pub. Fish. Aquat. Sci.* 108: 127–135.
- Deriso, R.B., and A. Parma. 1987. On the odds of catching fish with angling gear. *Trans. Amer. Fish. Soc.* 116: 244–256.
- Deriso, R.B., and A. M. Parma. 1988. Dynamics of age and size for a stochastic population model. *Can. J. Fish. Aquat. Sci.* 45: 1054–1068.
- Deriso, R.B., R.G. Punsly, and W.H. Bayliff. 1991. A Markov movement model of yellowfin tuna in the Eastern Pacific Ocean and some analyses for international management. *Fisheries Res.* 11: 375–395.
- Deriso, R.B., and T.J. Quinn II. 1983. The Pacific halibut resource and fishery in regulatory area 2, II. Estimates of biomass, surplus production, and reproductive value. *Int. Pac. Halibut Comm., Sci. Rep.* 67: 55–89.
- Deriso, R.B., T.J. Quinn II, and P.R. Neal. 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.* 42: 815–824.
- Dorazio, R.M., and P.J. Rago. 1991. Evaluation of a mark-recapture method for estimating mortality and migration rates of stratified populations. *Can. J. Fish. Aquat. Sci.* 48: 254–260.
- Doubleday, W.G. 1976a. Enhancing age-length keys. *Int. Council Northw. Atl. Fish, (ICNAF) Res. Doc. 75/99, Ser. 3585.*
- Doubleday, W.G. 1976b. A least-squares approach to analysing catch at age data. *Res. Bull., Int. Comm. Northw. Atl. Fish.* 12: 69–81.
- Doubleday, W.G., and D. Rivard (eds.). 1981. Bottom trawl surveys. *Can. Spec. Pub. Fish. Aquat. Sci.* 58.
- Doubleday, W.G., and D. Rivard (eds.). 1983. Sampling commercial catches of marine fish and invertebrates. *Can. Spec. Pub. Fish. Aquat. Sci.* 66.
- Doubleday, W.G., D. Rivard, and W.D. McKone. 1984. Estimation of partial recruitment and yield per recruit for an otter trawl fishery for deepwater redfish. *N. Amer. J. Fish. Manage.* 4: 15–31.
- Draper, N., and H. Smith. 1981. *Applied Regression Analysis*, 2nd edition. Wiley, New York.
- Dupont, W.D. 1983. A stochastic catch-effort method for estimating animal abundance. *Biometrics* 39: 1021–1033.
- Eames, M., T. Quinn, K. Reidinger, and D. Haring. 1981. Northern Puget Sound 1976 adult coho and chum tagging studies. *Washington Dep. Fisheries, Tech. Rep.* 64, Olympia, Washington.
- Eberhardt, L.L. 1970. Correlation, regression, and density dependence. *Ecology* 51: 306–310.
- Ebert, T.A. 1980. Estimating parameters in a flexible growth equation, the Richards function. *Can. J. Fish. Aquat. Sci.* 37: 687–692.
- Edgington, E.S. 1980. *Randomization Tests*. Marcel Dekker, New York.
- Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. *CBMS-NSF Reg. Comb. Ser. Appl. Math.* SIAM 38, Philadelphia, Pennsylvania.
- Efron, B., and R.J. Tibshirani. 1993. *An Introduction to the Bootstrap*. Chapman and Hall, New York.
- Eggers, D.M. 1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. *J. Fish. Res. Board Can.* 33: 1964–1971.
- Eggers, D.M., N.A. Rickard, D.G. Chapman, and R.R. Whitney. 1982. A methodology for estimating area fished for baited hooks and traps along a groundline. *Can. J. Fish. Aquat. Sci.* 39: 448–453.
- Ehrhardt, N.M., and J.S. Ault. 1992. Analysis of two length-based mortality models applied to bounded catch length frequencies. *Trans. Amer. Fish. Soc.* 121: 115–122.

- Erzini, K. 1990. Sample size and grouping of data for length-frequency analysis. *Fisheries Res.* 9: 355–366.
- Fagen, R., and W.W. Smoker. 1989. How large-capacity hatcheries can alter interannual variability of salmon production. *Fisheries Res.* 8: 1–11.
- Ferson, S. 1993. Using fuzzy arithmetic in Monte Carlo simulation of fishery populations. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 595–608.
- Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford.
- Fisher, M.E., and B.S. Goh. 1984. Stability results for delayed-recruitment models in population dynamics. *J. Math. Biol.* 19: 147–156.
- Fletcher, R. 1987. Practical Methods of Optimization, 2nd edition. Wiley-Interscience, New York.
- Fletcher, R.I. 1974. The quadric law of damped exponential growth. *Biometrics* 30: 111–124.
- Fletcher, R. I. 1975. A general solution for the complete Richards function. *Math. Biosci.* 27: 349–360.
- Fletcher, R.I. 1978a. Time-dependent solutions and efficient parameters for stock production models. *U.S. Fish. Bull.* 76: 377–388.
- Fletcher, R.I. 1978b. On the restructuring of the Pella-Tomlinson system. *U.S. Fish. Bull.* 76: 515–534.
- Fletcher, R.I. 1982. A class of nonlinear productivity equations from fishery science and a new formulation. *Math. Biosci.* 61: 279–293.
- Fletcher, R.I. 1987. Three optimization problems of year-class analysis. *J. Cons. Int. Explor. Mer* 43: 169–176.
- Fletcher, R. I., and R. B. Deriso. 1979. Appraisal of certain arguments, analysis, forecasts, and precedents contained in the utilities' evidentiary studies on power-plant insult to fish stocks of the Hudson River estuary. Vol. I. U.S. Environmental Protection Agency, Adjudicating Docket C/II-WP-77-01. New York.
- Fogarty, M.J., and S.A. Murawski. 1986. Population dynamics and assessment of exploited invertebrate stocks. *Can. Spec. Publ. Fish. Aquat. Sci.* 92: 228–244.
- Fogarty, M.J., M.P. Sissenwine, and E.B. Cohen. 1991. Recruitment variability and the dynamics of exploited marine populations. *Trends Ecol. Evol.* 6: 241–246.
- Ford, E. 1933. An account of the herring investigations conducted at Plymouth during the years from 1924–1933. *J. Mar. Biol. Assoc. U.K.* 19: 305–384.
- Foucher, R.P., and D. Fournier. 1982. Derivation of Pacific cod age composition using length-frequency analysis. *N. Amer. J. Fish. Manage.* 2: 276–284.
- Fournier, D.A. 1983. The use of age and length data for estimating the age structure of a collection of fish. *Can. Spec. Pub. Fish. Aquat. Sci.* 66: 206–208.
- Fournier, D. 1996. An introduction to AD Model Builder for use in nonlinear modeling and statistics. Otter Research Ltd., Nanaimo, BC, Canada.
- Fournier, D.A., and C.P. Archibald. 1982. A general theory for analyzing catch at age data. *Can. J. Fish. Aquat. Sci.* 39: 1195–1207.
- Fournier, D.A., and P.A. Breen. 1983. Estimation of abalone mortality rates with growth analysis. *Trans. Amer. Fish. Soc.* 112: 403–411.
- Fournier, D.A., and I.J. Doonan. 1987. A length-based stock assessment method utilizing a generalized delay-difference model. *Can. J. Fish. Aquat. Sci.* 44: 422–437.
- Fournier, D.A., and A.R. Warburton. 1989. Evaluating fisheries management models by simulated adaptive control—introducing the composite model. *Can. J. Fish. Aquat. Sci.* 46: 1002–1012.
- Fournier, D.A., J.R. Sibert, J. Majkowski, and J. Hampton. 1990. MULTIFAN: a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). *Can. J. Fish. Aquat. Sci.* 47: 301–317.

- Fox, W.W. 1970. An exponential yield model for optimizing exploited fish populations. *Trans. Amer. Fish. Soc.* 99: 80–88.
- Fox, W.W., Jr. 1975. Fitting the generalized stock production model by least-squares and equilibrium approximation. *U.S. Fish. Bull.* 73: 23–37.
- Francis, R.C. 1974. Relationship of fishing mortality to natural mortality at the level of maximum sustainable yield under the logistic stock production model. *J. Fish. Res. Board Can.* 31: 1539–1542.
- Francis, R.I.C.C. 1988a. Are growth parameters estimated from tagging and age-length data comparable? *Can. J. Fish. Aquat. Sci.* 45: 936–942.
- Francis, R.I.C.C. 1988b. Maximum likelihood estimation of growth and growth variability from tagging data. *New Zealand J. Marine Freshw. Res.* 22: 43–51.
- Francis, R.I.C.C. 1990. A maximum likelihood stock reduction method. *New Zealand Min. Agri. Fish., Fisheries Assess. Res. Doc.* 90/4, Wellington.
- Francis, R.I.C.C. 1990. Back-calculation of fish length: a critical review. *J. Fish Biol.* 36: 883–902.
- Francis, R.I.C.C. 1992. Use of risk analysis to assess fishery management strategies: a case study using orange roughy (*Hoplostethus atlanticus*) on the Chatham Rise, New Zealand. *Can. J. Fish. Aquat. Sci.* 49: 922–930.
- Francis, R.I.C.C. 1993a. Monte Carlo evaluation of risks for biological reference points used in New Zealand fishery assessments. *Can. Spec. Publ. Fish. Aquat. Sci.* 120: 221–230.
- Francis, R.I.C.C. 1993b. The interpretation of “Probability”: a response to Walters’ comments. *Can. J. Fish. Aquat. Sci.* 50: 882–883.
- Francis, R.I.C.C. 1995. An alternative mark-recapture analogue of Schnute’s growth model. *Fisheries Res.* 23: 95–111.
- Francis, R.I.C.C., and R. Shotton. 1997. “Risk” in fisheries management: a review. *Can. J. Fish. Aquat. Sci.* 54: 1699–1715.
- Frederick, S.W., and R.M. Peterman. 1995. Choosing fisheries harvest policies: when does uncertainty matter? *Can. J. Fish. Aquat. Sci.* 52: 291–306.
- Freon, P. 1988. Introduction of environmental variables into global production models. Pages 481–528 in T. Wyatt and M.G. Larraneta, eds., *Int. Symp. Long Term Changes Mar. Fish Pop.*, Vigo, Spain. Consejo Superior de Investigaciones Científicas.
- Freon, P., C. Mullon, and G. Pichon. 1990. Climprod: a fully interactive expert-system software for choosing and adjusting a global production model which accounts for changes in environmental factors. Pages 347–357 in T. Kauasaki, S. Tanaka, Y. Toba, and A. Taniguchi, (eds.), *Long-term variability of pelagic fish populations and their environment*. Pergamon Press, Oxford.
- Fry, F.E.J. 1949. Statistics of a lake trout fishery. *Biometrics* 5: 26–67.
- Fujioka, J.T. 1993. Sablefish. Pages 4-1 to 4-13 in Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1994. North Pacific Fishery Management Council, Anchorage, AK.
- Fujioka, J.T., J. Heifetz, and M.F. Sigler. 1997. Choosing a harvest strategy for sablefish, *Anoplopoma fimbria*, based on uncertain life-history parameters. NOAA Tech. Rep. NMFS 130: 247–251.
- Fukushima, M.F. 1996. Effects of density-dependence, environment, and species interaction during spawning and incubation on population dynamics of pink and sockeye salmon in the Auke Lake system, Southeast Alaska. Ph.D. Dissertation, Univ. of Alaska-Fairbanks, Juneau.
- Fuller, W.A. 1987. *Measurement Error Models*. Wiley, New York.
- Gabriel, W.L., M.P. Sissenwine, and W.J. Overholtz. 1989. Analysis of spawning stock biomass per recruit: an example for Georges Bank haddock. *N. Amer. J. Fish. Manage.* 9: 383–391.
- Gallant, A.R. 1987. *Nonlinear Statistical Models*. Wiley, New York.

- Gallucci, V.F., and T.J. Quinn II. 1979. Reparameterizing, fitting, and testing a simple growth model. *Trans. Amer. Fish. Soc.* 108: 14–25.
- Gallucci, V.F., S.B. Saila, D.J. Gustafson, and B.J. Rothschild (eds.). 1996. Stock Assessment: Quantitative Methods and Applications for Small-Scale Fisheries. CRC Press, Boca Raton, FL.
- Gani, J. 1973. Stochastic formulations for life tables, age distributions, and mortality curves. Pages 291–302 in M.S. Bartlett and R.W. Hoirns, eds., *The Mathematical Theory of the Dynamics of Biological Populations*. Academic Press, New York.
- Garcia, O. 1983. A stochastic differential equation model for the height growth of forest stands. *Biometrics* 39: 1059–1072.
- Garcia, S., P. Sparre, and J. Csirke. 1989. Estimating surplus production and maximum sustainable yield from biomass data when catch and effort time series are not available. *Fisheries Res.* 8: 13–23.
- Gavaris, S. 1980. Use of a multiplicative model to estimate catch rate and effort from commercial data. *Can. J. Fish. Aquat. Sci.* 37: 2272–2275.
- Gavaris, S. 1988. An adaptive framework for the estimation of population size. *Can. Atl. Fish. Sci. Adv. Comm. (CAFSAC) Research Doc.* 88/29.
- Gavaris, S., and C.A. Gavaris. 1983. Estimation of catch at age and its variance for groundfish stocks in the Newfoundland region. *Can. Spec. Publ. Fish. Aquat. Sci.* 66: 178–182.
- Geiger, H.J., and J.P. Koenings. 1991. Escapement goals for sockeye salmon with informative prior probabilities based on habitat considerations. *Fisheries Res.* 11: 239–256.
- Gelman, A., J.B. Carlin, H.S. Stern, and D.B. Rubin. 1995. *Bayesian Data Analysis*. Chapman and Hall, London.
- Gerrodette, T., D. Goodman, and J. Barlow. 1985. Confidence limits for population projections when vital rates vary randomly. *U.S. Fish. Bull.* 83: 207–217.
- Getz, W.M. 1985. Optimal and feedback strategies for managing multicohort populations. *J. Optimization Th. and App.* 46: 505–514.
- Getz, W. M., and R.G. Haight. 1989. *Population Harvesting: Demographic Models of Fish, Forest, and Animal Resources*. Princeton University Press, Princeton, New Jersey.
- Getz, W.M., and G.L. Swartzman. 1981. A probability transition matrix model for yield estimation in fisheries with highly variable recruitment. *Can. J. Fish. Aquat. Sci.* 38: 847–855.
- Givens, G.H., Raftery, A.E., and J.E. Zeh. 1993. Benefits of a Bayesian approach for synthesizing multiple sources of evidence and uncertainty linked by a deterministic model. *Rep. Int. Whal. Comm.* 43: 495–500.
- Goldberg, S. 1958. *Introduction to Difference Equations*. Wiley, New York.
- Gonzalez, S.A. 1987. Age and growth of *Concholepas concholepas* (Brugiere 1789) using microgrowth structure and spectral analysis. M.S. Thesis, University of Washington, Seattle.
- Goodyear, C.P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. *Can. Spec. Publ. Fish. Aquat. Sci.* 120: 67–82.
- Goodyear, C. P., and S. W. Christensen. 1984. Bias-elimination in fish population models with stochastic variation in survival of the young. *Trans. Amer. Fish. Soc.* 113: 627–632.
- Gordon, G., M. O'Callaghan, and G.M. Tallis. 1970. A deterministic model for the life cycle of a class of internal parasites of sheep. *Math. Biosci.* 8: 209–226.
- Gordon, G.N.G., N.L. Andrew, and S.S. Montgomery. 1995. Deterministic compartmental model for the eastern king prawn (*Penaeus plebejus*) fishery in New South Wales. *Mar. Freshw. Res.* 46: 793–807.
- Graham, M. 1935. Modern theory of exploiting a fishery and applications to North Sea trawling. *J. Cons. Int. Explor. Mer* 10: 264–274.
- Grant, W.E., J.H. Matis, and T.H. Miller. 1991. A stochastic compartmental model for migration of marine shrimp. *Ecol. Model.* 54: 1–15.

- Gribble, N., and M. Dredge. 1994. Mixed-species yield-per-recruit simulations of the effect of seasonal closure on a central Queensland coast prawn trawling ground. *Can. J. Fish. Aquat. Sci.* 51: 998–1011.
- Gudmundsson, G. 1986. Statistical considerations in the analysis of catch-at-age observations. *J. Cons. Int. Explor. Mer* 43:83–90.
- Gudmundsson, G. 1987. Time series models of fishing mortality rates. *Raunvisindastofnun Haskolans, Univ. Iceland, Reykjavik. Rep. RH-02-87.*
- Gudmundsson, G. 1994. Time series analysis of catch-at-age observations. *Appl. Stat.* 43: 117–126.
- Gudmundsson, G. 1995. Time series analysis of catch-at-length data. *ICES J. Mar. Sci.* 52: 781–795.
- Gulland, J.A. 1955. On the estimation of population parameters from marked members. *Biometrika* 42: 269–270.
- Gulland, J.A. 1961. Fishing and the stocks of Iceland. *Fish. Invest. Minist. Agric. Fish. Food, U.K., Series II, XXIII(4):* 1–52. London.
- Gulland, J.A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Workshop Group Report. *Int. Counc. Explor. Sea CM 1965, Doc. 3. Mimeo. Copenhagen.*
- Gulland, J.A. 1970. The fish resources of the ocean. *U.N. FAO Fish. Tech. Pap.* 97. Rome.
- Gulland, J.A. 1971. Science and fishery management. *J. Cons. Int. Explor. Mer* 33: 471–477.
- Gulland, J.A. 1978. Fishery management: new strategies for new conditions. *Trans. Amer. Fish Soc.* 107: 1–11.
- Gulland, J.A. 1983. *Fish Stock Assessment.* Wiley, Chichester, UK.
- Gulland, J.A., and L.K. Boerema. 1973. Scientific advice on catch levels. *U.S. Fish. Bull.* 71: 325–335.
- Gunderson, D.R. 1980. Using *r-K* selection theory to predict natural mortality. *Can. J. Fish. Aquat. Sci.* 37: 2266–2271.
- Gunderson, D.R. 1995. *Surveys of Fisheries Resources.* John Wiley and Sons, New York.
- Gutreuter, S. 1987. Considerations for estimation and interpretation of annual growth rates. Pages 115–126 in R.C. Summerfelt and G.E. Hall, eds., *The Age and Growth of Fish.* Iowa State University Press, Ames.
- Hagen, P.T., and T.J. Quinn II. 1991. Long-term growth dynamics of young Pacific halibut: evidence of temperature-induced variation. *Fisheries Res.* 11: 283–306.
- Haist, V., D.A. Fournier, and J.F. Schweigert. 1993. Estimation of density-dependent natural mortality in British Columbia herring stocks through SSPA and its impact on sustainable harvesting strategies. *Can. Spec. Publ. Fish. Aquat. Sci* 120: 269–282.
- Hamley, J.M. 1975. Review of gillnet selectivity. *J. Fish. Res. Board Can.* 32:1943–1969.
- Hampton, J. 1991a. Estimation of southern bluefin tuna *Thunnus maccoyii* growth parameters from tagging data, using von Bertalanffy models incorporating individual variation. *U.S. Fish. Bull.* 89: 577–590.
- Hampton, J. 1991b. Estimation of southern bluefin tuna *Thunnus maccoyii* natural mortality and movement rates from tagging experiments. *U.S. Fish. Bull.* 89: 591–610.
- Hampton, J., and D. Fournier. 1996. South Pacific albacore stock assessment using the regionalized SPARCLE model. Sixth South Pacific Albacore Research Workshop, Working Paper No. 4, South Pacific Commission, Noumea, New Caledonia.
- Hanumara, R.C., and N.A. Hoenig. 1987. An empirical comparison of a fit of linear and non-linear models for seasonal growth in fish. *Fisheries Res.* 5: 359–381.
- Harding, J.P. 1949. The use of probability paper for graphical analysis of polymodal frequency distributions. *J. Mar. Biol. Assoc. U.K.* 28: 141–153.
- Hasselblad, V. 1966. Estimation of parameters for a mixture of normal distributions. *Technometrics* 8: 431–444.

- Hastie, T.J., and R.S. Tibshirani. 1990. Generalized Additive Models. Chapman and Hall, New York.
- Hayes, D.B. 1993. A statistical method for evaluating differences between age-length keys with application to Georges Bank haddock, *Melanogrammus aeglefinus*. U.S. Fish. Bull. 91: 550–557.
- Hayes, D.B., J.K.T. Brodziak, and J.B. O'Gorman. 1995. Efficiency and bias of estimators and sampling designs for determining length-weight relationships of fish. Can. J. Fish. Aquat. Sci. 52: 84–92.
- Hearon, J. X. 1976. Properties of the Leslie population matrix. Bull. Math. Bio. 38: 199–203.
- Hearn, W.S., R.L. Sandland, and J. Hampton. 1987. Robust estimation of the natural mortality rate in a completed tagging experiment with variable fishing intensity. J. Cons. Int. Explor. Mer 43: 107–117.
- Heifetz, J. 1996. Dynamics of a migratory fish population with applications to the management of sablefish in the NE Pacific Ocean. Ph.D. Dissertation, Univ. of Alaska-Fairbanks, Juneau.
- Heifetz, J., D.M. Clausen, and J.N. Ianelli. 1994. Slope rockfish. In Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1995. North Pacific Fishery Management Council, Anchorage, Alaska.
- Heifetz, J., and J.T. Fujioka. 1991. Movement dynamics of tagged sablefish in the northeastern Pacific. Fisheries Res. 11: 355–374.
- Heifetz, J., J.T. Fujioka, and T.J. Quinn II. 1997. Geographic apportionment of sablefish harvest in the northeastern Pacific Ocean. NOAA Tech. Rep. NMFS 130: 229–237.
- Hennemuth, R.C., J.E. Palmer, and J.E. Brown. 1980. A statistical description of recruitment in 18 selected fish stocks. J. NW. Atl. Fish. Soc. 1: 101–111.
- Hewitt, R.P. 1985. Comparison between egg production method and larval census method for fish biomass assessment. U.S. Dept. Comm., NOAA Tech. Rep. NMFS 36: 95–99. Washington, DC.
- Hightower, J.E., and G.D. Grossman. 1987. Optimal policies for rehabilitation of overexploited fish stocks using a deterministic model. Can. J. Fish. Aquat. Sci. 44: 803–810.
- Hightower, J.E., and W.H. Lenarz. 1989. Optimal harvesting policies for the widow rockfish fishery. Amer. Fish. Soc. Symp. 6: 83–91.
- Hilborn, R. 1976. Optimal exploitation of multiple stocks by a common fishery: a new methodology. J. Fish. Res. Board Can. 33: 1–5.
- Hilborn, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. J. Fish. Res. Board Can. 36: 1477–1489.
- Hilborn, R. 1985. Fleet dynamics and individual variation: why some people catch more fish than others. Can. J. Fish. Aquat. Sci. 42: 2–13.
- Hilborn, R. 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Can. J. Fish. Aquat. Sci. 47: 635–643.
- Hilborn, R., and M. Ledbetter. 1985. Determinants of catching power in the British Columbia salmon purse seine fleet. Can. J. Fish. Aquat. Sci. 42: 51–56.
- Hilborn, R., E.K. Pikitch, and R.C. Francis. 1993. Current trends in including risk and uncertainty in stock assessment and harvest decisions. Can. J. Fish. Aquat. Sci. 50: 874–880.
- Hilborn, R., E.K. Pikitch, and M.K. McAllister. 1994. A Bayesian estimation and decision analysis for an age-structured model using biomass survey data. Fish. Res. 19: 17–30.
- Hilborn, R., and C.J. Walters. 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics, & Uncertainty. Chapman and Hall, New York.
- Hinton, M.G. 1996. Standardizing catch and effort statistics using physiological, ecological, or behavioral constraints, and environmental data, with applications to blue marlin *Makaira nigricans* and swordfish *Xiphias gladius* of the Pacific Ocean. Ph.D. Dissertation, Univ. Calif.-San Diego, La Jolla.

- Hoag, S.H., R.B. Deriso, and G. St-Pierre. 1984. Recent changes in halibut CPUE: Studies on area differences in setline catchability. *Int. Pac. Halibut Comm., Sci. Rep.* 71.
- Hoag, S.H., and R.J. MacNaughton. 1978. Abundance and fishing mortality of Pacific halibut, cohort analysis, 1935–1976. *Int. Pac. Halibut Comm., Sci. Rep.* 65.
- Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *U.S. Fish. Bull.* 82: 898–903.
- Hoenig, J.M., and D.M. Heisey. 1987. Use of a log-linear model with the EM algorithm to correct estimates of stock composition and to convert length to age. *Trans. Amer. Fish. Soc.* 116: 232–243.
- Hoenig, J.M., W.D. Lawing, and N.A. Hoenig. 1983. On estimating the total mortality rate from mean age, mean length, or median length. *Proc. Int. Council for Explor. of the Sea, Copenhagen, Denmark.*
- Hoenig, J.M., W.G. Warren, and M. Stocker. 1994. Bayesian and related approaches to fitting surplus production models. *Can. J. Fish. Aquat. Sci.* 51: 1823–1831.
- Hoenig, N.A., and R.C. Hanumara. 1982. A statistical study of a seasonal growth model for fishes. *Univ. Rhode I., Dept. Comp. Sci., Tech. Rep., Narragansett.*
- Hollowed, A.B., and B.A. Megrey. 1993. Evaluations of risks associated with application of alternative harvest strategies for Gulf of Alaska walleye pollock. *Univ. Alaska Sea Grant College Program, Rep. No. 93-02:* 291–320.
- Hollowed, A.B., E. Brown, J. Ianelli, P. Livingston, B. Megrey, and C. Wilson. 1997. Walleye pollock. In *Stock Assessment and Fishery Evaluation for the Gulf of Alaska, November 1997, North Pac. Fishery Manage. Council, Anchorage, AK.*
- Holling, C.S. 1966. The functional response of invertebrate predators to prey density. *Mem. Ent. Soc. Can.* 48: 1–86.
- Honma, M. 1974. Estimation of overall effective fishing intensity of tuna longline fishery. *Bull. Far Seas Fish. Res. Lab.*, No. 10: 63–85.
- Horbowy, J. 1992. The differential alternative to the Deriso difference production model. *ICES J. Mar. Sci.* 49: 167–174.
- Horwood, J.W. 1987. A calculation of optimal fishing mortalities. *J. Cons. Int. Explor. Mer* 43: 199–208.
- Horwood, J.W. 1993. Stochastic locally-optimal harvesting. *Can. Spec. Publ. Fish. Aquat. Sci* 120: 333–343.
- Horwood, J.W., and P. Whittle. 1986a. Optimal control in the neighborhood of an optimal equilibrium with examples from fisheries models. *I.M.A. J. Math. Appl. Med. Biol.* 3: 129–142.
- Horwood, J.W., and P. Whittle. 1986b. The optimal harvest from a multicohort stock. *I.M.A. J. Math. Appl. Med. Biol.* 3: 143–155.
- Hunter, J.R., and B.J. Macewicz. 1985. Measurement of spawning frequency in multiple spawning fishes. *U.S. Dept. Comm., NOAA Tech. Rep. NMFS* 36: 79–94.
- Hunter, J.R., N.C.H. Lo, and R.J.H. Leong. 1985. Batch fecundity in multiple spawning fishes. *NOAA Tech. Rep. NMFS* 36: 67–77.
- Huntsman, G.R., and W.E. Schaaf. 1994. Simulation of the impact of fishing on reproduction of a protogynous grouper, the Graysby. *N. Amer. J. Fish. Manage.* 14: 41–52.
- Huson, R.M., D. Rivard, W.G. Doubleday, and W.D. McKone. 1984. Impact of varying mesh size and depth of fishing on the financial performance of an integrated harvesting/processing operation for redfish in the Northwest Atlantic. *N. Amer. J. Fish. Manage.* 4: 32–47.
- Ianelli, J. 1996. An alternative stock assessment model of the eastern Bering Sea pollock fishery. Pages 81–104 in *Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea / Aleutian Islands regions, November 1996. North Pacific Fishery Management Council, Anchorage, Alaska.*

- Ianelli, J.N., and J. Heifetz. 1995a. Decision analysis of alternative harvest policies for the Gulf of Alaska Pacific ocean perch fishery. *Fisheries Res.* 24: 35–63.
- Ianelli, J.N., and J. Heifetz. 1995b. Erratum to Decision analysis of alternative harvest policies for the Gulf of Alaska Pacific ocean perch fishery. *Fisheries Res.* 24: 345–349.
- ICES. 1984. Report of the working group on long-term management measures. ICES C.M. 1984/Assess: 11. International Council for the Exploration of the Sea.
- ICES. 1993. Report of the working group on methods of fish stock assessments, Copenhagen 1987, Reykjavik 1988, and Nantes 1989. ICES Coop. Res. Rep. 191. International Council for Exploration of the Sea.
- IPHC. 1981. Annual Report 1980. International Pacific Halibut Commission.
- IPHC. 1985. Annual Report 1984. International Pacific Halibut Commission.
- Ishii, T. 1979. Attempt to estimate migration of fish population with survival parameters from tagging experiment data by the simulation method. *Inv. Pesq.* 43: 301–317.
- Ivlev, V.S. 1961. *Experimental Ecology of the Feeding of Fishes*. Yale Univ. Press, New Haven, Connecticut.
- Jacobson, L.D., and A.D. MacCall. 1995. Stock-recruitment models for Pacific sardine (*Sardinops sagax*). *Can. J. Fish. Aquat. Sci.* 52: 566–577.
- Jakobsen, T. 1992. Biological reference points for North-East Arctic cod and haddock. *ICES J. Mar. Sci.* 49: 155–166.
- Jakobsen, T. 1993a. Management of Northeast Arctic cod: past, present—and future? *Univ. Alaska Sea Grant College Program, Rep. No. 93-02*: 321–338.
- Jakobsen, T. 1993b. The behavior of F_{low} , F_{med} , and F_{high} in response to variation in parameters used for their estimation. *Can. Spec. Publ. Fish. Aquat. Sci.* 120: 119–126.
- Jensen, A.L. 1984a. Logistic surplus-production models with explicit terms for growth, mortality, and recruitment. *Trans. Amer. Fish. Soc.* 113: 617–626.
- Jensen, A.L. 1984b. Non-linear catch curves resulting from variation in mortality among subpopulations. *J. Cons. Int. Explor. Mer* 41: 121–124.
- Jensen, A.L. 1985. Comparison of catch curve methods for estimation of mortality. *Trans. Amer. Fish. Soc.* 114: 743–747.
- Jensen, R.V. 1987. Classical chaos. *Amer. Scientist* 75: 168–175.
- Jinn, J.H., J. Sedransk, and P. Smith. 1987. Optimal two-phase stratified sampling for estimation of the age composition of a fish population. *Biometrics* 43: 343–353.
- Johnson, S.J., and T.J. Quinn, II. 1987. Length frequency analysis of sablefish in the Gulf of Alaska. Contract report to Auke Bay National Laboratory. University of Alaska, School of Fisheries and Science, Tech. Rep. UAJ-SFS-8714. Juneau, Alaska.
- Jolicoeur, P. 1975. Linear regressions in fishery research: some comments. *J. Fish. Res. Board Can.* 32: 1491–1494.
- Jones, R. 1981. The use of length composition data in fish stock assessments (with notes on VPA and cohort analysis). U.N. FAO Fisheries Circ. 734, Rome.
- Kappenman, R. F. 1981. A method for growth curve comparisons. *U.S. Fish. Bull.* 79: 95–101.
- Karlin, S., and H.M. Taylor. 1975. *A First Course in Stochastic Processes*. Academic Press, New York.
- Kearney, R.E. 1991. Extremes in fish biology, population dynamics, and fisheries management: Pacific skipjack and southern bluefin tuna. *Rev. Aquat. Sci.* 4: 289–298.
- Kendall, Sir M., and A. Stuart. 1979. *Advanced Theory of Statistics*, vol. II: Inference and Relationship. Charles Griffin and Sons, Bucks, UK.
- Kennedy, W.J., Jr., and J.E. Gentle. 1980. *Statistical Computing*. Marcel Dekker, New York.
- Ketchen, K.S. 1950. Stratified subsampling for determining age distributions. *Trans. Amer. Fish. Soc.* 79: 205–212.
- Keyfitz, N. 1968. *Introduction to the mathematics of population*. Addison-Wesley, Reading, Massachusetts.

- Kimura, D.K. 1977. Statistical assessment of the age-length key. *J. Fish. Res. Board Can.* 34: 317–324.
- Kimura, D.K. 1980. Likelihood methods for the von Bertalanffy growth curve. *U.S. Fish. Bull.* 77: 765–776.
- Kimura, D.K. 1981. Standardized measures of relative abundance based on modeling log (CPUE) and their application to Pacific ocean perch (*Sebastodes alutus*). *J. Cons. Int. Explor. Mer* 39: 211–218.
- Kimura, D.K. 1985. Changes to stock reduction analysis indicated by Schnute's general theory. *Can. J. Fish. Aquat. Sci.* 42: 2059–2060.
- Kimura, D.K. 1988a. Analyzing relative abundance indices with log-linear models. *N. Amer. J. Fish. Manage.* 8: 175–180.
- Kimura, D.K. 1988b. Stock-recruitment curves as used in the stock reduction analysis model. *J. Cons. Int. Explor. Mer* 44: 253–258.
- Kimura, D.K. 1989a. Variability in estimating catch in numbers at age and its impact on cohort analysis. *Can. Spec. Pub. Fish. Aquat. Sci.* 108: 57–66.
- Kimura, D.K. 1989b. Variability, tuning, and simulation for the Doubleday-Deriso catch-at-age model. *Can. J. Fish. Aquat. Sci.* 46: 941–949.
- Kimura, D.K. 1990. Approaches to age-structured separable sequential population analysis. *Can. J. Fish. Aquat. Sci.* 47: 2364–2374.
- Kimura, D.K., J.W. Balsiger, and D.H. Ito. 1984. Generalized stock reduction analysis. *Can. J. Fish. Aquat. Sci.* 41: 1325–1333.
- Kimura, D.K., and S. Chikuni. 1987. Mixtures of empirical distributions: an iterative application of the age-length key. *Biometrics* 43: 23–35.
- Kimura, D.K., and J.V. Tagart. 1982. Stock reduction analysis: another solution to the catch equations. *Can. J. Fish. Aquat. Sci.* 39: 1467–1472.
- Kinas, P.G. 1993. Bayesian statistics for fishery stock assessment and management. Ph.D. Dissertation, University of British Columbia, Vancouver BC.
- Kinas, P.G. 1996. Bayesian fishery stock assessment and decision making using adaptive importance sampling. *Can. J. Fish. Aquat. Sci.* 53: 414–423.
- Kingsley, M.C.S. 1979. Fitting the von Bertalanffy growth equation to polar bear age-weight data. *Can. J. Zool.* 57: 1020–1025.
- Kingsley, M.C.S., V.F. Gallucci, and T.J. Quinn II. 1980. Comments: von Bertalanffy growth parameters. *Trans. Amer. Fish. Soc.* 109: 252–253.
- Kirkpatrick, M. 1984. Demographic models based on size, not age, for organisms with indeterminate growth. *Ecology* 65: 1874–1884.
- Kirkwood, G. P. 1983. Estimation of von Bertalanffy growth curve parameters using both length increment and age-length data. *Can. J. Fish. Aquat. Sci.* 40: 1405–1411.
- Kirkwood, G. P., and I.F. Somers. 1984. Growth of two species of tiger prawn *Penaeus esculentus* and *Penaeus semisulcatus* in the western Gulf of Carpentaria. *Aust. J. Mar. Freshw. Res.* 35: 703–712.
- Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. *J. Fish. Res. Board Can.* 25: 1303–1307.
- Koopman, B.O. 1980. Search and Screening. Pergamon Press, New York.
- Kope, R.G. 1992. Optimal harvest rates for mixed stocks of natural and hatchery fish. *Can. J. Fish. Aquat. Sci.* 49: 931–938.
- Koslow, J.A. 1989. Managing nonrandomly varying fisheries. *Can. J. Fish. Aquat. Sci.* 46: 1302–1308.
- Kruse, G., D.M. Eggers, R.J. Marasco, C. Pautzke, and T.J. Quinn II (eds.). 1993. Proc. Int. Symp. on Management Strategies for Exploited Fish Populations. Alaska Sea Grant College Program Rep. 93-02, University of Alaska-Fairbanks, Fairbanks.

- Kutkuhn, J.H. 1963. Estimating absolute age composition of California sardine landings. Calif. Fish. Bull. 120.
- Laevastu, T., and H.A. Larkins. 1981. Marine Fishery Ecosystem—Its Quantitative Evaluation and Management. Fishing News Books, Guildfoul.
- Lafferty, R., and T.J. Quinn, II. 1987. Population studies of Kenai River rainbow trout. Annual report to Sport Fish Division, Alaska Fish and Game. University of Alaska, School of Fisheries and Science, Tech. Rep. UAJ-SFS-8706. Juneau, AK.
- Lai, H.-L. 1987. Optimum allocation for estimating age composition using age-length key. U.S. Fish. Bull. 85: 179–185.
- Lai, H.-L., and V.F. Gallucci. 1988. Effects of parameter variability on length cohort analysis. J. Cons. Int. Explor. Mer 45: 82–92.
- Lapointe, M.F., and R.M. Peterman. 1991. Spurious correlations between fish recruitment and environmental factors due to errors in the natural mortality rate used in virtual population analysis (VPA). ICES J. Mar. Sci. 48: 219–228.
- Larkin, P.A. 1973. Some observations on models of stock and recruitment relationships for fishes. Conseil Int. Explor. Mer, Rapp. et Proc.-Verb. 164: 316–324.
- Larkin, P.A. 1977. An epitaph for the concept of maximum sustainable yield. Trans. Amer. Fish. Soc. 106: 1–11.
- Larkin, P.A., and I.G. McDonald. 1968. Factors in the population biology of the sockeye salmon of the Skeena River. J. Animal Ecol. 37: 229–258.
- Lasker, R. (ed.). 1985a. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. U.S. Dept. Comm., NOAA Tech. Rep. NMFS 36. Washington, DC.
- Lasker, R. 1985b. Introduction. U.S. Dept. Comm., NOAA Tech. Rep. NMFS 36: 1–3.
- Lassen, H. 1983. Estimation of stock size and fishing mortality when data on catches and abundance are available. ICES Stat. Comm. CM 1983/5: 14 pp.
- Laurec, A., and J.G. Shepherd. 1983. On the analysis of catch and effort data. J. Cons. Int. Explor. Mer 41: 81–84.
- Law, R., and M.T. Edley. 1990. Transient dynamics of populations with age- and size-dependent vital rates. Ecology 71: 1863–1870.
- Lawson, T.A., and R. Hilborn. 1985. Equilibrium yields and yield isopleths from a general age-structured model of harvested populations. Can. J. Fish. Aquat. Sci. 42: 1766–1771.
- Leaman, B.M. 1993. Reference points for fisheries management: the western Canadian experience. Can. Spec. Publ. Fish. Aquat. Sci 120: 15–30.
- Lee, R.M. 1912. An investigation into the methods of growth determination in fishes. Cons. Explor. Mer, Publ. De Circonference 63: 35 pp.
- Lefkovitch, L.P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21: 1–18.
- Leigh, G.M. 1988. A comparison of estimates of natural mortality from fish tagging experiments. Biometrika 75: 347–353.
- Leslie, P. H. 1945. One the use of matrices in certain population mathematics. Biometrika 3: 183–212.
- Leslie, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria Aalge* Pont.) J. Anim. Ecol. 35: 291–301.
- Levin, S. A., and C. P. Goodyear. 1980. Analysis of an age-structured fishery model. J. Math. Biol. 9:245–274.
- Levins, R. 1969. The effect of random variations of different types on population growth. Proc. Natl. Acad. Sci. 62: 1061–1065.
- Lewis, E.G. 1942. On the generation and growth of a population. Sankya: Indian J. Stat. 6: 93–96.
- Liang, D.F. 1982a. Exact and approximate nonlinear estimation techniques. In Advances in

- the techniques and technology of the application of nonlinear filters and Kalman filters. N.A.T.O. Advisory Group for Aerospace Research and Development. Rep. AGARD-AG-256, Neuilly Sur Seine, France.
- Liang, D.F. 1982b. Comparisons of nonlinear filters for systems with non-negligible nonlinearities. In Advances in the techniques and technology of the application of nonlinear filters and Kalman filters. N.A.T.O. Advisory Group for Aerospace Research and Development. Rep. AGARD-AG-256, Neuilly Sur Seine, France.
- Liang, D.F., and G.S. Christensen. 1978. Estimation for discrete nonlinear time-delayed systems and measurements with correlated and coloured noise processes. *Int. J. Control* 28: 1–10.
- Lierman, M., and R. Hilborn. 1997. Depensation in fish stocks: a hierachic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* 54: 1976–1984.
- Lindley, D.V. 1983. Theory and practice of Bayesian statistics. *The Statistician* 32: 1–11.
- Lipinski, M.R., and M.A. Roeleveld. 1990. Minor extension of the von Bertalanffy growth theory. *Fisheries Res.* 9: 367–371.
- Lo, N.C.H., L.D. Jacobson, and J.L. Squire. 1992. Indices of relative abundance from fish spotter data based on delta-lognormal models. *Can. J. Fish. Aquat. Sci.* 49: 2515–2526.
- Lowe, S.A., and G.G. Thompson. 1993. Accounting for uncertainty in the development of exploitation strategies for the Atka mackerel resource of the Aleutian Islands. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 203–231.
- Lowe, S.A., J.M. Terry, and J.T. Fujioka. 1991. Bioeconomic analysis of a minimum size limit for Gulf of Alaska sablefish using a yield per recruit model. *Fisheries Res.* 11: 307–320.
- Ludwig, D., and C.J. Walters. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. *Can. J. Fish. Aquat. Sci.* 38: 711–720.
- Ludwig, D., and C.J. Walters. 1982. Optimal harvesting with imprecise parameter estimates. *Ecol. Model.* 14: 273–292.
- Ludwig, D., and C. Walters. 1985. Are age-structured models appropriate for catch-effort data? *Can. J. Fish. Aquat. Sci.* 42: 1066–1072.
- Ludwig, D., and C.J. Walters. 1989. A robust method for parameter estimation from catch and effort data. *Can. J. Fish. Aquat. Sci.* 46: 137–144.
- MacCall, A.D. 1990. Dynamic Geography of Marine Fish Populations. University of Washington Press, Seattle.
- MacDonald, L.L., and S.A. Butler. 1982. Estimation of fish mortality. *Trans. Amer. Fish. Soc.* 111: 535–537.
- MacDonald, P.D.M. 1987. Analysis of length frequency distributions. Pages 371–384 in R.C. Summerfelt and G.E. Hall, eds., Age and Growth of Fish. Iowa State Univ. Press, Ames.
- MacDonald, P.D.M., and T.J. Pitcher. 1979. Age groups from size frequency data: a versatile and efficient method. *J. Fish. Res. Board Can.* 36: 987–1001.
- Mace, P.M., and M.P. Sissenwine. 1993. How much spawning per recruit is enough? *Can. Spec. Publ. Fish. Aquat. Sci.* 120: 101–117.
- Maéda, H. 1967. Distribution pattern of fish in relation to fishing method, with special reference to that of tuna along longline. Pages 1025–1041 in Symposium on Scombrid Fisherries, Part III. Marine Biol. Assoc. India, Mandapam Camp, India.
- Maguire, J.-J., and P.M. Mace. 1993. Biological reference points for Canadian Atlantic gadoid stocks. *Can. Spec. Publ. Fish. Aquat. Sci.* 120: 321–332.
- Mangel, M. 1982. Search effort and catch rates in fisheries. *Eur. J. Oper. Research* 11: 361–366.
- Mangel, M. 1985. Decision and Control in Uncertain Resource Systems. Academic Press, New York.
- Mangel, M., and J.H. Beder. 1985. Search and stock depletion: theory and applications. *Can. J. Fish. Aquat. Sci.* 42: 150–163.
- Mangel, M., and C.W. Clark. 1983. Uncertainty, search, and information in fisheries. *J. Cons. Int. Explor. Mer* 41: 93–103.

- Manley, B.F.J. 1990. Stage-structured Populations: Sampling, Analysis, and Simulation. Chapman and Hall, London.
- Mardia, K.V., J.T. Kent, and J.M. Bibby. 1979. Multivariate Analysis. Academic Press, London.
- Martin, I., and R.M. Cook. 1990. Combined analysis of length and age-at-length data. *J. Cons. Int. Explor. Mer* 46: 178–186.
- Matis, J.H., B.C. Patten, and G.C. White (eds.). 1979. Compartmental Analysis of Ecosystem Models. International Co-operative Publishing House, Fairland, Maryland.
- May, R.M. 1973. Stability and Complexity in Model Ecosystems. Princeton Univ. Press, Princeton, New Jersey.
- McAllister, M.K., and J.N. Ianelli. 1997. Bayesian stock assessment using catch-age data and the sampling-importance sampling algorithm. *Can. J. Fish. Aquat. Sci.* 54: 284–300.
- McAllister, M.K., and E.K. Pikitch. 1997. A Bayesian approach to choosing a design for surveying fishery resources: application to the eastern Bering Sea trawl survey. *Can. J. Fish. Aquat. Sci.* 54: 301–311.
- McAllister, M.K., E.K. Pikitch, A.E. Punt, and R. Hilborn. 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/ importance resampling algorithm. *Can. J. Fish. Aquat. Sci.* 51: 2673–2687.
- McCaughran, D.A. 1981. Estimating growth parameters for Pacific halibut from mark-recapture data. *Can. J. Fish. Aquat. Sci.* 38: 394–398.
- McCaughran, D.A. 1987. Growth in length of Pacific halibut. Pages 507–515 in R.C. Summerfelt and G.E. Hall, eds., *The Age and Growth of Fish*. Iowa State University Press, Ames.
- MSFMCA (Magnuson-Stevens Fishery Conservation and Management Act). 1996. U.S. Dept. Commerce, NOAA Tech. Mem. NMFS-F/SPO-23.
- McFarlane, G.A., and R.J. Beamish. 1990. Effect of an external tag on growth of sablefish (*Anoplopoma fimbria*), and consequences to mortality and age at maturity. *Can. J. Fish. Aquat. Sci.* 47: 1551–1557.
- McNeil, W.J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. *J. Fish. Res. Board Can.* 21: 1385–1396.
- McNew, R.W., and R.C. Summerfelt. 1978. Evaluation of a maximum likelihood estimator for analysis of length frequency distributions. *Trans. Amer. Fish. Soc.* 107: 730–736.
- McShane, P.E. 1992. Exploitation models and catch statistics of the Victorian fishery for abalone *Haliotis rubra*. *U.S. Fish. Bull.* 90: 139–146.
- Megrey, B.A. 1989. Review and comparison of age-structured stock assessment models. *Amer. Fish. Soc. Symp.* 6: 8–48.
- Meinhold, R.J., and N.D. Singpurwalla. 1983. Understanding the Kalman filter. *Amer. Stat.* 37: 123–127.
- Mendelsohn, R. 1978. Optimal harvesting strategies for stochastic, single species, multi-age class models. *Math. Biosci.* 41: 159–174.
- Mendelsohn, R. 1979. Determining the best trade-off between expected economic return and the risk of undesirable events when managing a randomly varying population. *J. Fish. Res. Board Can.* 36: 939–947.
- Mendelsohn, R. 1980. Using Markov decision models and related techniques for purposes other than simple optimization: analyzing the consequences of policy alternatives on the management of salmon runs. *U.S. Fish. Bull.* 78: 35–50.
- Mendelsohn, R. 1982. Discount factors and risk aversion in managing random fish populations. *Can. J. Fish. Aquat. Sci.* 39: 1252–1257.
- Mendelsohn, R. 1988. Some problems in estimating population sizes from catch-at-age data. *U.S. Fish. Bull.* 86: 617–630.
- Mesnil, B., and J.G. Shepherd. 1990. A hybrid age- and length-structured model for assessing regulatory measures in multiple-species, multiple-fleet fisheries. *J. Cons. Int. Explor. Mer* 47: 115–132.

- Methot, R.D. 1989. Synthetic estimates of historical abundance and mortality in northern anchovy. Amer. Fish. Soc. Symp. 6: 66–82.
- Methot, R.D. 1990. Synthesis model: an adaptive framework for analysis of diverse stock assessment data. Int. North Pac. Fish. Comm. Bull. 50: 259–277.
- Millar, R.B. 1992. Estimating the size selectivity of fishing gear by conditioning on the total catch. J. Amer. Stat. Assoc. 87: 962–968.
- Millar, R.B. 1995. The functional form of hook and gillnet selection curves cannot be determined from comparative catch data alone. Can. J. Fish. Aquat. Sci. 52: 883–891.
- Miller, R.G., Jr. 1966. Simultaneous Statistical Inference. McGraw-Hill, New York.
- Mills, M.J. 1985. Statewide harvest report. Alaska Dept. Fish Game, Federal Aid in Fish Restoration and Anadromous Fish Studies (F-10-1) 27.
- Misra, R.K. 1980. Statistical comparisons of several growth curves of the von Bertalanffy type. Can. J. Fish. Aquat. Sci. 37: 920–926.
- Moreau, J. 1987. Mathematical and biological expression of growth in fishes: recent trends and further developments. Pages 81–113 in R.C. Summerfelt and G.E. Hall, eds., The Age and Growth of Fish. Iowa State University Press, Ames.
- MRAG. 1992. The LFDA (Length Frequency Distribution Analysis) package user manual. Marine Resources Assessment Group Ltd., London.
- Mullen, A. 1994. Effects of movement on stock assessment in a restricted-range fishery. Can. J. Fish. Aquat. Sci. 51: 2027–2033.
- Mundy, P.R. 1982. Computation of migratory timing statistics for adult chinook salmon in the Yukon River, Alaska, and their relevance to fisheries management. N. Amer. J. Fish. Manage. 4: 359–370.
- Mundy, P.R. 1985. Harvest control systems for commercial marine fisheries management—theory and practice. Washington Sea Grant, Tech. Rep. WSG-85-1: 1–34.
- Mundy, P.R., K.K. English, W.J. Gazey, and K.E. Tarbox. 1993. Evaluation of the harvest management strategies applied to sockeye salmon populations of Upper Cook Inlet, Alaska, using run reconstruction analysis. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 107–139.
- Murawski, S.A. 1984. Mixed-species yield-per-recruitment analyses accounting for technological interactions. Can. J. Fish. Aquat. Sci. 41: 897–916.
- Murphy, G.I. 1960. Estimating abundance from longline catches. J. Fish. Res. Board Can. 17: 33–40.
- Murphy, G.I., and K.C. Elliott. 1954. Variability of longline catches of yellowfin tuna. U.S.F.W.S., Spec. Sci. Rep., Fisheries, No. 119.
- Murray, J.D. 1989. Mathematical Biology. Springer-Verlag, Berlin.
- Myers, R.A., and N.G. Cadigan. 1995. Statistical analysis of catch-at-age data with correlated errors. Can. J. Fish. Aquat. Sci. 52: 1265–1273.
- Myers, R.A., N.J. Barrowman, J.A. Hutchings, and A.A. Rosenberg. 1995. Population dynamics at low population levels. Science 269: 1106–1108.
- Myhre, R.J., and T.J. Quinn II. 1984. Comparison of efficiency of snap gear to fixed-hook setline gear for catching Pacific halibut. Int. Pac. Halibut Comm., Sci. Rep. 69.
- Nash, W.J. 1992. An evaluation of egg-per-recruit analysis as a means of assessing size limits for blacklip abalone (*Haliotis rubra*) in Tasmania. Pages 318–337 in S.A. Shepherd, M.J. Tegner, and S.A. Guzman del Proo, eds., Abalone of the World: Biology, Fisheries, and Culture. Fishing News Books, Cambridge, UK.
- NRC (National Research Council). 1994a. An Assessment of Atlantic Bluefin Tuna. National Academy Press, Washington, D.C.
- NRC (National Research Council). 1994b. Improving the Management of U.S. Marine Fisheries. National Academy Press, Washington, D.C.

- NRC (National Research Council). 1998a. Improving Methods for Fish Stock Assessment. National Academy Press, Washington, D.C.
- NRC (National Research Council). 1998b. Review of Northeast Fishery Stock Assessments. National Academy Press, Washington, D.C.
- Nelson, B., and T. J. Quinn II. 1987. Population parameters for rougheye rockfish (*Sebastodes aleutianus*). Proc. Int. Rockfish Symp., Alaska Sea Grant Rep. 87-2: 209–228.
- Neter, J., W. Wasserman, and M.H. Kutner. 1989. Applied Linear Regression Models, 2nd edition. Irwin, Homewood, Illinois.
- Neyman, J. 1949. On the problem of estimating the number of schools of fish. Univ. Calif. Publ. Stat. 1: 21–36.
- Norris, J.G. 1989. Comparative analysis of harvesting strategies for sablefish stocks off the coasts of Washington, Oregon, and California. Ph.D. Dissertation, Univ. of Washington, Seattle.
- Okubo, A. 1980. Diffusion and Ecological Problems: Mathematical Models. Springer-Verlag, New York.
- Olsen, S., and T. Laevastu. 1983. Factors affecting catch of longlines, evaluated by a simulation model of longline fishing. Draft manuscript for ICES Fish Capture Comm. 13 pp.
- Overholtz, W.J., S.F. Edwards, and J.K.T. Brodziak. 1993. Strategies for rebuilding and harvesting New England groundfish resources. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 507–527.
- Paloheimo, J.E. 1971. On a theory of search. Biometrika 58: 61–75.
- Paloheimo, J.E. 1980. Estimation of mortality rates in fish populations. Trans. Amer. Fish. Soc. 109: 378–386.
- Paloheimo, J.E., and L.M. Dickie. 1964. Abundance and fishing success. Conseil Int. Explor. Mer, Rapp. et Proc.-Verb. 155: 152–163.
- Palsson, H.P., D.E. Lane, and B. Kaufman. 1993. Bioeconomic methods for determining TAC's. Can. Spec. Publ. Fish. Aquat. Sci. 120: 357–372.
- Parker, K. 1985. Biomass model for the egg production method. U.S. Dept. Comm., NOAA Tech. Rep. NMFS 36: 5–6.
- Parma, A. 1990. Optimal harvesting of fish populations with nonstationary stock-recruitment relationships. Nat. Resource Model. 4: 39–76.
- Parma, A.M. 1993. Retrospective catch-at-age analysis of Pacific halibut: implications on assessment of harvesting policies. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 247–265.
- Parma, A.M., and R.B. Deriso. 1990. Experimental harvesting of cyclic stocks in the face of alternative recruitment hypotheses. Can. J. Fish. Aquat. Sci. 47: 595–610.
- Parma, A.M., and P.J. Sullivan. 1998. Stock assessment methodology: model documentation. International Pacific Halibut Commission, Report of Assessment and Research Activities 1997.
- Perrick, M.L. 1985. A method of analyzing catches and abundance indices from a fishery. ICCAT Working Document SCRS/85/35: 209–221.
- Parzen, E. 1960. Modern Probability Theory and Its Applications. John Wiley and Sons, New York.
- Parzen, E. 1962. Stochastic Processes. Holden-Day, San Francisco, CA.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39: 175–192.
- Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. Meeresforschung 28: 251–282.
- Pauly, D., and N. David. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforschung 28: 205–211.
- Pauly, D., and G. Gaschutz. 1979. A simple method for fitting oscillating length growth data with a program for pocket calculators. ICES C.M.G. 24.

- Pauly, D., and G.R. Morgan (eds.). 1987. Length-based Methods in Fisheries Research. ICLARM Conference Proceedings 13, International Center for Living Aquatic Resources Management, Manila, Philippines.
- Pawlak, C., and R.C. Hanumara. 1991. A comparison of non-linear growth models for fisheries. *Fisheries Res.* 11: 143–154.
- Pella, J.J. 1969. A stochastic model for purse seining in a two-species fishery. *J. Theor. Biol.* 22: 209–226.
- Pella, J.J. 1993. Utility of structural time series models and the Kalman filter for predicting consequences of fishery actions. Alaska Sea Grant College Program, Rep. No. 93-02: 571–593.
- Pella, J. 1996. Final report on Kalman filtering of biomass and recruitment indices from NRC data sets via the Deriso equation. NMFS Auke Bay Laboratory (manuscript). Auke Bay, Alaska.
- Pella, J.J., and C.T. Psaropoulos. 1975. Measures of tuna abundance from purse-seine operations in the eastern Pacific Ocean adjusted for fleet-wide evolution of increased fishing power, 1960–1971. *Int.-Amer. Trop. Tuna Comm. Bull.* 16: 283–400.
- Pella, J.J., and P.K. Tomlinson. 1969. A generalized stock production model. *Int.-Amer. Trop. Tuna Comm. Bull.* 13: 419–496.
- Pelletier, D., and A. Laurec. 1992. Management under uncertainty: defining strategies for reducing overexploitation. *ICES J. Mar. Sci.* 49: 389–401.
- Pennington, M. 1983. Efficient estimators of abundance, for fish and plankton surveys. *Biometrics* 39: 281–286.
- Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. *Can. J. Fish. Aquat. Sci.* 38: 1113–1119.
- Pianka, E.R. 1974. Evolutionary Ecology. Harper and Row, New York.
- Pikitch, E.K. 1987. Use of a mixed-species yield-per-recruit model to explore the consequences of various management policies for the Oregon flatfish fishery. *Can. J. Fish. Aquat. Sci.* 44 (Suppl. 2): 349–359.
- Piquelle, S., and G. Stauffer. 1985. Parameter estimation for an egg production method of anchovy biomass assessment. U.S. Dept. Comm., NOAA Tech. Rep. NMFS 36: 7–15.
- Pitcher, T.J., and P.D.M. MacDonald. 1973. Two models for seasonal growth in fishes. *J. Appl. Ecol.* 10: 599–606.
- Polacheck, T. 1990. Year around closed areas as a management tool. *Nat. Resource Model.* 4: 327–354.
- Pollard, J.H. 1973. Mathematical Models for the Growth of Human Populations. Cambridge Univ. Press, Cambridge.
- Polovina, J. 1986. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock. *U.S. Fish. Bull.* 84: 423–428.
- Pope, J.G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. *Res. Bull. Int. Comm. Northw. Atl. Fish.* 9: 65–74.
- Pope, J.G. 1975. Estimation of unknown natural mortality. ICNAF Dumm. Doc. 75/2.
- Pope, J.G. 1989. Multispecies extensions to age-structured assessment models. *Amer. Fish. Soc. Symp.* 6: 102–111.
- Pope, J.G., and J.G. Shepherd. 1982. A simple method for the consistent interpretation of catch-at-age data. *J. Cons. Int. Explor. Mer* 40: 176–184.
- Pope, J.G., and J.G. Shepherd. 1985. A comparison of the performance of various methods for tuning VPA's using effort data. *J. Cons. Int. Explor. Mer* 42: 129–151.
- Pope, J.G., and T.K. Stokes. 1989. Use of multiplicative models for separable virtual population analysis (VPA), integrated analysis, and the general VPA tuning problem. *Amer. Fish. Soc. Symp.* 6: 92–101.

- Power, J.H. 1991. Review of "Dynamic Geography of Marine Fish Populations." *Trans. Amer. Fish. Soc.* 120: 402.
- Prager, M.H. 1994. A suite of extensions to a nonequilibrium surplus-production model. *U.S. Fish. Bull.* 92: 374–389.
- Press, W.H., B.P. Flannery, S.A. Teukolsky, and W.T. Vetterling. 1989. *Numerical Recipes—The Art of Scientific Computing (Fortran Version)*. Cambridge University Press, Cambridge.
- Punsly, R.G., and R.B. Deriso. 1991. Estimation of the abundance of yellowfin tuna, *Thunnus albacares*, by age groups and regions within the eastern Pacific Ocean. *Int.-Amer. Trop. Tuna Comm. Bull.* 20: 99–131.
- Punsly, R.G., and H. Nakano. 1992. Analysis of variance and standardization of longline hook rates of bigeye (*Thunnus obesus*) and yellowfin (*Thunnus albacares*) tunas in the eastern Pacific Ocean during 1975–1987. *Int.-Amer. Trop. Tuna Comm. Bull.* 20: 167–184.
- Punt, A.E., and D.S. Butterworth. 1989. Results of first stage screening trials for a proposed whale stock management procedure. *Rep. Int. Whal. Comm.* (Special Issue 11): 191–197.
- Punt, A.E., P.A. Garratt, and A. Govender. 1993. On an approach for applying per-recruit methods to a protogynous hermaphrodite, with an illustration for the slinger *Chrysoblephus puniceus* (Pisces: Sparidae). *S. Afr. J. Mar. Sci.* 13: 109–119.
- Punt, A.E., and R. Hilborn. 1997. Fisheries stock assessment and decision analysis: a review of the Bayesian approach. *Rev. Fish Biol. Fisheries* 7. *in press*.
- Punt, A.E., M.K. McAllister, E.K. Pikitch, and R. Hilborn. 1994. Stock assessment and decision analysis for hoki (*Macruronus novaezelandie*) for 1994. *New Zealand Min. Agric. Fisheries, Fish. Assess. Res. Doc.* 94/13, Wellington.
- Quinn, T.J., II. 1980. Sampling for the abundance of schooling populations with line-transect, mark-recapture, and catch-effort methods. Ph.D. Dissertation, University of Washington, Seattle.
- Quinn, T.J., II. 1981. The use of Leslie-type age-structure models for the Pacific halibut population. Pages 217–242 in D.G. Chapman and V.F. Gallucci, eds., *Quantitative Population Dynamics*. International Co-operative Publishing House, Fairland, Maryland.
- Quinn, T.J., II. 1985a. Catch-per-unit-effort: a statistical model for Pacific halibut. *Can. J. Fish. Aquat. Sci.* 42: 1423–1429.
- Quinn, T.J., II. 1985b. Line transect estimators for schooling populations. *Fisheries Res.* 3: 183–199.
- Quinn, T.J., II. 1986. Are age-structured data and analysis necessary for fisheries management? *Proc. XIIth Int. Biomath. Conf.*, Seattle, Washington.
- Quinn, T.J., II. 1987. Standardization of catch-per-unit-effort for trends in catchability. *Nat. Resource Model.* 1: 279–296.
- Quinn, T.J., II. 1991. Review of Dynamic Geography of Marine Fish Populations by A.D. MacCall. *Copeia*, 1991, No. 3: 861–863.
- Quinn, T.J., II, E.A. Best, L. Bijsterveld, and I.R. McGregor. 1983a. Sampling Pacific halibut (*Hippoglossus stenolepis*) landings for age composition: history, evaluation, and estimation. *Int. Pac. Halibut Comm., Sci. Rep.* 68.
- Quinn, T.J., II, E.A. Best, L. Bijsterveld, and I.R. McGregor. 1983b. Port sampling for age composition of Pacific halibut landings. *Can. Sp. Pub. Fish. Aquat. Sci.* 66: 194–205.
- Quinn, T.J., II, and J.S. Collie. 1990. Alternative population models for eastern Bering Sea pollock. *Int. North Pac. Fish. Comm. Bull.* 50: 243–257.
- Quinn, T.J., II, R.B. Deriso, S.H. Hoag, and R.J. Myhre. 1984. A summary of methods of estimating annual surplus production for the Pacific halibut fishery. *Int. North Pac. Fish. Comm. Bull.* 42: 73–81.
- Quinn, T.J., II, R.B. Deriso, and S.H. Hoag. 1985. Methods of population assessment of Pacific halibut. *Int. Pac. Halibut Comm. Sci. Rep.* 72.

- Quinn, T.J., II, R.B. Deriso, and P.R. Neal. 1990a. Migratory catch age analysis. *Can. J. Fish. Aquat. Sci.* 47: 2315–2327.
- Quinn, T.J., II, R. Fagen, and J. Zheng. 1990b. Threshold management policies for exploited populations. *Can. J. Fisheries Aquat. Sci.* 47: 2016–2029.
- Quinn, T.J., II, and R. Gates. 1997. Estimation of salmon escapement: models with entry, mortality, and stochasticity. *Nat. Resource Model.* 10: 217–250.
- Quinn, T.J., II, S.H. Hoag, and G.M. Southward. 1982. Comparison of two methods of combining catch-per-unit-effort data from geographic regions. *Can. J. Fish. Aquat. Sci.* 39: 837–846.
- Quinn, T.J., II, and R.P. Marshall. 1989. Time series analysis: quantifying variability and correlation in Alaska salmon catches and environmental data. *Can. Spec. Pub. Fish. Aquat. Sci.* 108: 67–80.
- Quinn, T.J., II, and H.J. Niebauer. 1995. Relation of eastern Bering Sea walleye pollock recruitment to environmental and oceanographic variables. *Proc. International Symposium on Climate Change and Northern Fish Populations. Can. Sp. Pub. Fish. Aquat. Sci.* 121: 497–507.
- Quinn, T.J., II, and N.F. Szarzi. 1993. Determination of sustained yield in Alaska's recreational fisheries. *Alaska Sea Grant College Program, Rep. 93-02:* 61–84.
- Ralston, S. 1982. Influence of hook size in the Hawaiian deep-sea handline fishery. *Can. J. Fish. Aquat. Sci.* 39: 1297–1302.
- Ralston, S. 1987. Mortality rates of snappers and groupers. Pages 375–404 in J.J. Polovina and S. Ralston, eds., *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder, Colorado.
- Ralston, S. 1989. Effect of seasonal recruitment on bias of the Beverton-Holt length-based mortality estimator. *Amer. Fish. Soc. Symp.* 6: 190–197.
- Ratkowsky, D.A. 1986. Statistical properties of alternative parameterizations of the von Bertalanffy growth curve. *Can. J. Fish. Aquat. Sci.* 43: 742–747.
- Rao, C.R. 1958. Some statistical methods for comparison of growth curves. *Biometrics* 14: 1–17.
- Rao, C.R. 1973. *Linear Statistical Inference and Its Applications*. Wiley, New York.
- Reed, W.J. 1979. Optimal escapement levels in stochastic and deterministic harvesting models. *J. Env. Econ. Manage.* 6: 350–363.
- Reed, W.J. 1980. Optimal age-specific harvesting in a nonlinear population model. *Biometrics* 36: 579–593.
- Reed, W.J. 1986. Analyzing catch-effort data allowing for randomness in the catching process. *Can. J. Fish. Aquat. Sci.* 43: 174–186.
- Reilly, S.B. 1981. Population assessment and population dynamics of the California gray whale (*Eschrichtius robustus*). Ph.D. Dissertation, University of Washington, Seattle.
- Reish, R.L., R.B. Deriso, D. Ruppert, and R.J. Carroll. 1985. An investigation of the population dynamics of Atlantic menhaden (*Brevoortia tyrannus*). *Can. J. Fish. Aquat. Sci.* 42: 147–157.
- Restrepo, V.R., J.M. Hoenig, J.E. Powers, J.W. Baird, and S.C. Turner. 1992. A simple simulation approach to risk and cost analysis, with applications to swordfish and cod fisheries. *U.S. Fish. Bull.* 90: 736–748.
- Richards, F.J. 1959. A flexible growth function for empirical use. *J. Exper. Botany* 10: 290–300.
- Richards, L.J. 1987. Comparing imprecise abundance indices with a symmetric model. *Can. J. Fish. Aquat. Sci.* 44: 793–802.
- Richards, L.J. 1991. Use of contradictory data sources in stock assessments. *Fisheries Res.* 11: 225–238.
- Richards, L.J., and J.T. Schnute. 1986. An experimental and statistical approach to the question: Is CPUE an index of abundance? *Can. J. Fish. Aquat. Sci.* 43: 1214–1227.

- Richards, L.J., and J.T. Schnute. 1992. Statistical models for estimating CPUE from catch and effort data. *Can. J. Fish. Aquat. Sci.* 49: 1315–1327.
- Richards, L.J., J.T. Schnute, A.R. Kronlund, and R.J. Beamish. 1992. Statistical models for the analysis of ageing error. *Can. J. Fish. Aquat. Sci.* 49: 1801–1815.
- Richards, L.J., J.T. Schnute, and N. Olsen. 1997. Visualizing catch-age analysis: a case study. *Can. J. Fish. Aquat. Sci.* 54: 1646–1658.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 11: 559–623.
- Ricker, W.E. 1971. Critical statistics from two reproduction curves. *J. Fish. Res. Board Can.* 28: 333–341.
- Ricker, W.E. 1973. Linear regressions in fishery research. *J. Fish. Res. Board Can.* 30: 409–434.
- Ricker, W.E. 1975a. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191.
- Ricker, W.E. 1975b. A note concerning Professor Jolicoeur's comments. *J. Fish. Res. Board Can.* 32: 1494–1498.
- Ricker, W.E. 1982. Linear regression for naturally variable data. *Biometrics* 338: 859–860.
- Rivard, D. 1987. Biological production and surplus production models. *Fisheries Res. Branch, Ottawa, Ontario, Canada (manuscript)*
- Rivard, D. 1989. Overview of the systematic, structural, and sampling errors in cohort analysis. *Amer. Fish. Soc. Symp.* 6: 49–65.
- Rivard, D., and L.J. Bledsoe. 1978. Parameter estimation for the Pella-Tomlinson stock-production model under nonequilibrium conditions. *U.S. Fish. Bull.* 76: 523–534.
- Rivard, D., and J.-J. Maguire. 1993. Reference points for fisheries management: the eastern Canadian experience. *Can. Spec. Publ. Fish. Aquat. Sci.* 120: 31–58.
- Robbins, H., and S. Monro. 1951. A stochastic approximation method. *Ann. Math. Stat.* 22: 400–407.
- Robson, D.S. 1960. An unbiased sampling and estimation procedure for creel censuses of fishermen. *Biometrics* 16: 261–277.
- Robson, D.S. 1961. On the statistical theory of a roving creel census of fishermen. *Biometrics* 17: 415–437.
- Roff, D. A. 1980. A motion for the retirement of the von Bertalanffy function. *Can. J. Fish. Aquat. Sci.* 37: 127–129.
- Roff, D.A. 1983. Analysis of catch/effort data: a comparison of three methods. *Can. J. Fish. Aquat. Sci.* 40: 1496–1506.
- Ronholz, L.L., and D.K. Kimura. 1986. Atka mackerel. Pages 145–163 in R.G. Bakkala and J.W. Balsiger, eds., *Condition of groundfish resources of the eastern Bering Sea and Aleutian Islands region in 1986*. Nw. Ak. Fish. Cent., NMFS, NOAA, Seattle, Washington.
- Rosenberg, A.A., and J.R. Beddington. 1988. Length-based methods of fish stock assessment. Pages 83–103 in J.A. Gulland, ed., *Fish Population Dynamics*, 2nd edition. Wiley, Chichester, UK.
- Ross, G.J.S. 1970. The efficient use of function minimization in non-linear maximum likelihood estimation. *Appl. Stat.* 19: 205–221.
- Rotenberg, M. 1987. Effect of certain stochastic parameters on extinction and harvested populations. *J. Theor. Biol.* 124: 455–471.
- Rothschild, B.J. 1967. Competition for gear in a multiple species fishery. *J. Cons. Int. Explor. Mer.*, 31: 102–110.
- Rothschild, B.J. 1977. Fishing effort. Pages 96–115 in J.A. Gulland, ed., *Fish Population Dynamics*. Wiley, London.
- Rothschild, B.J. 1986. *Dynamics of Marine Fish Populations*. Harvard Univ. Press, Cambridge, Massachusetts.
- Rowling, K. 1994. Tiger flathead, *Neoplatycephalus richardsoni*. Pages 124–136 in (R.D.J.

- Tilzey, ed.) The South East Fishery Bureau of Resource Sciences, Australian Gov. Print. Service, Canberra, Australia.
- Rubin, D.B. 1987. The SIR algorithm—a discussion of Tanner and Wong's: the calculation of posterior distributions by data augmentation. *J. Amer. Stat. Assoc.* 82: 543–546.
- Rudstam, L.G., J.J. Magnuson, and W.M. Tonn. 1984. Size selectivity of passive fishing gear: a correction for encounter probability applied to gill nets. *Can. J. Fish. Aquat. Sci.* 41: 1252–1255.
- Ruppert, D., R.L. Reish, R.B. Deriso, and R.J. Carroll. 1984. Optimization using stochastic approximation and Monte Carlo simulation (with application to harvesting of Atlantic menhaden). *Biometrics* 40: 535–545.
- Ruppert, D., R.L. Reish, R.B. Deriso, and R.J. Carroll. 1985. A stochastic population model for managing the Atlantic menhaden (*Brevoortia tyrannus*) fishery and assessing risks. *Can. J. Fish. Aquat. Sci.* 42: 1371–1379.
- Saila, S.B., and J.M. Flowers. 1967. Elementary applications of search theory to fishing tactics as related to some aspects of fish behavior. U.N. F.A.O., Fisheries Rep. 62: 343–355.
- Saila, S.B., E. Lorda, and H.A. Walker. 1985. The analysis of parameter error propagation in simple fishery models. *Marine Resource Econ.* 1: 235–246.
- Sainsbury, K.J. 1980. Effect of individual variability on the von Bertalanffy growth equation. *Can. J. Fish. Aquat. Sci.* 37: 241–247.
- Sainsbury, K.J. 1982. Population dynamics and fishery management of the paua, *Haliotis iris* II. Dynamics and management as examined using a size class population model. *New Zealand J. Mar. Fresh. Res.* 16: 163–173.
- Sainsbury, K.J. 1988. The ecological basis of multispecies fisheries, and management of a demersal fishery in tropical Australia. Pages 349–382 in J.A. Gulland, ed., *Fish Population Dynamics*, 2nd edition. Wiley, New York.
- Salvado, C.A.M. 1993. Population field theory with applications to tag analysis and fishery modeling: the empirical Green function. *Can. J. Fish. Aquat. Sci.* 50: 2491–2512.
- Sampson, D.B. 1987. Variance estimators for virtual population analysis. *J. Cons. Int. Explor. Mer* 43: 149–158.
- Sampson, D.B. 1988a. Fish capture as a stochastic process. *J. Cons. Int. Explor. Mer* 45: 39–60.
- Sampson, D.B. 1988b. The stability of virtual population analysis cohort estimates. *J. Cons. Int. Explor. Mer* 44: 135–142.
- Sampson, D.B. 1990. A length-structured population model for southern fin whales and a test for density dependence. *J. Cons. Int. Explor. Mer* 46: 249–268.
- Sampson, D.B. 1991. Fishing tactics and fish abundance, and their influence on catch rates. *ICES J. Mar. Sci.* 48: 291–301.
- Sampson, D.B. 1994. Estimating the number of fish landed from their total weight and a sample average weight. *Can. J. Fish. Aquat. Sci.* 51: 2537–2548.
- Sandland, R.L., and C.A. Gilchrist. 1979. Stochastic growth curve analysis. *Biometrics* 35: 255–271.
- Schaefer, M.B. 1954. Some aspects of dynamics of populations important to the management of commercial marine fisheries. *Int. Amer. Trop. Tuna Comm. Bull.* 1: 25–56.
- Schaefer, M.B. 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. *Inter-Amer. Trop. Tuna Comm. Bull.* 2: 247–268.
- Schmitt, C.C., and B.E. Skud. 1978. Relation of fecundity to long-term changes in growth, abundance and recruitment. *Int. Pac. Halibut Comm., Sci. Rep.* 66.
- Schnute, J. 1977. Improved estimates from the Schaefer production model; theoretical considerations. *J. Fish. Res. Board Can.* 34: 583–603.
- Schnute, J. 1981. A versatile growth model with statistically stable parameters. *Can. J. Fish. Aquat. Sci.* 38: 1128–1140.

- Schnute, J. 1984. Linear mixtures: a new approach to bivariate trend lines. *J. Amer. Stat. Assoc.* 79: 1–8.
- Schnute, J. 1985. A general theory for the analysis of catch and effort data. *Can. J. Fish. Aquat. Sci.* 42: 414–429.
- Schnute, J. 1987. A general fishery model for a size-structured fish population. *Can. J. Fish. Aquat. Sci.* 44: 924–940.
- Schnute, J.T. 1991. The importance of noise in fish population models. *Fisheries Res.* 11: 197–223.
- Schnute, J.T. 1994. A general framework for developing sequential fisheries models. *Can. J. Fish. Aquat. Sci.* 51: 1676–1688.
- Schnute, J., and D.A. Fournier. 1980. A new approach to length frequency analysis: growth structure. *Can. J. Fish. Aquat. Sci.* 37: 1337–1351.
- Schnute, J.T., and R. Hilborn. 1993. Analysis of contradictory data sources in fish stock assessments. *Can. J. Fish. Aquat. Sci.* 50: 1916–1923.
- Schnute, J.T., and A.R. Kronlund. 1996. A management oriented approach to stock recruitment analysis. *Can. J. Fish. Aquat. Sci.* 53: 1281–1293.
- Schnute, J.T., and L.J. Richards. 1990. A unified approach to the analysis of fish growth, maturity, and survivorship data. *Can. J. Fish. Aquat. Sci.* 47: 24–40.
- Schnute, J.T., and L.J. Richards. 1995. The influence of error on population estimates from catch-age models. *Can. J. Fish. Aquat. Sci.* 52: 2063–2077.
- Schnute, J.T., L.J. Richards, and A.J. Cass. 1989a. Fish growth: investigations based on a size-structured model. *Can. J. Fish. Aquat. Sci.* 46: 730–742.
- Schnute, J.T., L.J. Richards, and A.J. Cass. 1989b. Fish survival and recruitment: investigations based on a size-structured model. *Can. J. Fish. Aquat. Sci.* 46: 743–769.
- Schnute, J.T., and J. Sibert. 1983. The salmon terminal fishery: a practical, comprehensive timing model. *Can. J. Fish. Aquat. Sci.* 40: 835–853.
- Schwarz, C.J., and J.B. Dempson. 1994. Mark-recapture estimation of a salmon smolt population. *Biometrics* 50: 98–108.
- Schwarz, C.J., J.F. Schweigert, and A. N. Arnason. 1993. Estimating migration rates using tag-recovery data. *Biometrics* 49: 177–193.
- Schweigert, J.F. 1993. Evaluation of harvesting policies for the management of Pacific herring stocks, *Clupea pallasi*, in British Columbia. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 167–190.
- Schweigert, J., and C.J. Schwarz. 1993. Estimating migration rates for Pacific herring (*Clupea pallasi*) using tag-recovery data. *Can. J. Fish. Aquat. Sci.* 50: 1530–1540.
- Schweigert, J.F., and J.R. Sibert. 1983. Optimizing survey design for determining age structure of fish stocks: an example from British Columbia Pacific herring. *Can. J. Fish. Aquat. Sci.* 40: 588–597.
- Schweigert, J.F., and J.R. Sibert. 1984. Reply to S.J. Smith. *Can. J. Fish. Aquat. Sci.* 41: 827–828.
- Seber, G.A.F. 1982. *The Estimation of Animal Abundance*, 2nd edition. Griffin, London.
- Seber, G.A.F. 1984. *Multivariate Observations*. Wiley, New York.
- Seber, G.A.F. 1986. A review of estimating animal abundance. *Biometrics* 42: 267–292.
- Seber, G.A.F., and C.J. Wild. 1989. *Nonlinear Regression*. Wiley, New York.
- Shardlow, T., R. Hilborn, R.M. Peterman, G.J. Steer, and M.J. Bradford. 1985. Density-dependent catchability coefficients. *Trans. Amer. Fish. Soc.* 114: 436–440.
- Sharpe, F.R. and A.J. Lotka. 1911. A problem in age-distribution. *Philosophical Magazine* 21: 435–438.
- Shelton, P.A. 1992. The shape of recruitment distributions. *Can. J. Fish. Aquat. Sci.* 49: 1754–1761.
- Shepherd, J.G. 1982. A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *J. Cons. Int. Explor. Mer* 40: 67–75.

- Shepherd, J.G. 1987a. A weakly parametric method for the analysis of length composition data. Pages 113–119 in D. Pauly and G.R. Morgan, eds., Length-based Methods in Fisheries Research (ICLARM), Manila, Philippines.
- Shepherd, J.G. 1987b. Towards a method for short-term forecasting of catch rates based on length compositions. Pages 167–176 in D. Pauly and G.R. Morgan, eds., Length-based Methods in Fisheries Research. Int. Center Liv. Aquat. Res. Manage. (ICLARM), Manila, Philippines.
- Shepherd, J.G., and M.D. Nicholson. 1986. Use and abuse of multiplicative models in the analysis of fish catch-at-age data. *Statistician* 35: 221–227.
- Shepherd, J.G., and M.D. Nicholson. 1991. Multiplicative modeling of catch-at-age data, and its application to catch forecasts. *J. Cons. Int. Explor. Mer* 41: 284–294.
- Shepherd, S.A., and P.A. Breen. 1992. Mortality in abalone: its estimation, variability, and causes. Pages 276–304 in S.A. Shepherd, M.J. Tegner, and S.A. Guzman del Proo, eds., Abalone of the World: Biology, Fisheries, and Culture. Fishing News Books, Cambridge, UK.
- Sibert, J.R., and D.A. Fournier. 1994. Evaluation of advection-diffusion equations for estimation of movement patterns from tag recapture data. Pages 108–121 in R. Shomura, J. Majkowski, and S. Langi, eds., Proceedings of the First FAO Expert Consultation on Interactions of Pacific Ocean Tuna Fisheries. FAO Fish. Tech. Pap., 336/1, Rome.
- Sigler, M.F. 1993. Stock assessment and management of sablefish *Anoplopoma fimbria* in the Gulf of Alaska. Ph.D. Dissertation, University of Washington, Seattle.
- Sigler, M.F., and J.T. Fujioka. 1993. A comparison of policies for harvesting sablefish, *Anoplopoma fimbria*, in the Gulf of Alaska. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 7–19.
- Sigler, M.F., J.T. Fujioka, and S.A. Lowe. 1997. Sablefish. In Stock Assessment and Fishery Evaluation for the Gulf of Alaska, November 1997, North Pac. Fishery Manage. Council, Anchorage, AK.
- Sims, S.E. 1982a. Algorithms for solving the catch equation forward and backward. *Can. J. Fish. Aquat. Sci.* 39: 197–202.
- Sims, S.E. 1982b. The effect of unevenly distributed catches on stock-size estimates using virtual population analysis (cohort analysis). *J. Cons. Int. Explor. Mer* 40: 47–52.
- Sims, S.E. 1984. An analysis of the effect of errors in the natural mortality rate on stock size estimates using virtual population analysis (cohort analysis). *J. Cons. Int. Explor. Mer* 41: 149–153.
- Sissenwine, M.P., and J.G. Shepherd. 1987. An alternate perspective on recruitment overfishing and biological reference points. *Can. J. Fish. Aquat. Sci.* 44: 913–918.
- Skalski, J.R., and J.A. Perez-Comas. 1993. Nonparametric maximum likelihood estimation of mesh size selectivity. *Fisheries Res.* 18: 321–334.
- Skud, B.E., and J.M. Hamley. 1978. Factors affecting longline catch and effort. *Int. Pac. Halibut Comm., Sci. Rep.* 64.
- Sluzcanowski, P.R. 1984. Modelling and optimal control: a case study based on the Spencer Gulf prawn fishery for *Peneaus latisulcatus* Kishinouye. *J. Cons. int. Explor. Mer* 41: 211–225.
- Smale, M.A., and W.W. Taylor. 1987. Sources of back-calculation error in estimating growth of lake whitefish. Pages 189–202 in R.C. Summerfelt and G.E. Hall, eds., The Age and Growth of Fish. Iowa State University Press, Ames.
- Smith, A.D.M. 1993. Risks of over- and under-fishing new resources. *Can. Spec. Publ. Fish. Aquat. Sci* 120: 261–267.
- Smith, A.D.M., and C.J. Walters. 1981. Adaptive management of stock recruitment systems. *Can. J. Fish. Aquat. Sci.* 38: 690–703.
- Smith, P.E., and R.P. Hewitt. 1985. Sea survey design and analysis for an egg production method of northern anchovy biomass assessment. U.S. Dept. Comm., NOAA Tech. Rep. NMFS 36: 17–26.

- Smith, P.J. 1989. Is two-phase sampling really better for estimating age composition? *J. Amer. Stat. Assoc.* 84: 916–921.
- Smith, S.J. 1980. Comparison of two methods of estimating the variance of the estimate of catch per unit effort. *Can. J. Fish. Aquat. Sci.* 37: 2346–2351.
- Smith, S.J. 1984. Comment on optimizing survey design for determining age structure of fish stocks. *Can. J. Fish. Aquat. Sci.* 41: 826–827.
- Smith, S. J., J.J. Hunt, and D. Rivard (eds.). 1993. Risk Evaluation and Biological Reference Points for Fisheries Management. *Can. Spec. Publ. Fish. Aquat. Sci.* 120.
- Somerton, D.A., and D.R. Kobayashi. 1992. Inverse method for mortality and growth estimation: a new method for larval fishes. *U.S. Fish. Bull.* 90: 368–375.
- Somerton, D.A., and M.F. Merritt. 1986. Method of adjusting crab catch per pot for differences in soak time and its application to Alaskan tanner crab *Chionoecetes bairdi* catches. *N. Amer. J. Fish. Manage.* 6: 586–591.
- Southward, G.M. 1976. Sampling landings of halibut for age composition. *Int. Pac. Halibut Comm., Sci. Rep.* 58.
- Sprent, P., and G.R. Dolby. 1980. The geometric mean functional relationship. *Biometrics* 36: 547–550.
- Ssentongo, G.W., and P.A. Larkin. 1973. Some simple methods of estimating mortality rates of exploited fish populations. *J. Fish. Res. Board Can.* 30: 695–698.
- Starr, P., and R. Hilborn. 1988. Reconstruction of harvest rates and stock contribution in gauntlet salmon fisheries: application to British Columbia and Washington sockeye (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* 45: 2216–2229.
- State of Alaska. 1996. Alaska State Constitution. Juneau, Alaska.
- Stauffer, G.D., and S.J. Piquelle. 1980. Estimates of the 1980 spawning biomass of the subpopulation of northern anchovy. *Nat. Mar. Fish. Serv., SW Fish. Center, La Jolla, California, Admin. Rep. LJ-80-09.*
- Stocker, M., and R. Hilborn. 1981. Short-term forecasting in marine fish stocks. *Can. J. Fish. Aquat. Sci.* 38: 1247–1254.
- Sullivan, P.J. 1992. A Kalman filter approach to catch-at-length analysis. *Biometrics* 48: 237–257.
- Sullivan, P.J., H.-L. Lai, and V.F. Gallucci. 1990. A catch-at-length analysis that incorporates a stochastic model of growth. *Can. J. Fish. Aquat. Sci.* 47: 184–198.
- Summerfelt, R.C., and G.E. Hall (eds.). 1987. *Age and Growth of Fish*. Iowa State Univ. Press, Ames.
- Sykes, Z. M. 1969. On discrete stable population theory. *Biometrics* 25: 285–294.
- Tanaka, S. 1956. A method of analyzing the polymodal frequency distribution and its application to the length distribution of porgy. *Bull. Tokai Reg. Fish. Res. Lab.* 14: 1–12.
- Templin, W. D., J.S. Collie, and T.J. Quinn II. 1996. Run reconstruction of the wild pink salmon fishery in Prince William Sound, 1990–1991. *Amer. Fish. Soc. Symp.* 18: 499–508.
- Texas Instruments, Inc. 1981. 1979 year-class report for the multi-plant impact study of the Hudson River estuary. Prepared for Consolidated Edison Co. of New York, Inc.
- Thompson, G.G. 1992. A Bayesian approach to management advice when stock-recruitment parameters are uncertain. *U.S. Fish. Bull.* 90: 561–573.
- Thompson, G.G. 1993. A proposal for a threshold stock size and maximum fishing mortality rate. *Can. Spec. Publ. Fish. Aquat. Sci.* 120: 303–320.
- Treble, R.J., R.W. Day, and T.J. Quinn II. 1993. Detection and effects on mortality estimates of changes in tag loss. *Can. J. Fish. Aquat. Sci.* 50: 1435–1441.
- Trites, A.W. 1991. Does tagging and handling affect the growth of northern fur seal pups (*Callorhinus ursinus*)? *Can. J. Fish. Aquat. Sci.* 48: 2436–2442.
- Tsoa, E., W.E. Shrank, and N. Roy. 1985. Generalizing fisheries models: an extension of Schaefer analysis. *Can. J. Fish. Aquat. Sci.* 42: 44–50.

- Tsou, T.S., and S.Y. Yeh. 1991. Studies on selection of standard years and abundance trends of the South Atlantic albacore based on 1967–1988 Taiwanese longline fishery data. ICCAT, Coll. Vol. Sci. Papers Vol. 34, SCRS/90/48:123–127.
- Tuljapurkar, S. D. 1982. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theor. Pop. Biol.* 21: 114–140.
- Tuljapurkar, S. D., and S. H. Orzack. 1980. Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theor. Pop. Biol.* 18: 314–342.
- Tyler, A.V., L.L. Sebring, M.C. Murphy, and L.F. Murphy. 1985. A sensitivity analysis of Deriso's delay-difference equation using simulation. *Can. J. Fish. Aquat. Sci.* 42: 836–841.
- Uhler, R.S. 1980. Least squares regression estimates of the Schaefer production model. *Can. J. Fish. Aquat. Sci.* 37: 1284–1294.
- Ulltang, O. 1977. Sources of errors in and limitations of virtual population analysis (cohort analysis). *J. Cons. Int. Explor. Mer* 37: 249–260.
- Usher, M.B. 1966. A matrix approach to the management of renewable resources, with special reference to selection forests. *J. Appl. Ecol.* 3: 355–367.
- Vaughan, D. S. 1977. Confidence intervals on mortality rates based on the Leslie matrix. Pages 128–149 in W. Van Winkle, ed., *Assessing the Effects of Power-Plant Induced Mortality on Fish Populations*. Pergamon Press, New York.
- Vaughan, D.S., and P. Kanciruk. 1982. An empirical comparison of estimation procedures for the von Bertalanffy growth equation. *J. Cons. Int. Explor. Mer* 40: 211–219.
- Vaughan, D. S., and S. B. Saila. 1976. A method for determining mortality rates using the Leslie matrix. *Trans. Amer. Fish. Soc.* 105: 380–383.
- Velleman, P.F., and D.C. Hoaglin. 1981. *Applications, Basics and Computing of Exploratory Data Analysis*. Duxbury Press, Belmont, California.
- Vetter, E.F. 1988. Estimation of natural mortality in fish stocks: a review. *U.S. Fish. Bull.* 86: 25–43.
- Von Foerster, H. 1959. Some remarks on changing populations. Pages 382–407 in F. Stohlman, Jr., ed., *The Kinetics of Cellular Proliferation*. Grune and Stratton, New York.
- Wald, A. 1940. The fitting of straight lines if both variables are subject to error. *Ann. Math. Stat.* 11: 284–300.
- Walford, L.A. 1946. A new graphic method of describing the growth of animals. *Biol. Bull.* 90: 141–147.
- Walter, G.G. 1973. Delay-differential equation models for fisheries. *J. Fish. Res. Board Can.* 30: 939–945.
- Walters, C.J. 1975. Optimal harvest strategies for salmon in relation to environmental variability and uncertain production parameters. *J. Fish. Res. Board Can.* 32: 1777–1784.
- Walters, C.J. 1981. Optimum escapements in the face of alternative recruitment hypotheses. *Can. J. Fish. Aquat. Sci.* 38: 678–689.
- Walters, C.J. 1985. Bias in the estimation of functional relationships from time series data. *Can. J. Fish. Aquat. Sci.* 42: 147–149.
- Walters, C.J. 1986. *Adaptive Management of Renewable Resources*. MacMillan, New York.
- Walters, C.J. 1987. Microcomputer stock assessment using Schnute's generalization of the Deriso delay-difference model (manuscript).
- Walters, C.J. 1990. A partial bias correction factor for stock-recruitment parameter estimation in the presence of autocorrelated environmental effects. *Can. J. Fish. Aquat. Sci.* 47: 516–519.
- Walters, C.J. 1993. Comment on R.I.C.C. Francis: computing probability distributions for risk analysis. *Can. J. Fish. Aquat. Sci.* 50: 881–882.
- Walters, C.J., and R. Hilborn. 1976. Adaptive control of fishing systems. *J. Fish. Res. Board Can.* 33: 145–159.

- Walters, C.J., and D. Ludwig. 1981. Effects of measurement errors on the assessment of stock-recruit relationships. *Can. J. Fish. Aquat. Sci.* 38: 704–710.
- Walters, C.J., and D. Ludwig. 1994. Calculation of Bayes posterior probability distributions for key population parameters. *Can. J. Fish. Aquat. Sci.* 51: 713–722.
- Walters, C., and D. Ludwig. 1987. Adaptive management of harvest rates in the presence of a risk averse utility function. *Nat. Resource Model.* 1: 321–337.
- Walters, C.J., and A. Parma. 1996. Fixed exploitation rate strategies for coping with effects of climate change. *Can. J. Fish. Aquat. Sci.* 53: 148–158.
- Walters, C.J., and A. Punt. 1994. Placing odds on sustainable catch using virtual population analysis and survey data. *Can. J. Fish. Aquat. Sci.* 51: 946–958.
- Weisberg, S., and R.V. Frie. 1987. Linear models for the growth of fish. Pages 127–143 in R.C. Summerfelt and G.E. Hall, eds., *The Age and Growth of Fish*. Iowa State University Press, Ames.
- Welch, D.W., and G.A. McFarlane. 1990. Quantifying growth of female Pacific hake (*Merluccius productus*): an example of measuring uncertainty and bias in non-linear parameter estimation. *Can. J. Fish. Aquat. Sci.* 47: 672–681.
- Wespestad, V. 1993. Walleye pollock. Pages 1-1 to 1-26 in Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands Region as projected for 1994. North Pacific Fishery Management Council, Anchorage, Alaska.
- Westrheim, S.J., and W.E. Ricker. 1978. Bias in using an age-length key to estimate age frequency distributions. *J. Fish. Res. Board Can.* 35: 184–189.
- Wetherall, J.A., J.J. Polovina, and S. Ralston. 1987. Estimating growth and mortality in steady-state fish stocks from length frequency data. Pages 53–74 in D. Pauly and G.R. Morgan, eds., *Length-based Methods in Fisheries Research*. ICLARM, Manila, Philippines.
- White, G.C., and I.L. Brisbin, Jr. 1980. Estimation and comparison of parameters in stochastic growth models for barn owls. *Growth* 44: 97–111.
- Whittle, P. 1982. Optimization over Time; Dynamic Programming and Stochastic Control, vol. 1. Wiley, Chichester, UK.
- Willis, D.W., K.D. McCloskey, and D.W. Gabelhouse, Jr. 1985. Calculation of stock density indices based on adjustments for efficiency of gill-net mesh size. *N. Amer. J. Fish. Manage.* 5: 126–137.
- Wismer, D.A., D.L. DeAngelis, and B.J. Shuter. 1985. An empirical model of size distributions of smallmouth bass. *Trans. Amer. Fish. Soc.* 114: 737–742.
- Xu, X., and R.B. Millar. 1993. Estimation of trap selectivity for male snow crab (*Chionoecetes opilio*) using the SELECT modeling approach with unequal sampling effort. *Can. J. Fish. Aquat. Sci.* 50: 2485–2490.
- Yeh, S.Y., T.S. Tsou, and H.C. Liu. 1991. Assessment of the South Atlantic albacore resource by using surplus production models, 1967–1988. ICCAT, Coll. Vol. Sci. Papers Vol. 34, SCRS/90/59: 166–170.
- York, A. E. 1987. On comparing the population dynamics of fur seals. In J.P. Croxall and R. L. Gentry, eds., *Status, biology, and ecology of fur seals*. NOAA Tech. Rep. NMFS 51, U.S. Department of Commerce, NTIS, Springfield, Virginia.
- Zebdi, A. 1991. Identification of environmental causes of recruitment variation in the herring stock of Sitka Sound, Alaska. M.S. Thesis, University of Alaska Fairbanks, Juneau.
- Zeh, J.E., D. Ko, B.D. Krogman, and R. Sonntag. 1986. A multinomial model for estimating the size of a whale population from incomplete census data. *Biometrics* 42: 1–14.
- Zhang, C.I., and P.I. Sullivan. 1988. Biomass-based cohort analysis that incorporates growth. *Trans. Amer. Fish. Soc.* 117:180–189.
- Zheng, J., F.C. Funk, G.H. Kruse, and R. Fagen. 1993a. Evaluation of threshold management strategies for Pacific herring in Alaska. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 141–165.

- Zheng, J., M.C. Murphy, and G.H. Kruse. 1995. A length-based population model and stock-recruitment relationships for red king crab, *Paralithodes camtschaticus*, in Bristol Bay, Alaska. Can. J. Fish. Aquat. Sci. 52: 1229–1246.
- Zheng, J., T.J. Quinn II, and G.H. Kruse. 1993b. Comparison and evaluation of threshold estimation methods for exploited fish populations. Univ. Alaska Sea Grant College Program, Rep. No. 93-02: 267–289.
- Zheng, J., and C.J. Walters. 1988. Population dynamics and stock assessment of Wanshan Spring *Decapterus maradsi* (T.&S.) in South China Sea. Fisheries Res. 6: 217–231.

Index

- abundance, estimation of. *See* catch-age estimation of abundance
See also delay-difference model parameter estimation; index of abundance; length-based assessment methods; migration; production; spawner-recruit parameter estimation; survey information acceptable biological catch (ABC), 433–434, 472 acoustic surveys, 433 AD Model Builder, 354–355 ADAPT method of catch-age analysis, 353 adaptive importance sampling (AIS) in catch-age estimation of abundance, 354 in spawner-recruit estimation, 125 adaptive management and decision analysis, 483 definition of active and passive types, 458 effects on production model estimation, 76 for harvest control in semelparous populations, 123 and optimization of harvest, 454, 458 related to goals, objectives, and constraints, 444 additive error. *See* error structure advection in models of migration, 421 age composition estimation when estimating the catch, 302–303 by length frequency analysis, 295–301 and sample size considerations, 306–311 with separate length and age samples, 311–317 with simple random sampling, 301–302 with two-stage random sampling, 303–306 age of entry, 239 with biological reference points, 462–464, 473 in yield per recruit model variations, 264
See also recruitment age-length key, 304, 311, 313, 316, 363 age-structured model, 268, 364 for biological reference points, 459, 479 for catch-age estimation of abundance, 339 fecundity and maturity, 200, 205 for geographic apportionment, 433 with discrete Leslie matrix, 276 with migration, 407, 408, 410, 428 for migratory per recruit analyses, 435 with nonlinear discrete Leslie-type, 289 for optimization of harvest, 453 for per-recruit and year-class analysis, 239–267 as related to stage-structured matrix models, 369–372 and risk, uncertainty, and decision analysis, 484 for simple theory of mortality, 10 of spawning stock and egg production per recruit, 259

- aging error
 in catch-age estimation of abundance, 335, 355
 in the Deriso-Parma size and age model, 380
 in estimation of age composition, 295, 316
 Akaike information criterion (AIC), 165
 Allen-Clark abundance models, 208–212
 allocation, 437
 issues in harvest goals, 442, 443
 issues in yield per recruit models, 267
 of samples in age composition, 303, 304, 306–311
 allometric relationship, 129
 applied to estimation of natural mortality M , 361
 in Beverton-Holt year-class models, 240, 248
 for fecundity and maturity, 203
 in the LVB growth model, 139, 140, 142
 from mark-recapture data, 162
 with scale and otolith measurements, 180
 in size-age models, 143, 146–148, 150, 152, 153, 155
 in stochastic models with recruits by size group, 253
 for weight-length models, 129–131
 Alverson-Carney method of estimation of natural mortality M , 361
 amensalism, 9
 anabolism, 128, 140
 angling models, 40, 42, 43, 45–48
 annual death fraction, 10, 13
 annual surplus production (ASP), 67–71.
See also production
 apportionment
 of catch in migratory per recruit analyses, 435, 436
 by geographic strata, 432–434
 Atka mackerel, 131, 361, 478
 autocorrelation
 in delay-difference model estimation, 236
 effect on optimization of harvest, 449, 453
 in production model estimation, 78
 in spawner-recruit estimation, 101, 117
 in stochastic linear matrix models, 279
 with variation in growth, 195, 199
 auxiliary data
 use in catch-age estimation of abundance, 317
 use in estimation of migration, 414
 back-calculation method
 for catch-age estimation of abundance, 323, 326, 328, 352, 353
 for length-based assessment methods, 380–382
 limitations for scale and otolith analysis, 180–182
 for run reconstruction, 429
 Baranov catch equation, 12
 in Beverton-Holt year-class models, 243
 in catch-age models, 318, 324, 325, 333
 in delay-difference models, 221, 223
 in generic per recruit models, 256, 257
 in length-based assessment methods, 383
 in migratory cohort and catch-age methods, 426
 in models for estimation of migration, 416, 420
 in a stochastic model with recruits by size group, 251
 basin model, 403, 404
 batch spawners, 206
 Bayesian
 approach in least squares analysis, 225
 approach to models of the fishing process, 40–42
 decision analysis, 483–484
 delay-difference model parameter estimation, 225, 233–235
 estimation of age composition, 306, 310
 Kalman Filter development, 235–238
 methods for catch-age estimation of abundance, 354–355
 optimization methods in harvest calculations, 457–458
 spawner-recruit posterior distribution, 124–127
 stochastic size and age structured models, 373, 376
 Bayesian information criterion (BIC), 165
 Bellman equation for optimization of harvest, 456–458
 Bernardelli matrix in Leslie matrix discrete models, 276
 Bernoulli
 differential equation for population growth, 7
 distribution for outliers in mark-recapture data, 158
 Bertalanffy growth model. *See* LVB growth model
 beta function, 248

- Beverton-Holt
 method in size-structured analysis, 364–367
 method for spawning and egg production per recruit, 259
 model used in optimization of harvest, 458
 models used in biological reference points, 471, 482
 per-recruit and year-class models, 241–249
 per-recruit model generalized, 250, 255
 recruit models used in delay-difference models, 214, 233
 recruit models used in nonlinear Leslie-type models, 290
 spawner-recruit models, 87–90, 92, 93, 95–99, 122–123
 spawner-recruit parameter estimation, 100, 102, 104, 112, 125
bias
 in back-calculation of scale and otolith measurements, 182
 in catch-age estimation of abundance, 319, 321, 328, 338, 342–344, 350, 353, 453, 454
 considerations for the LVB growth model, 138, 152
 considerations with mark-recapture data, 158, 163
 in delay-difference model parameter estimation, 236
 effect on weighting indices, 483
 in estimation of age composition, 303–305, 311, 316
 in estimation of migration, 413
 in estimation of natural mortality M , 362
 in length-based assessment methods, 382, 390
 in the method of geographic apportionment, 432
 in methods for catch-effort and the fishing process, 19, 36
 in production model parameter estimation, 67, 78–82
 with simple method of size-structured analysis, 365–367
 in spawner-recruit parameter estimation, 91, 100, 101, 103, 108, 110, 116, 117, 125, 478
 and variation in growth, 188, 190, 198
 in weight-length models, 131
 binomial distribution, 14, 202, 283
 bioeconomic considerations, 267, 437, 446, 447
 biological objective in management goals, 445
 biological reference points (BRPs), 459–482
 with age-structured parameter F_{st} , 479–480
 related to natural mortality parameter M , 460–462
 and relations among F_m , F_{max} , F_p , 464–468
 and spawning population, 263, 474–479
 and spawning population per recruit, 472–474
 and threshold reference points, 480–482
 with yield-effort parameters F_m and F_{ey} , 459–460
 with yield-per-recruit parameter $F_{0.1}$, 468–472
 with yield-per-recruit parameter F_{max} , 462–464
biomass dynamics. *See* delay-difference models; production models
biomass-based policy
 of geographic apportionment of catch, 433, 434
 for harvest adjustment, 440–442
bluefin tuna, 190, 419, 421
bootstrap method
 in catch-age estimation of abundance, 342–345, 355
 in catch-effort standardization, 33
 in estimation of migration, 417
 in production model parameter estimation, 78, 80
 to quantify risk, 484
 in spawner-recruit parameter estimation, 101
Box-Cox transformation
 for catch-effort data, 30–32
 for size, 373
Brody-LVB growth model
 for biological reference points, 471
 in a stochastic model with recruits by size group, 250
 in year-class models, 248
Brody growth parameter, 133, 298
bycatch, 437, 443
 cacometric yield curve, 245, 246
CAGEAN computer program, 319, 342, 355
 calibration as used with catch-age data, 337, 338, 352, 353

- cannibalism, 86, 89
 carrying capacity
 in migration population models, 399, 403
 in model dynamics for semelparous populations, 118, 119
 optimization methods, 449
 in simple population growth models, 5–9
 in spawner-recruit models, 95
CASA computer program for catch-length analysis, 385
 catabolism, 128, 140
 catch
 in Allen-Clark abundance models, 209, 210
 in Beverton-Holt year-class models, 241–248
 in biological reference points, 459, 462–464, 468, 472, 473, 479–481
 for catch-age estimation of abundance, 317–326, 328, 330–339, 342–345, 348–355
 for catch-effort and fishing process models, 15–19, 22–28, 30, 36, 38–49
 in delay-difference models 220–225, 227, 229, 233, 236, 237
 in Deriso-Schnute biomass models, 212–217
 for estimation of age composition, 301–306, 310
 for estimation of migration, 398, 413, 414, 416, 420, 421
 for estimation of natural mortality M , 357–360
 and fecundity and maturity, 206
 forecasting in linear matrix models, 291
 in generic per recruit models, 255–258
 with geographic apportionment, 432–434
 goals, objectives, and constraints, 442–447
 harvest policies and equilibrium concepts, 438–441
 in length-based assessment methods, 380–385, 387, 389–392, 395–397
 in migration population models, 401–405
 in migratory cohort and catch-age analyses, 421–423, 426–428
 in migratory per recruit analyses, 435, 436
 in model dynamics for semelparous populations, 118, 122, 123
 optimization methods, 447–450, 453–456, 459
 in production model parameter estimation, 68, 74, 82
 risk, uncertainty, and decision analysis, 483–485
 in run reconstruction, 428, 429, 432
 in the simple theory of mortality, 11–15
 in size-structured basic models, 364, 365, 368
 in spawner-recruit models, 98, 100, 104, 114
 in stochastic linear matrix models, 283, 284
 in a stochastic model with recruits by size group, 250–253
 in stochastic size and age structured models, 377–380
 in theory of stock productivity, 50, 51, 56
 from yield per recruit model variations, 264, 265, 267
 catch at age. *See* catch-age
 catch curve, 317, 319–323, 330–332, 355, 357, 360
 catch-age, 295, 364
 data in estimation of age composition, 303, 305, 306
 data in estimation of migration, 398
 data for estimation of natural mortality M , 360
 data in migratory cohort and catch-age analyses, 421–423, 426, 428
 geographic apportionment, 432
 input for Kalman filter, 236
 and production model parameter estimation, 68
 related to length-based assessment methods, 382, 385, 387, 390, 391, 395
 results related to delay-difference model, 227, 229
 results used in linear matrix models, 291
 in stochastic linear matrix models, 284
 catch-age estimation of abundance, 317–356
 with auxiliary information, 333–349
 bias and retrospective analysis in, 453, 454
 computer programs for, 355–356
 with general catch-age relationship, 317–319
 by miscellaneous alternative approaches, 350–355
 by relative abundance analysis, 330–333
 by stratified catch-age analysis, 349–350
 by virtual population analysis or cohort analysis, 323–330
See also catch curve

- catch-effort and the fishing process, 15–49
 and catchability differing between individuals, 40–42
 complex models for, 28–36
 of marks for estimation of natural mortality M , 358
 methods compared to catch-age methods, 342
 in migratory cohort and catch-age analyses, 421
 and regional considerations, 17–18
 sampling considerations, 25–28
 with schooling and search, 36–40
 standardization and gear selectivity, 18–25
 with stochastic fishing models, 42–49
catch-length analysis. *See* length-based assessment methods
catch limit. *See* quota
catchability coefficient
 in bioeconomic objective functions, 446
 in catch-age models, 336–351
 in delay-difference models, 220, 225, 236, 237
 in length-based assessment models, 385
 in methods to estimate natural mortality M , 358, 360
 in migration population models, 402, 416, 426
 in models of catch-effort data, 15–25, 28, 40, 41
 in production models, 56, 68, 74, 82
cell division, 2, 4
Central Limit Theorem, 283
central tendency, measure of, 31–35, 198, 281
chaotic dynamics, 121
characteristic equation
 for Allen-Clark abundance models, 210
 for continuous linear matrix models, 293
 for Deriso-Schnute biomass models, 213
 for Leslie matrix discrete model, 271, 275, 276
 for nonlinear discrete Leslie-type models, 288
closed areas to fishing, 436
closed population, 31, 46, 358, 412
closures for optimization of harvest, 449
cod, 77, 99
coefficient of variation
 in delta method for growth models, 164, 167, 171
 effect on harvest policies, 454
 in estimation of age composition, 302
 for geometric intrinsic growth equation, 279, 280
 for log-normal error in spawner-recruit models, 102, 113
 in a sablefish simulation model, 478
 in variation in growth model, 185
Cohen-Fishman growth model, 197, 199, 374
cohort
 defined for simple theory of mortality, 10
 included in continuous linear matrix models, 292
 included in delay-difference models, 220
 modeled with stochastic size-age models, 374–378
 in per-recruit and year-class models, 239–267
 related to theory of stock productivity, 51
 results used for biological reference points, 462, 467–469, 478, 479
 stochastic mortality and multinomial distribution, 281, 283, 284
 use in estimation of migration, 398, 421
 use in estimation of natural mortality M , 357, 359, 361
cohort analysis, 324–330, 350–352
 consequence for age composition sample size, 310
 for run reconstruction, 399
 of tagging data to estimate natural mortality M , 359
See also catch-age estimation of abundance; length-based assessment methods; migration
collapse of population
 with autocorrelations, 449
 and log utility functions, 485
 and methods based on spawning stock per recruit, 263
 related to biological reference points, 473, 477, 482
commensalism, 9
compartmental model, 400, 404
compensatory mortality
 effect on biological reference points, 466, 477, 481
 effect on dynamics for semelparous populations, 118, 119, 121
 in spawner-recruit models, 98
See also density dependence

- competition
 in catch-effort and the fishing process, 28, 36, 40, 45–48
 in generic per recruit models, 257
 in simple and multispecies models, 5, 9
 in spawner-recruit models, 87
- computer simulation. *See* simulation
- confidence interval
 for Beverton-Holt year-class models, 245, 249
 for catch-age estimation of abundance, 321
 for catch-effort and the fishing process, 22, 32, 33, 35
 for comparison of growth models, 165, 172, 177
 for estimation of age composition, 302
 for LVB growth model, 136, 143
 for production model estimation, 78
 for size-age models, 146, 152–154
 for stochastic linear matrix models, 281
 for weight-length models, 131
- conflicts, 437
- conjugate function, 373
- conservation, 222, 437, 442, 443, 447
- constant catch policy 76, 438, 441, 448, 450, 453, 458
- constant escapement
 in Allen-Clark abundance models, 211
 in dynamics for semelparous populations, 123
 for optimization of harvest, 440, 442, 444, 449, 450, 454
 in production model parameter estimation, 76
- constant recruitment implication, 87
- constant fishing mortality
 in Beverton-Holt year-class models, 241
- equilibrium results for delay-difference models, 223
 in generic per recruit models, 255
 harvest policy, 438–454, 458
 in a production model, 65
- constant harvest. *See* constant catch
- constant harvest rate. *See* constant fishing mortality
- constant quota. *See* constant catch
- constant yield. *See* constant catch
- continuous linear matrix models, 292–295
- contradictory data, 353, 482, 483
- control theory, 443
- cost
 considerations in age and size sampling, 306, 309–311
 in management goals and objectives, 443, 446, 447, 458
- crab, 18, 268
- creel survey, 27
- Cushing
 recruit model in a delay-difference model, 223, 224
 recruit model in harvest optimization, 444
- spawner-recruit models, 93, 96–98
- spawner-recruit parameter estimation, 103, 104, 111–115
- Darroch's method for estimation of migration, 412–415
- decision analysis, 458, 482–484
- decision table, 484
- delay-difference model, 208, 364
 as Allen-Clark abundance models, 209–211
 for biological reference points, 459–461, 472
 as Deriso-Schnute biomass models, 212–218
 with further generalizations, 220
 with Horbowy's approach, 218–220
 with mortality models, 220–223
 optimization of harvest, 449
 partial recruitment in, 220
 as size-structured models, 364, 368
 with stock reduction analysis, 223–224
 with use of a net growth parameter, 218
- delay-difference model parameter estimation, 224–238
- in combined measurement and process error models, 231–235
- with Kalman filters, 235–238
- with a measurement error model, 224–226
 with a process error model, 226–231
- delta method
 in catch-age estimation of abundance, 320, 326
 in catch-effort and the fishing process, 32, 49
- for comparison of growth models, 167
- in estimation of age composition, 303, 305
- in estimation of migration, 413

- in production model parameter estimation, 80
 in spawner-recruit parameter estimation, 101
 in weight-length models, 130
- DeLury method for estimation of abundance, 336, 358
- density dependence
 effects on biological reference points, 461, 482
 estimated for geometric intrinsic growth equation, 279, 280
 in growth, 85, 96, 182, 183
 in migration population models, 411
 in natural mortality, 85
 in nonlinear discrete Leslie-type models, 284, 290
 in spawner-recruit models, 85, 87–91, 93, 96
 in surplus production models, 82, 85
- density independence
 effects on biological reference points, 479
 estimated for spawner-recruit models, 106, 111
 in Leslie matrix discrete model, 274
 in migration population models, 411
 and nonlinear discrete Leslie-type models, 287, 288
 and relation of surplus production to recruitment, 82, 85
 in spawner-recruit models, 87, 89, 92
 and spawning stock and egg production per recruit, 262
- depensatory mortality
 effects on biological reference points, 461, 468, 473, 477, 481, 482
 effects on optimal harvest, 449
 in spawner-recruit models, 94, 99, 118, 119
 in theory of stock productivity, 64
See also density dependence
- depletion
 effects in catch-effort relationship, 28, 37, 41, 46, 48
 of prey, 93, 94
 of stocks and biological reference points, 473
- Deriso-Parma stochastic size and age structured models, 373–380
- Deriso-Schnute biomass models, 212–218
 and Deriso's model, 212–215
- and moments of the weight distribution of adults, 216–218
 and Schnute's extension, 215–216
See also delay-difference model
- Deriso-Schnute spawner-recruit model
 derivation, 93–95
 parameter estimation, 103, 104, 106
- difference equation, 1, 128
 for dynamics for semelparous populations, 118
 for Leslie matrix discrete model, 269, 273
 for the LVB growth model, 133, 139
 for migration population models, 400, 403
 for production model parameter estimation, 75–78
 for relation of surplus production to recruitment, 85
 for simple population growth models, 1–3
 for spawner-recruit models, 94
 for stochastic size and age structured models, 374
 for variation in growth, 182, 191, 193
See also delay-difference models
- differential equation, 1, 128
 for alternative delay-difference model, 218, 219
 for Beverton-Holt year-class models, 242
 for continuous linear matrix models, 292
 for dynamics for semelparous populations, 118, 119
 for estimation of migration, 419–421
 for the LVB growth model, 132, 140, 141
 for migration population models, 402–404
 for production model parameter estimation, 74, 75
 for relation of surplus production to recruitment, 85
 for run reconstruction, 432
 for simple population growth models, 1–3, 5, 7, 8
 for size-age models, 145–147, 149
 for size-structured basic models, 368
 for spawner-recruit models, 87, 89, 90, 94, 98
 for theory of mortality, 10–13
 for theory of stock productivity, 53, 55, 61–64
 for variation in growth, 182, 183, 191, 193, 196

- diffusion
 in migration population models, 402–405
 in migratory cohort and catch-age analyses, 428
 in models of migration, 416, 421
 disaggregated data. *See* stratified catch-age analysis
 discard mortality, 26, 263, 264
 discount rate, 446, 447, 455
 discrete-time optimization methods, 455
 disease, 5, 360
 dispersion. *See* diffusion
 dome-shaped curves, 89, 90, 466
 double sampling, 303–306. *See also* sampling considerations
 dynamic geography, 403
 dynamic pool model, 239, 461, 462, 474
 dynamic programming for optimal harvest calculations, 455–458, 485
 dynamics for semelparous populations, 117–124
- E-M (expectation-maximization) algorithm, 316, 353
 early life survival
 and biological reference points, 479, 480
 and fecundity and maturity, 204, 205
 in forecasting in linear matrix models, 291
 in Leslie matrix discrete model, 273
 in migration population models, 408
 in spawner-recruit models, 86, 87, 98
 in stage-structured matrix models, 372
 time-varying, 278
See also recruitment
 ecological relationships. *See* multispecies
 economic objectives, 446
 ecosystem, 9, 437, 443
 efficient yield, 459
 egg loss, 418
 egg production and reproduction
 in Allen-Clark abundance models, 208
 and biological reference points, 472, 479
 in catch-age models, 337, 342
 in continuous linear matrix models, 292–294
 in Deriso-Schnute biomass models, 214
 in the egg production method, 204–207
 and fecundity and maturity, 202–207
 in Leslie matrix discrete model, 268, 269, 272, 274–277
 in migration population models, 407, 408, 411
 in migratory per recruit analyses, 436
 in nonlinear discrete Leslie-type models, 284–287, 289, 290
 and optimization of harvest, 448, 449, 453
 in simple population models, 8, 11
 in spawner-recruit models, 86–89, 93, 96, 98, 100
 in spawning stock and egg production per recruit, 258–263
 in stage-structured matrix models, 369–372
 in stochastic linear matrix models, 280, 281
 in a stochastic model with recruits by size group, 253
 stochastic linear matrix models, 279
 in time-varying linear matrix models, 278
 Ehrhardt-Ault method in size-structured analysis, 365–367
 eigenvalue
 for Leslie matrix discrete model, 269, 271–273, 275, 276
 for migration population models, 404, 410, 411
 and nonlinear discrete Leslie-type models, 288, 289
 for stage-structured matrix models, 371, 372
 for stochastic linear matrix models, 279
 eigenvector
 for Leslie matrix discrete model, 269, 271–275, 277
 for migration population models, 410, 411
 for stage-structured matrix models, 371, 372
 use in comparison of growth models, 173
 ELEFAN, 301, 363
 emigration. *See* migration
 enhancement, 225, 297
 environment
 and biological reference points, 471, 477, 478
 in catch-effort and the fishing process, 17, 37
 considerations in estimation of natural mortality M , 360
 in dynamics for semelparous populations, 123
 in forecasting in linear matrix models, 291
 in harvest policies and equilibrium concepts, 442
 in models of stock productivity, 66

- in nonlinear discrete Leslie-type models, 287
- in optimization of harvest, 448, 449, 454
- and risk, uncertainty, and decision analysis, 483
- related to scale and otolith measurements, 181, 182
- in simple population growth models, 8
- in spawner-recruit models, 86, 91, 92
- in spawner-recruit model estimates, 102, 106, 108, 111, 117
- variation in growth, 182
- environmental impact assessment, 287
- equilibrium, 437
 - in Allen-Clark abundance models, 209–212
 - in alternative delay-difference models, 222, 223
 - and biological reference points, 459–461, 464, 467, 475–477, 479, 480, 482
 - concepts in harvest policies, 438–446
 - in continuous linear matrix models, 294
 - in delay-difference model parameter estimation, 226, 229, 230, 233–235
 - in Deriso-Schnute biomass models, 213–215
 - in dynamics for semelparous populations, 118, 119, 121, 122
 - and estimation of natural mortality M , 357
 - and forecasting in linear matrix models, 291
 - and geographic apportionment, 433, 434
 - in harvest optimization methods, 449, 455, 458
 - in length-based assessment methods, 390, 392
 - in Leslie matrix discrete model, 275
 - in migration population models, 400
 - in nonlinear discrete Leslie-type models, 285–290
 - in production model parameter estimation, 66–68, 72–77, 79, 81, 82
 - for relation of surplus production to recruitment, 85
 - in simple population growth models, 9
 - in spawner-recruit Bayesian model, 125
 - and spawning stock and egg production per recruit, 262
 - in stochastic linear matrix models, 280
 - in theory of stock productivity, 51–56, 58, 59, 61–66
- error structure
 - for analysis of growth with tagging data, 155, 157, 161
 - for analysis of size-age models, 146, 153
 - for Bayesian analysis of spawner-recruit, 125
 - for catch-age estimation of abundance, 352, 353
 - for comparison of growth models, 164, 170
 - for estimation of migration, 416
 - for fecundity and maturity analysis, 202–204
 - for length-based assessment methods, 384, 385, 391
 - for LVB growth model, 135, 142, 143
 - for migratory cohort and catch-age analyses, 426
 - modeled as a logistic error structure, 332
 - for production model parameter estimation, 69–73, 78, 80
 - for spawner-recruit parameter estimation, 100, 103, 104, 109, 116
 - for a stochastic model with recruits by size group, 253
 - for variation in individual's growth, 186, 188, 189, 196, 197
 - for weight-length models, 129–131
- errors-in-variables model, 108
- escapement
 - in Allen-Clark abundance models, 210–212
 - for a Bayesian analysis of spawner-recruit, 125, 126
 - in Deriso-Schnute biomass models, 214
 - in dynamics for semelparous populations, 123
 - and geographic apportionment, 433
 - in harvest policies, 440, 442, 444, 449, 450, 454, 458
 - and production model parameter estimation, 76
 - for run reconstruction, 428, 429, 432
 - for spawner-recruit parameter estimation, 100, 104
- eumetric yield curve, 246
- expected value
 - in models for variation in growth, 185, 186, 188, 193, 194, 196, 197
 - in models with mark-recapture data, 157, 160

expected value (*continued*)

- in models with migration population models, 404
- parameterizations in growth models, 137, 138
- in stochastic linear matrix models, 279, 281
- as used in catch-effort and the fishing process, 31, 39, 43, 49
- as used in delay-difference model parameter estimation, 237, 238
- as used in harvest optimization, 446, 448, 454, 456, 483, 484
- as used in spawner-recruit parameter estimation, 103, 110, 115
- for theory of mortality, 14, 15
- exploitable abundance, biomass, and surplus production, 339
- exploratory data analysis, 339
- exponential growth law, 1, 75
- extinction
 - and dynamics for semelparous populations, 121
 - and harvest policies, 439
 - and migration population models, 411
 - and theory of stock productivity, 55

F-test

- for comparison of growth models, 164, 167, 169, 171, 177, 180
- for size-age models, 150, 155

$F_{0.1}$

- in Beverton-Holt year-class models, 246
- and biological reference points, 459, 460, 468–473, 475, 477, 478

fecundity, 202–204. *See also* egg production

fertility, 268, 269, 290–294. *See also* fecundity

fertilization of eggs, 202, 204

filters. *See* Kalman filters

finite time optimization, 455

Fisher-Behrens comparison of growth models, 166, 173

Fishery Management Council, 392, 473

fishng effort

in Beverton-Holt year-class models, 241

in biological reference points, 468

in catch-age estimation of abundance, 336, 342, 343, 352

in catch-effort and the fishing process, 15–18, 26, 28, 36, 37, 40–42

in delay-difference model parameter estimation, 235

in delay-difference models—some alternatives, 220, 222

in Deriso-Schnute biomass models, 214

in estimation of migration, 413, 414, 416

in estimation of natural mortality M , 357–359

in generic per recruit models, 257

in goals and objectives of management, 446

in length-based assessment methods, 385, 391

in migration population models, 402, 405

in migratory cohort and catch-age analyses, 426, 427

in optimization of harvest, 454

in production model parameter estimation, 67, 72–74, 76, 77, 81

in theory of stock productivity, 50, 52, 54, 59, 60, 62, 64

fishng mortality

in Beverton-Holt year-class models, 241, 242, 244, 246, 248

and biological reference points, 459, 461–464, 468, 470–472, 474–477, 479–482

in catch-age estimation of abundance, 317–319, 321, 324–326, 328, 333, 334, 336, 338, 339, 342, 344, 348–354

in catch-effort and the fishing process, 15, 16, 23, 24, 28

in continuous linear matrix models, 294

in delay-difference models—some alternatives, 221, 223

in dynamics for semelparous populations, 118

in estimation of migration, 416, 420, 421

in estimation of natural mortality M , 355, 357–359

in generic per recruit models, 255–258

in goals and objectives of management, 443, 446

in harvest policies and equilibrium concepts, 438–442

in length-based assessment methods, 380, 382–386, 392

in migration population models, 403, 405

in migratory cohort and catch-age analyses, 426, 427

in migratory per recruit analyses, 434, 436

- in nonlinear discrete Leslie-type models, 287
 in optimization of harvest, 448–450, 453, 455, 458
 in production model parameter estimation, 67, 73, 77, 79
 in size-structured basic models, 365, 368
 in spawning stock and egg production per recruit, 261, 263
 in stochastic size and age structured models, 372, 375, 379
 in theory of mortality, 11, 13, 15
 in theory of stock productivity, 50–52, 54, 56, 58, 59, 61, 63–66
 in time-varying linear matrix models, 278
 in yield per recruit model variations, 264, 265, 267
 fishing power, 18, 25
 fixed cost in estimation of age composition, 309, 310
 fixed escapement. *See* constant escapement
 Fletcher quadratic production model, 62, 70, 80
 F_{\max}
 in Beverton-Holt year-class models, 246
 and biological reference points, 462–464, 466–473, 475, 477, 478
 Ford growth equation, 215, 216
 Ford growth parameter, 133, 138, 139, 212
 Ford plot, 134
 forecast
 and AIC versus BIC criteria, 165
 of catch-effort with time series, 36
 with delay-difference models, 222, 223
 equation for age-specific dynamics, 331
 equation for production model, 75
 equation for stage-structured matrix models, 371
 equation for stochastic linear matrix models, 279
 equation for time-varying linear matrix models, 278
 with linear matrix models, 290–292
 Fournier and Archibald catch-age method, 336, 338
 Fowler's method for threshold estimation, 482
 gamma spawner-recruit model, 97
 gear saturation in catch-effort and the fishing process, 28
 gear selectivity. *See* selectivity issues; selectivity models
 gear type
 considered in catch-age estimation of abundance, 335, 349, 350, 353
 considered in catch-effort and the fishing process, 16, 18, 19, 24, 25
 considered in migratory cohort and catch-age analyses, 426
 general linear
 catch-effort models, 18, 19, 22, 23, 25
 method for comparison of growth models, 165, 167
 method for estimation of age composition, 316
 method for modeling mark-recapture data, 158
 method for size-age models, 150
 model of scale and otolith measurements, 182
 general population model of surplus production, 85
 generalized additive model, 19, 92
 generic per recruit models, 255–258
 GENEST computer program for delay-difference model, 226, 227
 geographic apportionment, 432–434
 geometric growth law, 1
 germinal age, 326, 328
 Gibbs sampling method for Bayesian calculations, 125
 goals of management, 442–447
 Gompertz growth model
 with comparison of growth models, 165
 for fecundity and maturity, 202
 for production model parameter estimation, 66, 70, 73, 80, 82
 for relation of surplus production to recruitment, 85
 in size-age models, 145–148, 150, 153, 155
 in stochastic size and age structured models, 374
 in theory of stock productivity, 56, 61, 62, 66
 for variation in growth, 192
 Gompertz-Fox production model
 and parameter estimation, 66, 70, 73, 80, 82
 and relation of surplus production to recruitment, 85
 theory, 56, 61, 62, 66

- gonadal index for estimating natural mortality M , 362
- goodness-of-fit
- in catch-age estimation of abundance, 331
 - in estimation of age composition, 299
 - in LVB growth model, 143
 - in size-age models, 152
- Graham-Schaefer production model
- and biological reference points, 460, 482
 - parameter estimation, 66, 67, 69, 71, 72, 74–78, 80–82
 - related to Allen-Clark abundance models, 212
 - related to delay-difference model parameter estimation, 230
 - relation of surplus production to recruitment, 82, 85
 - related to spawner-recruit models, 96
 - theory of stock productivity, 52, 55, 56, 58, 60–62, 65, 66
- grayling, 413, 414
- growth, 128–200
- for alternative delay-difference models, 218–220, 222, 223
 - for alternative yield per recruit models, 265, 266
 - for Beverton-Holt year-class models, 245, 248
 - and biological reference points, 459–462, 472, 477, 482
 - and choosing the best model, 164–165
 - and comparison of growth models, 164–180
 - density-dependent. *See* density dependence
 - for Deriso-Schnute biomass models, 212–216
 - estimated along with migration, 416
 - estimated in delay-difference models, 224, 225, 227
 - estimated with mark-recapture data, 155–158, 161–163
 - estimated in production models, 75
 - estimated with scales and otoliths, 180, 181
 - and fecundity and maturity, 200–203
 - in a generic per recruit model, 256, 257
 - for length-based assessment methods, 380, 382–390, 392, 395, 397
 - modeled as a function of age, 143, 145–150, 152–155
 - as modeled with the LVB growth model, 132–135, 138–142
 - as modeled in production models, 50, 51, 53, 55, 61, 62
 - models for size of individuals, 128–199
 - physiology, 128
 - of a population in continuous linear matrix models, 293, 294
 - of a population in a Leslie matrix model, 273–275
 - of a population in stochastic linear matrix models, 279–281
 - of a population with migration, 399, 403, 404
 - for relation of surplus production to recruitment, 82, 85
 - for simple population growth models, 1–9
 - for spawner-recruit models, 93, 96, 98
 - for stage-structured matrix models, 369–372
 - for a stochastic model with recruits by size, 250, 251, 253
 - for stochastic size and age population models, 372, 374, 376, 378–380
 - use in estimation of natural mortality M , 357, 361, 362
 - as used in estimation of age composition, 295–301, 305, 316
 - as used in size-structured population models, 363–399
 - and variation in growth, 182–186, 188, 190–197, 199
 - and weight-length models, 129–131
- growth overfishing, 477
- habitat area 17, 433
- habitat suitability. *See* basin model
- haddock, 362, 472
- hake, 152, 460
- handling mortality, 265
- harvest. *See* catch
- harvest optimization, 437–485
- goals, objectives, and constraints, 442–446
 - methods, 447–458
 - polices and equilibrium concepts, 438–441
 - and risk, uncertainty, and decision analysis, 482–485
- See also* constant catch; constant escape-
ment; constant fishing mortality
- herring, 413, 481, 482

- Hessian, 355, 417
- Hilborn method of production model estimation, 82
- Hilborn's method of migration estimation, 413, 414
- homing, 398, 400, 406
- hooks, 15–18, 36, 40, 44–48
- Horbowy's approach for delay-difference models, 218
- Hotelling T^2 statistic, 171–174, 177
- hydroacoustic
- use in catch-age estimation of abundance, 348
 - use in delay-difference model parameter estimation, 226
 - use in geographic apportionment, 433
- hyperdepletion, 28
- hyperstability, 28
- identical error assumption, 114
- IMMAGE method for length-based assessment, 390
- immigration. *See* migration
- independent error. *See* error structure
- index of abundance, 16–49, 353, 483. *See also* catchability coefficient
- individual variation in growth
- considerations with mark-recapture data, 155, 158, 163
 - models, 184–190
- inflection point
- in double logistic selectivity curve, 391
 - in models for fecundity and maturity, 201, 202
 - in models of stock productivity, 60
 - in size-age models, 140–141, 145–150, 153, 154, 164
 - as a threshold reference point, 481, 482
- instantaneous growth parameter, 3, 134. *See also* growth
- instantaneous rate of change
- in LVB growth model, 140
 - in models of stock productivity, 51
 - in simple population growth models, 2, 3, 5
 - in size-age models, 148
- instantaneous total mortality, 10
- integral average, 12, 74, 89
- integrated
- Gompertz growth model, 374
 - equations in theory of stock productivity, 51, 60
- methods for catch-age estimation of abundance, 317
- quantities in delay-difference models, 232
- quantities in per recruit models, 256
- quantities for production model estimation, 51, 60, 67
- interest rate, 447
- interference competition, 40, 45, 46
- intrinsic growth fraction, 273–275
- intrinsic rate of increase
- for biological reference points, 481, 482
 - in continuous linear matrix models, 294
 - in migration population models, 399, 400
 - in simple population growth models, 6, 8, 9
- irreducible matrix, 372, 410, 411
- isometric relationship, 241
- in Beverton-Holt year-class models, 244, 246
 - in biological reference points, 463, 469
 - in delay-difference models—some alternatives, 219, 220
 - in estimation of natural mortality M , 361
 - in models of fecundity and maturity, 203
 - in LVB growth model, 139–141
 - in size-age models, 148, 150
 - in spawning stock and egg production per recruit, 259, 260
 - in stochastic model with recruits by size group, 250, 253
 - in weight-length models, 129–131
- isopleth, 245
- iterative reweighted least squares, 170, 353
- iteroparous, 117, 118, 289, 448
- jackknife method, 33, 80, 101
- Kalman filters
- for catch-age estimation of abundance, 353
 - derivation and models, 235–237
 - for length-based assessment methods, 385
 - for production model parameter estimation, 77
- knife-edge maturity, 259
- knife-edge recruitment. *See* recruitment
- knife-edge selectivity, 241. *See also* selectivity issues; selectivity models
- Laplace transform, 293
- larvae, 86, 87, 206, 398
- latent productivity, 50–52

- Laurec-Shepherd catch-age method, 352
 learning
 effects on catch-effort relationship, 18
 modeled in optimization methods, 458
 as related to production models, 76
 least squares estimation method
 for age composition, 316
 for catch-age models, 333, 335, 336, 339,
 342, 352
 for comparison of growth models, 165,
 167, 169–172, 174
 for delay-difference models, 224
 for fecundity and maturity, 202
 for growth using mark-recapture data,
 156–158
 for length-based assessment, 385, 390
 for LVB growth model, 135, 136, 142,
 143
 for migratory cohort and catch-age analy-
 ses, 426, 427
 for production models, 71, 73, 78, 80
 for size-age models, 146, 150, 152, 153
 for spawner-recruit models, 103, 104,
 112, 113, 117
 for variation in growth, 186, 195
 for weight-length models, 130, 131
 Lee's phenomenon, 182
 Lefkovitch model for stage-structured popu-
 lations, 371
 length cohort analysis. *See* length-based as-
 essment methods
 length composition analysis, 363
 length frequency
 analysis (LFA) for age composition, 295–
 301, 306, 311, 316, 317
 distribution analysis (LFDA), 363
 for estimation of natural mortality M ,
 357, 360
 for length-based assessment methods,
 380, 382, 383, 387, 388
 and LVB growth model, 138
 and size-structured basic models, 364
 length-based assessment methods, 380–397
 for catch-length and length-based synthe-
 sis, 382–397
 for length cohort analysis, 380–382
 length-weight relationship, 129–132
 Leslie matrix discrete model, 268–278
 LFDA, 363
 life history parameter
 for biological reference points, 472, 477,
 482
 in estimation of natural mortality M , 357,
 360–362
 view of relation of growth and natural
 mortality, 241
 lifetime egg production, 261, 274
 lifetime yield, 245, 261
 likelihood function
 for analysis of catch-effort and the fishing
 process, 30–35, 45, 48
 for analysis of fecundity and maturity,
 202
 for analysis of variation in growth, 184,
 189, 190, 192, 193, 195, 197
 for Bayesian considerations in spawner-
 recruit, 124, 125
 for catch-age estimation of abundance,
 321, 331–333, 335, 336
 for comparison of growth models, 164,
 165, 169–171, 174, 177, 180
 and decision analysis, 483
 for delay-difference model parameter
 estimation, 215, 224, 232, 233, 235,
 237
 for estimation of age composition, 295–
 297, 316, 317
 for estimation of migration, 412–414,
 416–419
 for growth analysis with mark-recapture
 data, 163
 for length-based assessment methods,
 383, 390–392
 for migratory cohort and catch-age analy-
 ses, 428
 for production model parameter estima-
 tion, 78
 for size-age models, 137, 152, 155
 for spawner-recruit parameter estimation,
 113, 114, 117
 for stochastic size and age structured mod-
 els, 373, 379, 380
 likelihood ratio, 169–170. *See also* likeli-
 hood function
 limited access, 437
 limited entry, 442
 line transect, 37, 38, 337, 432, 433
 linearization
 of Allen-Clark abundance models, 210
 of Deriso-Schnute biomass models,
 213
 in Kalman filters, 237, 238
 of spawner-recruit models, 100–103
 logbook, 26, 76

- logistic
 error structure and transformation, 332
 growth in a delay-difference model, 220
 law of population growth, 4–9
 model for biological reference points, 460
 model dynamics for semelparous populations, 118, 121
 model of maturity, 201, 202
 model of migratory populations, 399, 400, 403
 model in optimization of harvest, 458, 459
 models for size selectivity, 25, 384, 390–392
 model of stock productivity, 52, 53, 55
 size-age models, 148, 150
 spawner-recruit models, 87, 93, 95, 99
- lognormal distribution
 in Bayesian considerations in spawner-recruit, 125
 in biological reference points, 478
 in catch-age estimation of abundance, 319, 335–337
 in catch-effort and the fishing process, 18, 25, 30, 32, 34, 35
 in delay-difference model parameter estimation, 233
 in estimation of age composition, 296
 in estimation of migration, 416
 in fecundity and maturity, 203
 in length-based assessment methods, 385
 in migratory cohort and catch-age analyses, 426, 427
 in optimization methods, 448, 454, 456, 457
 in simple population growth models, 8
 in spawner-recruit models, 92, 102, 104
 in stochastic linear matrix models, 279–281, 283
 in a stochastic model with recruits by size group, 253
 of variation in growth, 189, 190, 198, 199
- longline models of the fishing process, 16, 18, 42, 46–49
- Lotka-Volterra model, 9
- lowess data smoothing, 92
- LQ approximation in dynamic programming, 458
- Ludwig-Walters method for estimation of spawner-recruit models, 91
- LVB (Ludwig von Bertalanffy) growth model, 132–143
 applied in length-based assessment methods, 382, 384, 386, 392
 and combining weight-length and length-age models, 139–143
 as a difference equation for weight-age, 139
 for length-age relation, 132–139
 in size-structured basic models, 364, 365, 369
 in a stochastic model with recruits by size group, 250, 253
 as used in estimation of natural mortality M , 357
- LVB allometric. *See* allometric relationship
- LVB isometric. *See* isometric relationship
- mackerel, 131, 361, 478
- Magnuson-Stevens Act (MSFCMA), 442
- Malthus on simple population growth models, 2, 4
- Malthusian parameter R , 2
- management, 437–485
 and basin models, 404
 and biological reference points, 459–481
 and the fishing process, 36
 and geographic apportionment, 432, 433
 goals, objectives, and constraints, 442–446
 harvest policies and equilibrium concepts, 438–442
 optimization methods, 447–458
 policies compared in production models, 76
- risk, uncertainty, and decision analysis, 482–485
- of semelparous populations, 123
- and slot limits, 265
- marine mammal, 439
- mark-recapture data
 applied to variation in growth, 184, 187–190, 192
 in catch-age estimation of abundance, 337
 contrasted with size-age data, 158
 in estimation of age composition, 303
 in estimation of migration, 406, 412–418, 421
 in estimation of natural mortality M , 357, 358
- in geographic apportionment, 432, 433
 for growth models, 134, 148, 155–164

Markov

- assumption compared in migration, 413
- chains for Bayesian parameter estimation, 233, 234, 354
- matrix in run reconstruction, 428
- processes in the fishing process, 42
- processes in migration population models, 400, 404, 406
- processes in spawner-recruit models, 87
- processes in stochastic linear matrix models, 283
- matrix form**
 - reduced in Allen-Clark abundance models, 208
 - in estimation of migration, 413
 - in length-based assessment methods, 384
 - in Leslie matrix discrete model, 272
 - in migration population models, 401, 404, 409, 410
 - in stage-structured matrix models, 370
- maturity**
 - and biological reference points, 472, 473
 - and catch-age estimation of abundance, 337
 - in dynamics for semelparous populations, 117, 118
 - and fecundity, 200–206
 - in migratory per recruit analyses, 435, 436
 - models, 201, 202
 - in nonlinear discrete Leslie-type models, 285, 289
 - in spawning stock and egg production per recruit, 259–263
 - and yield per recruit model variations, 265–267
- maximin yield, 472
- maximum economic yield, 458
- maximum likelihood.** *See* likelihood function
- maximum productivity
 - in delay-difference models, 230
 - in harvest policies and equilibrium concepts, 438
 - in spawner-recruit models, 88, 98
 - in theory of stock productivity, 52–54, 56, 57, 61, 62, 66
- maximum recruitment, 88–90, 95–98
- maximum sustainable yield (MSY) and catch (MSC)
 - for Allen-Clark abundance models, 210
 - in connection with management, 443
 - for Deriso-Schnute biomass models, 214

as a harvest policy, 442

in spawner-recruit models, 98, 122, 123
in theory of stock productivity, 52

May's method for threshold estimation, 482

MCMC (Markov Chain Monte Carlo) algorithm, 233, 234, 354

mean age of reproduction, 275, 294

mean generation length, 275–277, 280, 294
measurement error

for catch-age estimation of abundance, 335

for delay-difference model estimation, 224, 226, 228, 230

in mark-recapture growth analysis, 158
for migratory cohort and catch-age analyses, 423, 427

in production model parameter estimation, 69, 77

for spawner-recruit parameter estimation, 108–117

See also error structure

meta-analysis, 360

Metropolis algorithm, 233, 234

migration, 398–434

age-structured population models, 407–412

and catch-age estimation of abundance, 317, 326

deterministic, non-age-structured models, 399–404

effect on estimation of natural mortality M , 358–360

estimation of migration, 412–421

and geographic apportionment, 434

included in catch-age analysis, 423–428

included in cohort analysis, 421–423

included in per recruit analyses, 434–436

and movement, 398

stochastic, non-age-structured models, 404–407

migration estimation

with Darroch's method and extensions, 412–414

with Hilborn's method and extensions, 414–419

with miscellaneous methods, 419–421

minimum integrated average expected loss, 224

minimum size limit

considerations in biological reference points, 463, 471

- effect on catch-age estimation of abundance, 342
 effect on migratory per recruit analyses, 434, 436
 in a stochastic model with recruits by size group, 253
 in yield per recruit model variations, 263, 267
See also knife-edge selectivity
 mixed stock, 398, 428, 432
 mixture distribution, 295
 moments of the weight distribution, 216
 Monte Carlo methods
 in catch-age estimation of abundance, 354
 for comparison of growth models, 165
 in delay-difference model parameter estimation, 233, 236
 explained for stochastic linear matrix models, 281
 in forecasting in linear matrix models, 290, 291
 in optimization of harvest, 453
 in decision analysis, 484
See also MCMC algorithm
 mortality. *See* fishing mortality; natural mortality
 movement. *See* migration
 multiregional considerations, 371, 409
 multispecies
 considerations in harvest optimization, 449, 455, 459, 471
 migration population models, 399
 models of the fishing process, 45–47
 population growth models, 9
 VPA discussed, 360
 yield per recruit models, 266
 multinomial distribution
 for catch-age estimation of abundance, 331, 332, 335
 in catch-effort and the fishing process, 45, 48
 for estimation of age composition, 296, 297, 302, 317
 for estimation of migration, 416, 419
 in length-based assessment methods, 385, 391
 in stochastic linear matrix models, 284
 in theory of mortality, 14
 multiple objectives, 459
 mutualism, 9
 natural mortality
 in Allen-Clark abundance models, 209, 210
 in Beverton-Holt year-class models, 242, 243, 245
 in biological reference points, 460, 461, 479, 482
 in catch-age estimation of abundance, 317–319, 323–326, 328, 330, 334, 338, 339, 342, 349, 351
 in continuous linear matrix models, 294
 in delay-difference model parameter estimation, 224, 225, 227
 in delay-difference models—some alternatives, 220, 221, 223
 in Deriso-Schnute biomass models, 214
 estimation methods, 355–362
 in estimation of migration, 413, 416, 419–421
 in generic per recruit models, 255, 257
 in length-based assessment methods, 383, 386, 392
 in migration population models, 401, 402, 405
 in migratory cohort and catch-age analyses, 421–423, 426, 427
 and optimization of harvest, 448
 and surplus production models, 82, 85
 in size-structured basic models, 365, 369
 in theory of mortality, 11, 13, 15
 and theory of stock productivity, 50
 in yield per recruit model variations, 264
 natural mortality estimation
 with catch curve analysis, 357
 by collection of dead organisms, 360
 with LFA and related analyses, 357–358
 with life-history or meta-analysis, 360–362
 with mark-recapture experiments, 358–360
 by use of population models; multispecies VPA, 360
 negative binomial distribution, 416
 nonlinear discrete Leslie-type models, 284–290
 nonlinearity
 in catch-effort and the fishing process, 46
 in delay-difference model parameter estimation, 231
 measures in catch-age estimation of abundance, 342

- nonlinearity (*continued*)**
- measures in LVB growth model, 138
 - measures in size-age models, 152
- nonreporting**, 359, 416
- normal distribution**
- in biological reference points, 478
 - in catch-age estimation of abundance, 332
 - in catch-effort and the fishing process, 18, 30–35
 - for comparison of growth models, 166, 169–171, 174
 - in delay-difference model parameter estimation, 232, 236, 237
 - in estimation of age composition, 296
 - in estimation of migration, 416
 - in length-based assessment methods, 392
 - in models of variation in growth, 189–192, 198
 - in simple population growth models, 8
 - in spawner-recruit parameter estimation, 102, 112
 - in stochastic linear matrix models, 283
 - in stochastic model with recruits by size group, 253
- numerical integration**, 78, 99
- nursery grounds**, 398
- objective function**
- in catch-age estimation of abundance, 331, 333, 335, 351, 354
 - for comparison of growth models, 177
 - for estimation of age composition, 297–299, 301
 - for length-based assessment, 390, 391
 - for management objectives, 442–447, 449, 450, 453–456, 481, 482
 - for production model parameter estimation, 78
- See also* optimization
- ogive**, 262, 263
- oil spill example**, 277
- open population**, 358, 413
- optimal control**, 444, 455, 458, 459
- optimization**
- in Deriso-Schnute biomass models, 214
 - with fixed-parameter harvest control, 449–454
 - of harvest, 447–459
 - with time-varying harvest controls, 454–459
 - optimum yield (OY), 442, 443
- otolith**, 128
- analysis, 180, 181
 - use in estimation of age composition, 303, 310, 311, 317
- over-compensation**, 98, 119, 121
- overfishing**, 437
- and catch-effort interpretation, 17
 - in connection with biological reference points, 473, 476–478, 481
 - in connection with management goals, 442, 443
 - and geographic apportionment, 432–434
 - and harvest policies and equilibrium concepts, 440
- Pacific halibut**, 11, 17, 30, 48, 72, 74, 143, 146, 153, 180, 257, 278, 295, 302, 306, 319, 320, 342, 345, 354, 398, 423, 427, 433, 453
- Pacific herring**, 413, 481
- Pacific ocean perch**, 434
- Pacific salmon**, 114, 398, 406, 428, 429, 433, 440, 445, 458
- parasite-host**, 9
- Pareto optimal**, 459
- parsimonious model selection**, 152, 155, 160, 164, 165
- partial differential equation**
- for continuous linear matrix models, 292
 - for migration population models, 402, 403
 - for size-structured models, 368
- passive adaptive management**, 458
- Pauly's method of estimating natural mortality M** , 362
- Pella-Tomlinson production model**
- derivation, 56–61, 63, 66
 - parameter estimation, 66, 69, 70, 73, 74, 80–82
 - and relation of surplus production to recruitment, 85
 - as a size-age model, 148
- penalty weights**
- in catch-age estimation of abundance, 332, 335–339, 350
 - in estimation of age composition, 298, 299, 301
 - in length-based assessment methods, 391
 - in management objective functions, 445, 446, 453

- per recruit analysis
 with Beverton-Holt year-class models, 241, 243–246, 249
 for biological reference points, 461–464, 466–468, 470–475, 477, 478, 481, 482
 of discard mortality, 263–264
 and forecasting in linear matrix models, 290
 for generic yield models, 255, 257, 258
 and harvest policies and equilibrium concepts, 440, 458
 for migratory populations, 434–436
 for multi-species and multiple fisheries, 266–267
 and nonlinear discrete Leslie-type models, 286, 287
 relation to size-structured basic models, 364, 365, 368
 by sex of animal, 265–266
 of spawning stock and egg production, 258–263
 of a stochastic model with recruits by size group, 250, 253
 for stochastic size and age structured models, 378, 379
 for trophy fish and slot limits, 264–265
 of yield for some model variations, 263–267
 perfect information, 76
 performance measure in decision analysis, 483–485
 Perron-Frobenius theorem, 272, 277, 371, 372
 perturbation method, 458. *See also* linearization
 phase-plane analysis, 9, 400
 pink salmon, 100, 104, 108, 111–113, 116, 123, 418, 432
 planning horizon in harvest policies, 444–446, 450, 453, 455, 456
 plus group, 325, 338, 351, 352
 Poisson distribution, 30, 98, 416
 policy. *See* management
 polynomial model for size-age relationship, 143, 180
 population dynamics, definition of, 1
 population statistics, 129, 184, 204, 339
 posterior distribution
 in catch-age estimation of abundance, 354
 in delay-difference model parameter estimation, 233
 in risk, uncertainty, and decision analysis, 483
 in spawner-recruit analysis, 124, 125
 See also Bayesian
 Prager's nonequilibrium method of production model estimation, 77
 prawn, 19, 33, 35
 predator
 effects on natural mortality, 334, 357
 effects in simple optimization of harvest, 449, 459
 induced depensation, 99, 119
 in a longline model, 48
 and prey model solution, 93, 94
 and prey simple population models, 9
 search analogy for the fishing process, 37
 present value, 354, 447
 primitive matrix, 371, 372, 410, 411
 prior distribution
 in spawner-recruit analysis, 125, 127
 in catch-age estimation of abundance, 354
 in delay-difference model parameter estimation, 233
 in risk, uncertainty, and decision analysis, 483
 See also Bayesian
 pristine population
 in application of Allen-Clark abundance model, 212
 as initial condition of population, 223, 224, 392
 parameter in theory of stock productivity, 52, 56, 57, 61, 62
 for use in biological reference points, 460, 481, 482
 See also carrying capacity
 probability distribution. *See* likelihood function
 process error
 in Bayesian analysis of spawner-recruit, 124
 for catch-age estimation of abundance, 335, 336, 353–355
 for delay-difference model parameter estimation, 224, 226, 230–235
 for fecundity and maturity analysis, 203
 for length-based assessment methods, 383, 385
 for migratory cohort and catch-age analyses, 426, 427
 for production model parameter estimation, 77, 78
 for spawner-recruit parameter estimation, 92, 108, 111, 115, 117

- production
- as annual surplus production, 67–68
 - concepts for biological reference points, 459, 460, 470, 472, 474, 475, 481, 482
 - and difference equations for surplus production, 75–77
 - dynamics for semelparous populations, 118, 121–123
 - estimated with catch-age models, 345
 - estimated with delay-difference models, 236
 - estimation with equilibrium approximation, 73–74
 - and harvest policies, 438, 440
 - included in management objectives, 443
 - model parameter estimation, 66–82
 - model theory, 50–66
 - models in harvest optimization, 449, 454, 458
 - parameter in spawner-recruit models, 87–89, 95, 98, 101
 - relation of surplus production to recruitment, 82, 85
 - and surplus production—biomass relationship, 68–71
 - and surplus production—fishing effort relationship, 72
 - See also* egg production
- productivity. *See* latent productivity; maximum productivity; production progeny. *See* egg production; recruitment projection. *See* forecast
- proto-cooperation, 9
- pulse-fishing, 454
- purse seine, 18, 42, 43, 215, 233
- quantitative population dynamics, 1
- Quinn-Collie threshold production model, 65, 71, 80
- quota, 76, 241, 449, 483
- rainbow trout, 27, 158, 190, 257, 261, 299, 303, 464, 471, 473
- razor clams, 361, 479
- rebuilding
- with biological reference points, 477
 - in harvest policies, 434, 441, 453, 458
 - in management goals objectives, 443, 446
 - and production model parameter estimation, 82
- recreational fishing, 264, 443, 479
- recruitment, 86, 208, 239, 241
- in Allen-Clark abundance models, 208–212
 - in alternative delay-difference models, 218, 220–223
 - in Beverton-Holt year-class models, 241, 242, 245, 248, 249
 - and biological reference points, 460–464, 466, 472, 475–481
 - and catch-age estimation of abundance, 317–326, 333–339, 342–345, 348–351, 354
 - and delay-difference model parameter estimation, 224, 225, 229, 233, 235, 237
- in Deriso-Schnute biomass models, 212, 213, 217
- dynamics for semelparous populations, 119, 122, 123
- and estimation of age composition, 295, 297–299, 301
- and estimation of natural mortality M , 355, 357, 358
- and fecundity and maturity, 204, 206
- in generic per recruit models, 256–258
- and geographic apportionment, 433, 434
- and harvest policies, 442, 444, 448–450, 453–455, 458
- in length-based assessment methods, 381–387, 391, 392, 395
- in migration population models, 399, 404
- in migratory cohort and catch-age analyses, 422, 423, 426, 427
- in migratory per recruit analyses, 435, 436
- in nonlinear discrete Leslie-type models, 284–287
- overfishing, 476
- and production model parameter estimation, 71–74, 80
- relation to surplus production, 82, 85
- in size-structured basic models, 364–368
- in spawner-recruit models, 86–99
- and spawner-recruit parameter estimation, 100–127
- and spawning stock and egg production per recruit, 258, 260–263
- in stage-structured matrix models, 370–372
- in a stochastic model with recruits by size group, 249–253
- in stochastic size and age structured models, 375, 379
- and theory of mortality, 10–15
- and theory of stock productivity, 50, 51

- variability and management, 454, 472
and yield per recruit model variations, 264–266
red noise, 449
reef fishes, 265
reference point, 436, 440, 459–481
refuge, 436
region
 in catch-effort standardization, 17, 26, 27, 37
 and estimation of migration, 412–420
 and geographic apportionment, 432–434
 and migration population models, 399–411
 and migratory cohort and catch-age analyses, 421–427
 and migratory per recruit analyses, 434–436
 and stage-structured matrix models, 369, 371
regression method
 for biological reference points, 482
 of catch-age estimation of abundance, 319–321, 352
 of catch-effort analysis, 19, 22, 28, 36
 of comparison of growth models, 165, 166, 169, 170, 174
 of estimation of natural mortality M , 357, 358, 360, 361
 of fecundity and maturity analysis, 203
 of partitioning recruits by size group, 253
 of production model parameter estimation, 69–76, 80
 of scale and otolith analysis, 180–182
 of size-age analysis, 146, 152
 of spawner-recruit parameter estimation, 100–105, 108, 110, 116, 117
 of variation in growth analysis, 194
 of weight-length analysis, 136, 131
 See also likelihood function
relative abundance analysis, 330
replacement. *See* equilibrium
replacement line
 in Allen-Clark abundance models, 209
 for biological reference points, 474, 477
 for model of semelparous populations, 119, 122
 for nonlinear discrete Leslie-type models, 290
reproduction. *See* egg production
reproductive value, 274–277, 461, 479
residence time, 404, 436
retrospective analysis, 453, 454
revenue, 446, 447
Richards growth equation, 147, 154, 157
Ricker spawner-recruit model
 in biological reference points, 470, 475
 in catch-age estimation of abundance, 337, 342, 348
 in delay-difference models, 222, 227
 derived, 89–93, 95–99
 for dynamics of semelparous populations, 118, 119, 121–123
 in nonlinear discrete Leslie-type models, 285–287, 290
 and optimization of harvest, 438, 444, 450
parameter estimation, 100–104, 108, 112–116, 125
 and production models, 71, 80, 85
risk, 437
 accounted for in optimization of harvest, 453, 454, 459
 of capture, 40, 47
 and decision analysis, 482–485
 and harvest policies, 440, 442
 quantified in management objective, 444, 446
 related to geographic apportionment, 433, 434
Robbins-Munro method. *See* stochastic approximation
robustness issues
 in biological reference points, 477, 482
 in catch-age estimation of abundance, 321, 326, 328, 336, 339, 348, 354
 in comparison of growth models, 166, 167, 173, 174
 in delay-difference model parameter estimation, 225, 230
 in estimation of age composition, 301
 in generic per recruit models, 256
 in spawner-recruit models, 91
 in weight-length models, 131
rockfish, 2, 4, 135, 174, 180, 434
root normal transformation, 30, 33
rougheye rockfish, 135, 174
run reconstruction, 398–399, 428–432
sablefish, 241–245, 253, 260, 263, 354, 416, 433, 463, 471, 473, 478, 481
salmon, 100, 104, 108, 111–118, 121, 123, 125, 398, 398, 406, 413, 418, 440, 445, 458
sample reuse method 168, 174

- sampling considerations
 in catch-age estimation of abundance, 335–337, 342, 352, 354
 in catch-curve analysis, 321
 in catch-effort analysis, 25, 26, 30, 32, 42
 in comparison of growth models, 166, 169, 170, 172, 173
 in estimation of age composition, 295, 297, 301–303, 305, 306, 308–311, 316, 317
 in estimation of migration, 413, 418
 in fecundity and maturity, 200, 202, 206
 in geographic apportionment, 432
 in length-based assessment methods, 391
 in LVB growth model analysis, 138
 in mark-recapture data, 160
 in optimization of harvest, 459
 in production model parameter estimation, 76
 in scale and otolith measurements, 180, 182
 in spawner-recruit parameter estimation, 102
 in stochastic size and age structured models, 379
 in variation in growth analysis, 184, 190
 in weight-length analysis, 131
 sardine, 92, 180–182, 371
 scale and otolith measurements, 134, 180–182, 303
 Schnute growth model, 138, 148, 150, 153, 155, 156
 Schnute's extension to delay-difference models, 215
 Schnute's nonequilibrium method of production model estimation, 74
 Schnute-Richards growth model, 154
 schooling
 and catch-effort and the fishing process, 36, 37, 39, 40, 48
 and dynamics for semelparous populations, 119
 search theory, 43
 search time, 37
 seasonal issues
 in catch-age estimation of abundance, 328
 in generic per recruit models, 257
 in migratory cohort and catch-age analyses, 423
 in run reconstruction, 429
 in simple population growth models, 6
 in variation in growth, 182–184
 SELECT method for selectivity, 25
 selectivity issues
 in Beverton-Holt year-class models, 241, 242
 and biological reference points, 462, 464, 468, 472, 479
 in catch-age estimation of abundance, 320, 331, 333–335, 338, 339, 342, 344, 348–351, 354
 in catch-effort and the fishing process, 18, 23, 25
 in estimation of age composition, 299
 in estimation of natural mortality M , 358
 in generic per recruit models, 255–257
 in geographic apportionment, 432, 433
 in length-based assessment methods, 384–386, 388–392, 395, 397
 in migratory cohort and catch-age analyses, 426, 427
 in nonlinear discrete Leslie-type models, 287
 in optimization of harvest, 449, 453, 455
 in size-structured basic models, 365
 in spawning stock and egg production per recruit, 260, 263
 in a stochastic model with recruits by size group, 250–252
 in stochastic size and age structured models, 375, 377, 379
 in yield per recruit model variations, 263, 267
 selectivity models, 25, 333, 334, 391, 392
 semelparous population dynamics, 117–123
 separability assumption, 331
 in catch-age estimation of abundance, 331, 334, 335, 349, 350, 352–354
 in geographic apportionment, 432
 in length-based assessment methods, 383, 391
 in migratory cohort and catch-age analyses, 427
 in stochastic size and age structured models, 375
 sex change, 265, 266
 sex ratio
 and fecundity and maturity, 205–207
 and stochastic linear matrix models, 280
 and time-varying linear matrix models, 278
 sex-specific
 estimation of age composition, 295
 fecundity and maturity, 204, 205

- Sharpe-Lotka continuous linear matrix models, 292, 293
- shrimp, 19, 22, 265
- simple population growth models, 1–10
 as the geometric and exponential growth laws, 1–4
 as the logistic model, 4–6
 and multi-species extensions, 9–10
 with time-varying parameters, 6–9
- simple random sampling, 301–302. *See also* sampling considerations
- simulation methods
 for biological reference points, 478, 481, 482
 in catch-age estimation of abundance, 321, 342, 354
 in delay-difference model parameter estimation, 226
 in estimation of migration, 413
 in geographic apportionment, 433
 in optimization of harvest, 453, 454
 in production model parameter estimation, 74, 76
 in stochastic linear matrix models, 281
 in variation in growth analysis, 190
 in yield per recruit model variations, 266
- sinusoid
 effects on harvest optimization, 449
 environment in simple population growth models, 8
 recruitment in a Deriso-Schnute biomass model, 217
 time-varying linear matrix models, 278
 variation in growth, 183, 184
- SIR algorithm, 233
- size limit. *See* minimum size limit; slot limit
- size-age models, 143–155
 ad hoc, 143–145
 allometric, 143
 Gompertz, 145–147
 and the Pella-Tomlinson model, 148
- Richards, 147–148
- Schnute, 148–154
- Schnute-Richards, 154–155
- Verhulst, 147–148
See also Brody-LVB growth model; LVB growth model
- size-structured population models, 363–397
 basic, 364–369
 delay-difference, 220
 length-based assessment, 380–397
- stage-structured, 369–371
- stochastic, 372–379
- stochastic with recruits by size group, 250
- stochastic size and age structured, 378
- skipjack tuna, 416, 421
- slot limit, 264, 265
- snapper, 46, 306, 310, 311, 357
- social objectives, 447
- sockeye salmon, 100, 125, 118
- spatial distribution. *See* region; migration
- spatiotemporal considerations, 398
- spawner-recruit model, 86–100
 Beverton-Holt, 87–89
 Cushing, 93
 definition of compensatory, 98
 definition of depensatory, 99
 Deriso-Schnute, 93–96
 gamma, 97–98
 miscellaneous, 98–100
 Ricker, 89–93
 Shepherd, 96–97
 Thompson, 99
- spawner-recruit parameter estimation, 100–117
 and autocorrelated errors, 101–103, 117
 and linear regression approach, 100–101
 and measurement error approach, 108–117
 and nonlinear regression approach, 103–108
- spawning area, 86, 98, 206, 398
- spawning biomass
 in Deriso-Schnute biomass models, 214
 in migratory per recruit analyses, 436
 in multispecies per-recruit models, 267
 related to fecundity and maturity, 204–207
 in spawner-recruit parameter estimation, 100
 as in spawning stock and egg production per recruit, 259–263, 461, 462, 472–474, 481
- spawning population biological reference points, 474
- spawning population per recruit biological reference points, 472
- spawning stock, 86
 based harvest policy compared, 440
 biological reference points, 461, 464, 472–474, 476–478, 481
 and catch-age estimation of abundance, 339

- spawning stock (*continued*)
 delay-difference models, 214, 221, 222, 228, 230
 dynamics for semelparous populations, 122, 123
 and egg production per recruit, 258–263
 and geographic apportionment, 433
 and migratory per recruit analyses, 436
 and production model parameter estimation, 71
 related to management goals, 445
 and spawner-recruit models, 86–89, 91–93, 95, 98, 99
 and spawner-recruit parameter estimation, 100, 101, 108
 and yield per recruit trade-offs, 473
 species interaction. *See* multispecies
 stability
 analysis of Allen-Clark abundance models, 209–211
 analysis of Deriso-Schnute biomass models, 213
 analysis of Leslie matrix discrete model, 276, 277
 analysis of migration population models, 410
 analysis of nonlinear discrete Leslie-type models, 288–290
 of catch-effort versus abundance, 28
 of time-varying linear matrix models, 278
 stable population, 273
 age structure in Leslie matrix discrete model, 273–277
 age structure for migration population models, 410
 in continuous linear matrix models, 293, 294
 in migration population models, 410
 size structure in stage-structured matrix models, 372
 stage-structured matrix population models, 369–372
 standardization
 and catch-age estimation of abundance, 349
 of catch-effort indices, 18, 19, 23, 25, 26
 state space model, 354
 state variable or vector, 236, 237, 443, 455–458
 stationarity
 and harvest control, 454
 in length-based assessment methods, 382
 in migration population models, 410, 411
 in size-structured basic models, 364
 in stage-structured matrix models, 372
 stationary, 274
 assumption for size-structured basic models, 364
 continuous linear matrix models, 294
 correlation process in growth, 193–195, 197, 199
 policy for optimization of harvest, 456
 population and harvest considerations, 454, 477, 478
 results for stochastic size and age structured models, 378
 statistical significance, 101, 102, 113, 150
 stochastic approximation method, 453
 stochastic growth, definition of, 191
 stochastic linearization for Kalman filter, 237
 stochastic model
 for catch-age estimation of abundance, 336
 for catch-effort and the fishing process, 8, 16, 30, 42, 43, 46
 and delay-difference models, 221
 of growth in length-based assessment methods, 382, 384, 388
 with linear matrices, 279–284
 and migratory per recruit analyses, 436
 for movement, 404
 with recruits by size group, 249–255
 of simple population growth, 13, 15
 as a size-structured basic models, 369
 of size and age structured dynamics, 372–380
 of variation in growth, 195–197, 199
 stochastic process, 13, 15, 43
 stock concept, 50, 442
 stock reduction analysis, 223, 224
 stock-recruitment models. *See* spawner-recruit models
 stock synthesis analysis, 355, 356, 382, 387–397
 stratified catch-age estimation of abundance, 349–350
 stream life, 432
 Student's *t* distribution, 126, 166, 171
 subsistence, 333
 surplus production. *See* production

- survey information
 for catch-age estimation of abundance, 338, 353
 for catch-effort and the fishing process, 16, 25
 for egg production method, 206
 for estimation of age composition, 295, 302, 310
 for geographic apportionment, 433, 434
 for length-based assessment methods, 385, 392
 for spawner-recruit parameter estimation, 104
 survival. *See* fishing mortality; natural mortality
 sustainability
 in Allen-Clark abundance models, 210
 in Beverton-Holt year-class models, 246
 with biological reference points, 462, 473, 480
 in Deriso-Schnute biomass models, 214
 in dynamics for semelparous populations, 122, 123
 and goals, objectives, and constraints, 443
 and harvest policies and equilibrium concepts, 439, 442
 and optimization methods, 455
 in relation to surplus production, 85
 in spawner-recruit models, 98
 in theory of stock productivity, 52
 sustainable or sustained yield
 in Allen-Clark abundance models, 210
 in Deriso-Schnute biomass models, 214
 as a management goal, 442, 443
 for models of semelparous populations, 123
 in spawner-recruit models, 98
 in theory of stock productivity, 52
 synthetic cohort, 321, 357, 467
- tag loss and shedding
 and estimation of migration, 412, 414, 416, 420, 421
 and estimation of natural mortality M , 358, 359
 tagging mortality, 358, 416
 tagging. *See* mark-recapture data
 terminal abundance
 in catch-age estimation of abundance, 323–326, 330, 342, 350–353
 in estimation of natural mortality M , 359
- in migratory cohort and catch-age analyses, 421–423, 426, 427
 tests of common matrices, 174
 theory of mortality, 10–15
 and deterministic theory of fishing, 11–13
 and stochastic theory of fishing, 13–15
 theory of stock productivity, 50–66
 and Fletcher quadratic model, 62–64
 and Gompertz-Fox model, 61–62
 and Graham-Schaefer model, 52–56
 and models with environmental variables, 66
 and Pella-Tomlinson model, 56–61
 and threshold models, 64–66
 Thompson spawner-recruit model, 99
 thresholds
 in biological reference points, 459, 477, 478, 480–482
 in catch-age estimation of abundance, 338
 in dynamics for semelparous populations, 118, 119
 in harvest policies and equilibrium concepts, 439–442
 in optimization methods, 449, 453, 454, 458
 in production model parameter estimation, 66, 71, 73, 80, 82
 in spawner-recruit models, 96
 in theory of stock productivity, 64–66
 tiger flathead, 421
 tiger prawns, 33
 time series
 in biological reference points, 477–479, 481
 in catch-age estimation of abundance, 354, 355
 in catch-effort and the fishing process, 36
 in delay-difference model parameter estimation, 224–226, 232, 235, 236
 in delay-difference models—some alternatives, 223
 in migration population models, 404
 in optimization of harvest, 449, 459
 in production model parameter estimation, 67, 77
 in spawner-recruit parameter estimation, 100, 117
 in spawning stock and egg production per recruit, 262
 in theory of stock productivity, 66
 time-varying linear matrix models, 278–279

- total allowable catch (TAC), 433
 transit time, 404
 transition matrix
 and geographic apportionment, 433
 for length-based assessment methods, 384, 386, 397
 for migration population models, 404
 as a spawner-recruit model, 87
 for stage-structured matrix models, 370, 372
 for stochastic linear matrix models, 281
 trawl survey data
 applied in catch-age estimation of abundance, 348
 in catch-effort and the fishing process, 16, 25, 33
 for geographic apportionment, 434
 trophy fish, 264, 265
 TSER catch-age method, 355
 tuna, 19, 42, 116, 166, 177, 190, 191, 213, 214, 233, 359, 398, 406, 416, 419, 421, 428, 436
 tuned VPA catch-age method, 352, 355
 tuning method in catch-age analysis, 317, 428
 two-stage sampling, 303–306. *See also* sampling considerations
 uncertainty, 437
 about prior distribution in spawner-recruit analysis, 127
 associated with stock reduction method, 224
 included in Beverton-Holt year-class models, 245, 249
 issues in biological reference points, 460
 issues in forecasting in linear matrix models, 291
 issues in geographic apportionment, 434
 issues in harvest policies and equilibrium concepts, 442
 included in harvest optimizations, 454
 presented in catch-age estimation of abundance, 354
 related to risk and decision analysis, 482–485
 Usher stage-structured model, 371
 utility function, 124, 444, 453–456, 485
 validation issues in growth, 158, 181, 182
 variation in growth, 182–200
 and comparison of methods, 197–200
 as seasonal growth, 183–184
 as stochastic growth, 191–197
 Velleman's robust smoother, 256
 Verhulst growth model, 147
 virtual population analysis (VPA), 317, 323, 324, 350, 352, 353, 355
 von Bertalanffy growth model. *See* LVB growth model
 vulnerability
 and catch-effort and the fishing process, 42
 and estimation of migration, 416
 and estimation of natural mortality M , 358
 as contrasted with selectivity, 388, 391
 and spawning stock and egg production per recruit, 263
 Walford plot, 134
 walleye pollock, 28, 65, 226, 230, 326, 338, 348, 354, 478, 482
 weight at age, 139–143
 in alternative delay-difference models, 221
 in Beverton-Holt year-class models, 244
 and catch-age estimation of abundance, 317, 342
 and estimation of age composition, 305
 and fecundity and maturity, 204
 and generic per recruit models, 256
 and length-based assessment methods, 390
 and migratory per recruit analyses, 435, 436
 and yield per recruit model variations, 267
 See also size-age models
 weight-length models, 129–132
 weighting of data
 issues in, 335
 related to measurement error, 433, 434
 See also penalty weights
 weighting term. *See* penalty weights
 whale, 38, 125, 211, 212, 368, 433
 white noise, 448
 XSA catch-age method, 355
 year-class. *See* recruitment
 yellowfin tuna, 19, 214, 233, 359, 406, 436
 yield per recruit. *See* per recruit analysis