

# **Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture**

Kenneth P. Burnham

David R. Anderson

Gary C. White

Cavell Brownie

Kenneth H. Pollock



*American Fisheries Society*

Monograph 5

**Publication and Funding of this Monograph  
were made possible by a grant from**

**Chelan County Public Utility District**

**Wenatchee, Washington 98801**

**American Fisheries Society Monographs: ISSN 0362-1715  
Library of Congress Catalog Card Number: 87-070785  
ISBN 0-913235-41-5**

**Copyright 1987 by the  
American Fisheries Society  
5410 Grosvenor Lane  
Bethesda, Maryland 20814**

**Design and Analysis  
Methods for Fish Survival  
Experiments Based on  
Release-Recapture**

**Kenneth P. Burnham**

*Department of Statistics  
North Carolina State University, Raleigh, North Carolina 27695*

**David R. Anderson**

*Colorado Cooperative Fish and Wildlife Research Unit  
Colorado State University, Fort Collins, Colorado 80523*

**Gary C. White**

*Department of Fishery and Wildlife Biology  
Colorado State University, Fort Collins, Colorado 80523*

**Cavell Brownie and Kenneth H. Pollock**

*Department of Statistics  
North Carolina State University, Raleigh, North Carolina 27695*

American Fisheries Society Monograph 5  
ISSN 0362-1715

Bethesda, Maryland  
1987

# Contents

<b>Preface</b>	<b>xi</b>
<b>Part 1. Introduction</b>	<b>1</b>
1.1. Introduction	1
1.1.1. Simple Example	1
1.1.2. Historical Note	3
1.1.3. Objectives	4
1.1.4. Reader's Guide	5
1.2. Statistical Concepts	6
1.2.1. Maximum Likelihood Theory	6
1.2.1.1. Point estimation	10
1.2.1.2. Estimation of sampling variances and covariances	12
1.2.1.3. Method of expectation	14
1.2.1.4. Hypothesis testing	16
1.2.2. Components of Variance	22
1.2.2.1. Spatial and temporal variation	22
1.2.2.2. Sampling variation	23
1.3. Release-Recapture Protocols and Data	25
1.3.1. Introduction	25
1.3.2. Capture Histories and Data Arrays	28
1.3.2.1. CH matrix	28
1.3.2.2. Full $m$ -array	32
1.3.2.3. Reduced $m$ -array	33
1.3.3. Four Major Protocols	36
1.3.3.1. First capture history protocol	37
1.3.3.2. Unknown capture history protocol	38
1.3.3.3. Complete capture history protocol	39
1.3.3.4. Partial capture history protocol	39
1.4. Release-Recapture Modeling Concepts, Notation, and Assumptions	42
1.4.1. Introduction to Release-Recapture Concepts	43
1.4.2. Release-Recapture Notation	45
1.4.2.1. Notation for data	45
1.4.2.2. Notation for parameters	48
1.4.3. Release-Recapture Models	49
1.4.3.1. Modeling approach	49

## CONTENTS

1.4.3.2. Model structures	50
1.4.4. Assumptions	51
1.4.5. Data Analysis Philosophy	54
1.5 Treatment-Control Mortality Concepts	56
1.5.1. Introduction	56
1.5.2. Direct versus Indirect Mortality Effects	57
1.5.3. Total Treatment Mortality	58
1.5.4. Problems with Defining a Treatment Effect on Survival	62
<b>Part 2. Protocols for Studies with a Control and One Treatment</b>	<b>64</b>
2.1. Models, Hypotheses, and Tests: an Overview	64
2.1.1. Overview of Hypothesis Tests	64
2.1.2. Sequence of Treatment Effects Corresponding to TEST 1	66
2.1.3. Goodness of Fit Testing Within a Treatment Group	71
2.1.3.1. TEST 1	71
2.1.3.2. TEST 2	71
2.1.3.3. TEST 3	74
2.1.4. Discussion	77
2.2. First Capture Histories	78
2.2.1. Introduction	78
2.2.2. Model Structure and Expectations	78
2.2.3. Likelihood Function	80
2.2.4. Estimable Parameters	83
2.2.5. Minimal Sufficient Statistics	83
2.2.6. Analysis	84
2.2.7. Tests of Assumptions	86
2.2.8. Extended Sequence of Models $H'_{2\phi}, H'_{3\phi}, \dots, H'_{k-1,\phi}$	93
2.2.9. Relative Recovery Rate Method	97
2.2.10. Discussion	97
2.3. Unknown Capture Histories	100
2.3.1. Introduction	100
2.3.2. Model Structure	101
2.3.3. Estimable Parameters	106
2.3.4. Discussion	108
2.3.5. Theory for the Unknown Capture History Protocol	108
2.4. Complete Capture Histories	112
2.4.1. Introduction	112
2.4.2. Model $H_{k-1,\phi}$	112
2.4.3. Model Sequence	116
2.4.4. Model $H_0$	116
2.4.5. Model $H_{1\phi}$	117
2.4.6. Model $H_{2\phi}$	120
2.4.7. Comments on Models $H_{2\phi}$ to $H_{k-1,\phi}$	125

## CONTENTS

2.4.8. On Alternative Forms of the Estimators	126
2.4.9. Tests of Assumptions	127
2.4.9.1. TEST 1.R1	128
2.4.9.2. TEST 1.T2	128
2.4.9.3. TEST 1.R2	128
2.4.10. Comprehensive Example	129
2.4.11. Likelihood Function for Models $H_{k-1,\phi}$ , $H_{2p}$ , $H_{1\phi}$	143
2.5. Partial Capture Histories	146
2.5.1. Introduction	146
2.5.2. Scheme A	147
2.5.2.1. Introduction and presentation of data	147
2.5.2.2. Models $H_0$ , $H_{1\phi}$ , $H_{2p}$ , $H_{2\phi}$ , ..., $H_{k-1,\phi}$	148
2.5.2.3. Testing between models	148
2.5.2.4. Goodness of fit tests	148
2.5.2.5. Comparing survival for treatment and control groups	148
2.5.2.6. Example	149
2.5.3. Scheme B	155
2.5.3.1. Introduction and presentation of data	155
2.5.3.2. Models	156
2.5.3.3. Testing between models	158
2.5.3.4. Goodness of fit tests	160
2.5.3.5. Comparing survival among treatment and control groups	161
2.5.3.6. Example	161
2.5.3.7. Statistical theory	168
2.6. Summary of Models and Protocols	172
<b>Part 3. Theory for Studies with Two or More Treatments</b>	<b>174</b>
3.1. Theory for the Complete Capture History Protocol	174
3.1.1. Probability Distribution for One Data Set	174
3.1.2. Theory Under the Sequence of Models	178
3.1.3. Parameter Estimators, Variances, and Covariances	185
3.1.3.1. Pooling rule	185
3.1.3.2. Parameter estimators and their variances	188
3.1.3.3. Covariances under model $H_{j\phi}$	189
3.1.3.4. Covariances under models $H_{j\phi}$ and $H_0$	190
3.1.4. Goodness of Fit Tests	192
3.1.4.1. TEST 3	192
3.1.4.2. TEST 2	194
3.1.4.3. Comment on uniqueness	195
3.1.4.4. Comment on optimality	195
3.1.5. Tests Between Models (TEST 1)	196
3.2. Modifications for Other Protocols	198
3.2.1. Scheme A, Partial Capture Histories	198
3.2.2. Scheme B, Partial Capture Histories	198

## CONTENTS

3.2.3. First Capture Histories	200
3.2.4. Some Extensions	201
3.2.4.1. Relationship to temporal banding studies	201
3.2.4.2. Deeper insights	202
3.3. Variances and Covariances of $\hat{S}$	204
3.3.1. Some Variance Formulae	204
3.3.2. Covariances	206
3.4. Adjustments for Statistical Bias	207
3.4.1. Survival Rate Estimators, $\hat{\phi}$	208
3.4.2. Capture Probability Estimators, $\hat{p}$	209
3.4.3. Treatment Effect Estimators, $\hat{S}$	210
3.5. Transformations of $\hat{S}$ , $\hat{\phi}$ , and $\hat{p}$	211
3.5.1. Log-Transform for $\hat{\phi}$ and $\hat{S}$	211
3.5.2. Log-Odds Transform for $\hat{p}$	214
3.6. Computing Theoretical Biases, Standard Errors, and Test Powers	214
3.7. Testing Losses on Capture for a Treatment Effect	217
3.8. Handling Effects	218
3.9. Bias Reduction by Peeling for First Capture History and Unknown Capture History Protocols	221
3.9.1. Model Bias and Peeling for the First Capture History Protocol	222
3.9.2. Model Bias and Peeling for the Unknown Capture History Protocol	225
3.10. Synthetic Example of Multiple Treatments	226
<b>Part 4. Importance of Replication</b>	<b>240</b>
4.1. Introduction	240
4.1.1. Need for Replication and Multiple Lots	240
4.1.2. Replication and Multiple Lots	241
4.1.2.1. Replication	241
4.1.2.2. Sublots	242
4.1.2.3. Multiple lots	242
4.1.3. Empirical Variance Estimation without Replication	243
4.1.3.1. Quasi-likelihood theory	243
4.1.3.2. Variance-inflation factor method	245
4.1.4. Example with Multiple Lots	246
4.1.4.1. Description of the study	246
4.1.4.2. Example data	246
4.1.4.3. Model selection	249
4.1.4.4. Point estimation	249
4.1.4.5. Variance estimation	251
4.2. Empirical Variance Estimation	252
4.2.1. Estimation of the Variance-Inflation Factor	252
4.2.2. Replication Only	254
4.2.3. Random Multiple Lots Only	257
4.2.4. Treatment Effect as a Relative Risk	259

## CONTENTS

4.3. Estimation of Variance Components	260
4.3.1. Some Theory	260
4.3.2. Simple Example	266
4.3.3. More Complex Example	269
4.4. Example with Four Groups and 10 Lots	276
<b>Part 5. Properties of Procedures</b>	279
5.1. Introduction	279
5.2. Estimator Bias	281
5.3. Measures of Precision	285
5.4. Estimator Robustness	285
5.5. Heterogeneity	286
5.6. Estimator Efficiency	287
5.7. Power of Tests	289
5.8. Confidence Interval Coverage	292
5.9. Analytical-Numerical Approximations	292
<b>Part 6. Planning Experiments</b>	296
6.1. Introduction	296
6.1.1. Desirability of a Pilot Experiment	296
6.1.2. Review of Assumptions	297
6.2. Selection of an Experimental Protocol	300
6.2.1. Complete Capture History Protocol	300
6.2.2. Partial Capture History Protocol	301
6.2.3. Unknown Capture History Protocol	301
6.2.4. First Capture History Protocol	301
6.3. Effort and Sample Size Considerations	302
6.3.1. Introduction	302
6.3.2. Relative Numbers of Releases	303
6.3.2.1. Two groups	303
6.3.2.2. The case of more than two groups	307
6.3.2.3. Comments	313
6.3.3. Relative Recapture Effort	313
6.3.4. Relative Allocation of Effort to Releases and Recaptures	315
6.3.5. Numbers of Releases	317
6.3.6. Numerical Evaluation of Some Design Features: an Example	319
6.4. Multiple Lots	324
6.4.1. Introduction	324
6.4.2. Replication	324
6.4.3. Use of More Complex Designs	326
6.5. Coping with External Variables	327
6.5.1. Introduction	327
6.5.2. Stratification	327
6.5.3. Blocking	328

## CONTENTS

6.5.4. Randomization and Balance	328
6.5.5. Timing of Recapture Effort	328
6.5.6. Use of Sublots	329
6.5.7. Partitioning Recaptures by Site	329
6.5.8. Attention to Detail and Quality Control	329
6.6. Refining the Design by Simulation	329
<b>Part 7. Application of Theory</b>	<b>331</b>
7.1. Introduction	331
7.2. Lead-Dosing Experiments on Mallards	332
7.3. Lead-Dosing Study of Northern Pintails	335
7.4. Pesticide Dosing of Starlings	343
7.5. Partitioning Lazuli Bunting Data	348
7.6. Changes in Group Membership - Desert Tortoise Data	361
<b>Part 8. Extensions and Other Comments on Methodology</b>	<b>372</b>
8.1. Introduction	372
8.2. Studies with More Than Two Groups	372
8.2.1. Ordered Treatments	373
8.2.1.1. Direct modeling of treatment effect	373
8.2.1.2. Indirect modeling of treatment effect	375
8.2.2. Two Factors Each at Two or More Levels	377
8.3. Testing for Treatment Effects in a General Capture-Recapture Setting	378
8.3.1. Robust Designs that Allow for Heterogeneity and Trap Response	381
8.3.2. Testing for Age-Specific Treatment Effects	382
8.4. Other Procedures	382
8.4.1. Regression Methods	382
8.4.2. Release of Dead Fish	383
<b>Part 9. Comprehensive Computer Software</b>	<b>387</b>
9.1. Program Capabilities and Options	387
9.1.1. Input of Information	395
9.1.2. Program Output	399
9.1.3. Monte Carlo Simulator	399
9.2. Examples	406
9.3. Interface with Program SURVIV	408
9.4. Executing RELEASE	409
9.5. Programming Details	410
9.5.1. Source Code	410
<b>Summary</b>	<b>412</b>
<b>References</b>	<b>414</b>

## CONTENTS

<b>Unpublished Reports</b>	421
<b>Acknowledgments</b>	423
<b>Glossary</b>	424
<b>Index</b>	432

## Preface

This monograph presents design and analysis methods for a large class of survival experiments based on release-recapture of marked populations. We developed the underlying theory primarily to address fishery issues involving spillways, hydroelectric turbines, bypass systems, and related structures on the Columbia River in the northwestern United States. Many other applications exist, however. Treatment might include dosing of lead or various pesticides to determine the chronic effect of a contaminant on survival. The general theory is for the analysis of multiple interrelated release-recapture data sets; the methods presented herein apply to any experiments involving treatment and control groups of marked animals.

During the past 20 to 25 years, much literature has appeared on the estimation of population parameters based on capture-recapture sampling. One branch of the literature includes bird-banding and fish-tagging studies where the data are from a single, terminal, harvest-related recovery, as synthesized by Brownie et al. (1985). During the same time period, other literature appeared on studies dealing with multiple recaptures of marked animals, often referred to as capture-recapture sampling for open populations, or "Jolly-Seber models" after two of the leading contributors. Seber (1982) reviewed this literature. The links between these two major developments were outlined by Brownie et al. (1985) and Brownie and Pollock (1985).

A general theory for ecological experiments and studies in which marked animals are used relies on both of the above bodies of literature plus other developments (e.g., White et al. 1982). Overall, this subject and the literature on which it is based are fairly complex and diverse. Until recently, the separate approaches and models were developed in isolation, usually using different literature, notation, and context. In the past 10 years a coalescing of this work has led to the recognition that most "capture-recapture" models are special cases of a more general theory. Today, the entire area of capture-recapture is being unified under one umbrella of theory, which provides the context for the developments we present here.

As an example of progress in the theory and computation for capture-recapture sampling, one might consider the analysis done by Hammersley (1953), who presented a method for estimating the death rate in open-population models and applied it to data on the alpine swift *Apus melba* banded in Switzerland during 1920-1950. His estimation method involved a 28 x 28 matrix and a complex iterative process. Minor iterative cycles were embedded in major cycles and were done on a desk calculator. Approximately six major cycles were required for the swift data, and each required about 10 days of hand computation. The inversion of the matrix required about 4 hours of SEAC computer time (at the U.S. National Bureau of Standards). Hammersley estimated that this inversion could have been done in "about 2 months" on a desk calculator. In summary, Hammersley's method required about

100 person-days of computation on desk calculators of the day for this large data set.

Biologists now enjoy the sophisticated formalism of the Jolly-Seber model and the many extensions and restrictions that have been published in the past 21 years. The Jolly-Seber method itself also benefited from the work of Hammersley (see Cormack 1968). Many Jolly-Seber models have parameter estimators in closed form, and estimates can be computed in a few minutes on a calculator if the data are summarized in a suitable form. Monte Carlo studies have investigated the small-sample properties of the Jolly-Seber class of models, and much is now known about the analysis theory of capture-recapture sampling data. The improved models and theory are accompanied by tremendous advances in computer technology. Commonly available desktop computers now can fully analyze the alpine swift data in about 20 seconds of computer time.

Program RELEASE, which can be run on IBM-compatible microcomputers, was developed to allow biologists to focus on design, data collection, analysis, and inference, rather than on computational details. This software is powerful and easy to use, but it can be misused if the material in this monograph is not understood. To avoid potential misuse, we encourage understanding and careful consideration of the material in this monograph (the Reader's Guide in Section 1.1.5 should prove useful). We hope readers will examine the theory and examples to gain familiarity with the basis of the methods presented. Practice running program RELEASE with example data sets would be helpful in understanding some of the issues covered. Readers are encouraged to compare theory and application and gain familiarity with the Monte Carlo features of the software.

Additional research and applications should be stimulated by this monograph. Biologists and statisticians need to work together more closely to ensure that additional well-designed, empirical studies result. We hope to see the various research findings published in refereed, primary journals. The lack of publication in primary journals has been a problem in the past (e.g., Fletcher 1985), as much of the fisheries research on the Columbia River has appeared in the gray literature.

The material in this monograph can be understood by persons with two or three upper division courses in statistics and some elementary computer skills. The less background one has in these subjects, the more one may have to struggle. The main prerequisites are an interest in the topic, an interest in science and experimentation, and a curiosity about sound and thorough inference procedures.

We express our sincere thanks to the Chelan County Public Utility District, Wenatchee, Washington, for funding the research that led to the publication of this monograph. The District was both unselfish and extremely farsighted in allocating funds to develop rigorous design and analysis methods for this class of experiments.