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Rebecca A. Buchanan

Release-Recapture Models for Migrating Juvenile and Adult Salmon
in the Columbia and Snake Rivers using PIT-Tag and Radiotelemetry
Data

Rebecca A. Buchanan

A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

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Abstract

Release-Recapture Models for Migrating Juvenile and Adult Salmon in the
Columbia and Snake Rivers using PIT-Tag and Radiotelemetry Data

Rebecca A. Buchanan

Chair of the Supervisory Committee:
Professor John R. Skalski
School of Aquatic and Fisheries Sciences

Release-recapture models for two types of tagging data from migrating salmonids in the Columbia and Snake rivers are presented. The first model uses both juvenile and adult PIT-tag data to analyze the seaward and spawning migrations through the hydrosystem. This branching model accommodates transported smolts, known removals, and multiple adult age classes. Juvenile inriver survival, adult return rates, adult inriver survival, and transportation effects can be estimated from this model, as well as smolt-to-adult return rates (SARs) and the adult age composition. An example of summer Chinook salmon (*Oncorhynchus tshawytscha*) released in the Snake River upstream of Lower Granite Dam in 1999 is analyzed. The relative system-wide transportation effect measure was $\hat{R}_{sys} = 1.232$ ($\widehat{SE} = 0.036$), while the SAR to Lower Granite Dam was estimated to be $\widehat{SAR} = 0.0193$ ($\widehat{SE} = 0.001$). Overall upriver adult survival for the release group was estimated at $\hat{S}_A = 0.8175$ ($\widehat{SE} = 0.022$).

The second model analyzes radiotelemetry data from adult salmon to estimate perceived system survival and unaccountable loss during the upriver adult migration. Detections are available at the base and top of dams, and in tributary mouths. A sequence of models is presented, ranging from simple to complex, incorporating memory effects of tributary visits and fallback events. Models are compared using a data set of spring/summer Chinook salmon radio-tagged as adults at Bonneville Dam in 1996. Because these adults came from multiple spawning sites, the estimate of perceived survival from Bonneville to Lower Granite

Dam was low, at $\hat{S}_{sys} = 0.10$ ($\widehat{SE} = 0.01$). Unaccountable loss, $\hat{\mu}_R = 0.28$ ($\widehat{SE} = 0.02$), was considered the more appropriate performance measure for the adult migration in the case of non-known source fish.

A secondary purpose of this dissertation was to compare the analysis of adult data from radiotelemetry and PIT tags. The models in Chapter 3 indicate that for estimating large-scale quantities such as system survival and unaccountable loss, PIT tags may offer comparable information to radio tags. If the projected PIT-tag detection systems in tributary mouths become available and reliable, PIT tags may reasonably replace the more expensive radio tags in estimating large-scale quantities reflecting the adult migration.

TABLE OF CONTENTS

List of Figures	vii
List of Tables	viii
Chapter 1: Introduction	1
1.1 Release-Recapture Studies	1
1.2 Motivation of the Problem	5
1.3 Scope of Work	13
1.3.1 PIT-Tag Life-Cycle Model	13
1.3.2 Adult Radio-Tag Model	15
Chapter 2: Juvenile-Adult PIT-Tag Model	19
2.1 Introduction	19
2.1.1 Model Overview	19
2.1.2 Model Assumptions	21
2.2 Underlying Model	23
2.3 Estimable Model	27
2.3.1 Parameterization	27
2.3.2 Capture Histories and Likelihood	35
2.3.3 Generalization	46
2.4 Quantities of Interest	52
2.4.1 Transportation Effects	55
2.4.1.1 Isolated Site- and Age-specific TBR for Tagged and Un-	
tagged Fish (R_{ij})	56
2.4.1.2 Isolated Site-specific TBR for Tagged and Untagged Fish (R_i)	57
2.4.1.3 Contextual Site-specific TBR for Tagged Fish (RC_i)	59
2.4.1.4 Contextual Site-specific TBR for Untagged Fish (RC_i^U) . . .	62
2.4.1.5 System-wide TBR for Tagged Fish (R_{sys})	63
2.4.1.6 System-wide TBR for Untagged Fish (R_{sys}^U)	65
2.4.1.7 Conditional System-wide TBR for Tagged Fish (R_{cond}) . . .	66

2.4.1.8	Scenarios	67
2.4.1.8.1	Scenario A	68
2.4.1.8.2	Scenario B	69
2.4.1.9	Which TBR to Use	70
2.4.2	Adult Return Rates	72
2.4.2.1	Ocean Return Rate for Non-transported Fish (O_{NT})	72
2.4.2.2	Site-specific Ocean Return Rate for Transported Fish (O_{T_i})	73
2.4.2.3	Site-specific Smolt-to-Adult Return Rate for Tagged Fish ($SAR_{(K)}$)	74
2.4.2.4	Site-specific Smolt-to-Adult Return Rate for Untagged Fish ($SAR_{(K)}^U$)	76
2.4.3	Return Age Distributions	77
2.4.3.1	Return Age Distribution for Tagged Fish (A_j)	77
2.4.3.2	Return Age Distribution for Untagged Fish (A_j^U)	79
2.4.3.3	Conditional Adult Return Rate for Tagged Fish (μ_j)	79
2.4.3.4	Conditional Adult Return Rate for Untagged Fish (μ_j^U)	82
2.4.4	Inriver Adult Survival	82
2.4.4.1	Inriver Adult Survival for Tagged Fish (S_A)	82
2.4.4.2	Inriver Adult Survival for Untagged Fish (S_A^U)	84
2.5	Conceptual Issues	84
2.5.1	Fixing Parameters	84
2.5.2	Identifying Detection Sites	86
2.5.3	Collapsing age classes	87
2.6	Comparison with Current Practices	90
2.6.1	Juvenile Survival	90
2.6.2	Adult Return Rates	91
2.6.3	Transportation Effect	92
2.6.4	Adult Survival	97
2.7	1999 Summer Chinook Salmon Example	98
2.8	Summary	106
Chapter 3:	Adult Radio-Tag Model	108
3.1	Introduction	108
3.2	Data	113
3.2.1	Example Data Set: 1996 Chinook Salmon	113
3.2.2	Data Collection and Processing	116

3.3	Statistical Methods	127
3.3.1	Overview	127
3.3.2	Performance Measures	131
3.3.3	Model Assumptions	133
3.4	Model 0: Single Dam Detections	138
3.4.1	Data Description	138
3.4.2	Notation	139
3.4.3	Likelihood	141
3.4.4	Performance Measures	142
3.4.5	1996 Chinook Data Set	143
3.4.6	Results	145
3.5	Model 1: No Tributary Detections	145
3.5.1	Data Description	146
3.5.2	Notation	146
3.5.3	Likelihood	149
3.5.4	Performance Measures	150
3.5.5	1996 Chinook Data Set	151
3.5.6	Results	152
3.6	Model 2: Terminal Tributary Model	153
3.6.1	Data Description	154
3.6.2	Notation	154
3.6.3	Likelihood	157
3.6.4	Performance Measures	159
3.6.5	1996 Chinook Data Set	160
3.6.6	Results	162
3.7	Model 3: Tributary Model	164
3.7.1	Data Description	166
3.7.2	Model 3a: Memory-Free Tributary Model	166
3.7.2.1	Notation	166
3.7.2.2	Likelihood	168
3.7.2.3	Performance Measures	170
3.7.2.4	1996 Chinook Data Set	172
3.7.2.5	Results	174
3.7.3	Model 3b: Memory Tributary Model	176
3.7.3.1	Notation	176

3.7.3.2	Likelihood	179
3.7.3.3	Performance Measures	182
3.7.3.4	1996 Chinook Data Set	183
3.7.3.5	Results	185
3.8	Model 4: Fallback Model with Terminal Tributary Detections	187
3.8.1	Data Description	188
3.8.2	Notation	189
3.8.3	Likelihood	198
3.8.4	Performance Measures	201
3.8.5	1996 Chinook Data Set	203
3.8.6	Results	208
3.9	Model 5: Fallback and Tributary Model	211
3.9.1	Data Description	212
3.9.2	Model 5a: Fallback and Memory-Free Tributary Model	213
3.9.2.1	Notation	213
3.9.2.2	Likelihood	216
3.9.2.3	Performance Measures	220
3.9.2.4	1996 Chinook Data Set	222
3.9.2.5	Results	227
3.9.3	Model 5b: Short-term Fallback and Tributary Memory Model	231
3.9.3.1	Notation	233
3.9.3.2	Likelihood	242
3.9.3.3	Performance Measures	253
3.9.3.4	1996 Chinook Data Set	256
3.9.3.5	Results	265
3.9.4	Model 5c: Long-term Fallback Memory and Short-term Tributary Memory Model	269
3.9.4.1	Notation	270
3.9.4.2	Likelihood	276
3.10	Model 6: Fallback and Memory Tributary Model with Trap Data	276
3.10.1	Data and Assumptions	277
3.10.2	Notation	279
3.10.3	Likelihood	280
3.10.4	Performance Measures	282
3.10.5	1996 Chinook Data Set	282

3.10.6 Results	285
3.11 Discussion	287
3.11.1 Summary of Models	289
3.11.2 Model Results	295
3.11.3 Model Limitations	297
3.11.4 Data Issues	299
3.11.5 Conclusion	300
Chapter 4: Conclusion	302
4.1 Summary of Work and Ramifications	302
4.1.1 Juvenile-Adult PIT-tag model	302
4.1.2 Adult Radio-tag model	304
4.2 Benefits of Modeling Approach	306
4.3 Contribution to the Release-Recapture Field	308
References	310
Appendix A: Radiotelemetry Data for Sample Adult Chinook salmon	319
Appendix B: Variance formulas for \hat{S}_{sys} and $\hat{\mu}_R$	332
B.1 Variance formulas for \hat{S}_{sys}	332
B.1.1 Model 0	332
B.1.2 Models 1 and 2	332
B.1.3 Model 3a	333
B.1.4 Model 3b	336
B.1.5 Model 4	340
B.1.6 Model 5a	344
B.1.7 Models 5b and 6	351
B.2 Variance formulas for $\hat{\mu}_R$	366
B.2.1 Model 0	366
B.2.2 Model 1	366
B.2.3 Model 2	366
B.2.4 Model 3a	368
B.2.5 Model 3b	371
B.2.6 Model 4	376
B.2.7 Model 5a	380

B.2.8 Models 5b and 6	388
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LIST OF FIGURES

Figure Number	Page
1.1 Map of Columbia River Basin	7
2.1 Schematic 1 of underlying model, development example	28
2.2 Schematic 2 of underlying model, development example	29
2.3 m -array for development example	42
2.4 Contribution of capture history 3011 to m -array	43
2.5 m -array for development example with 2 adult age classes	44
2.6 Relationship between m -array and g statistics	47
2.7 TBR Scenarios	68
2.8 1999 summer Chinook salmon data set schematic	100
3.1 Simple adult migration paths	111
3.2 Complex adult migration paths	112
3.3 Simplification of complex adult migration path	120
3.4 Fallback followed by exit to tributary	121
3.5 Pre-fallback versus post-fallback migration paths	123
3.6 Data Simplification Example Number 1	124
3.7 Data Simplification Example Number 2	125
3.8 Data Simplification Example Number 3	126
3.9 Order of tributary removal and fallback data reduction	128
3.10 Fallback events parameterized with f_i	130
3.11 Migration paths with fallback between base and top of dam detections.	190
3.12 $R\ FB\ D_{2T}$ schematic	195
3.13 Migration paths for Model 5b	236
3.14 Dam and tributary labels	244

LIST OF TABLES

Table Number	Page
2.1 Parameters in underlying model, development example	26
2.2 Estimable Parameters, development example	33
2.3 Codes used in capture histories	35
2.4 Capture histories and probabilities, development example	36
2.5 Summary statistics, development example	39
2.6 Minimal sufficient statistics, development example	45
2.7 Estimable parameters, generalized model	48
2.8 Summary statistics, generalized model	50
2.9 Minimal sufficient statistics, generalized model	51
2.10 Maximum likelihood estimators, generalized model	52
2.11 m -array for 1999 summer Chinook salmon data set	102
2.12 Parameter estimates for 1999 summer Chinook salmon data set	103
2.13 TBR values for 1999 summer Chinook salmon data set	105
2.14 Performance measures for 1999 summer Chinook salmon data set	106
3.1 Locations of Tributary Detections	114
3.2 Detection summaries from full 1996 radio-tag data	115
3.3 Parameters in Model 0	140
3.4 Summary statistics for Model 0	142
3.5 Minimal sufficient statistics for Model 0	142
3.6 Observed summary statistics for Model 0	144
3.7 Maximum likelihood estimates from Model 0	145
3.8 Parameters in Model 1	148
3.9 Summary statistics for Model 1	149
3.10 Minimal sufficient statistics for Model 1	149
3.11 Observed summary statistics for Model 1	151
3.12 Maximum likelihood estimates from Model 1	153
3.13 Parameters in Model 2	157
3.14 Summary statistics for Model 2	158

3.15	Minimal sufficient statistics for Model 2	158
3.16	Observed summary statistics for Model 2	160
3.17	Maximum likelihood estimates from Model 2	164
3.18	Parameters in Model 3a	168
3.19	Summary statistics for Model 3a	169
3.20	Minimal sufficient statistics for Model 3a	169
3.21	Maximum likelihood estimators for Model 3a	170
3.22	Observed summary statistics for Model 3a	172
3.23	Maximum likelihood estimates from Model 3a	175
3.24	Parameters in Model 3b	178
3.25	Summary statistics for Model 3b	180
3.26	Minimal sufficient statistics for Model 3b	180
3.27	Observed summary statistics for Model 3b	183
3.28	Maximum likelihood estimates from Model 3b	186
3.29	Parameters in Model 4	196
3.30	Summary statistics for Model 4	199
3.31	Minimal sufficient statistics for Model 4	200
3.32	Observed summary statistics for Model 4, $K = 7$	206
3.33	Observed summary statistics for Model 4, $K = 4$	207
3.34	Maximum likelihood estimates from Model 4, $K = 7$	208
3.35	Maximum likelihood estimates from Model 4, $K = 4$ dams	210
3.36	Parameters in Model 5a	215
3.37	Summary statistics for Model 5a	218
3.38	Minimal sufficient statistics for Model 5a	218
3.39	Observed summary statistics for Model 5a, $K = 7$	223
3.40	Observed summary statistics for Model 5a, $K = 4$	226
3.41	Maximum likelihood estimates from Model 5a, $K = 7$	228
3.42	Maximum likelihood estimates from Model 5a, $K = 4$ dams	230
3.43	Parameters in Model 5b	239
3.44	Summary statistics for Model 5b	247
3.45	Minimal sufficient statistics for Model 5b	250
3.46	Observed summary statistics for Model 5b, $K = 7$	262
3.47	Observed summary statistics for Model 5b, $K = 4$	264
3.48	Maximum likelihood estimates from Model 5b, $K = 7$	265
3.49	Maximum likelihood estimates from Model 5b, $K = 4$ dams	268

3.50 Parameters in Model 5c	274
3.51 Observed summary statistics for Model 6, $K = 7$	283
3.52 Maximum likelihood estimates from Model 6, $K = 7$	285
3.53 Model comparisons	289
A.1 Radiotelemetry data for sample Chinook salmon	319

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DEDICATION

This work is dedicated to my grandparents, Edward and Annabel Buchanan, and Jack and Winnie Forbes.

Chapter 1

INTRODUCTION

1.1 Release-Recapture Studies

Recapture studies of marked animals have been used many times to estimate demographic parameters of animal populations in the past century; for examples, see Jackson (1939), Darroch (1958), Darroch (1959), Cormack (1964), Jolly (1965), Seber (1965), Burnham et al. (1987), Pollock et al. (1990), and Lebreton, Burnham, Clobert and Anderson (1992). A basic study design is release-recapture, also called capture-recapture. Release-recapture studies use live recaptures of individually marked animals, which are usually re-released upon capture. There are at least 2 sampling periods and often more; sampling periods are very short relative to the study duration, and may be considered discrete in time. Unmarked individuals may be captured, marked, and released at sampling periods after the initial release.

The classic statistical models used to analyze recapture data are the “Cormack-Jolly-Seber” (CJS) or “Jolly-Seber” (JS) models, developed by Cormack (1964), Jolly (1965), and Seber (1965). The CJS and JS models were developed for open populations, with the CJS model incorporating emigration (or death), and the JS model incorporating either immigration (or birth), emigration (or death), or both. Survival and capture or detection probabilities may be time-dependent, but are assumed equal among individuals at any given sampling time. With these and other assumptions, the models’ likelihoods are multinomial, and may be expressed as the product of conditional likelihoods representing data on captures of marked and unmarked animals, releases of newly marked and previously marked animals, and losses on capture. Estimators are typically derived via maximum likelihood, and variances and covariances via the information matrix and Taylor series (i.e., the delta

method). The JS model allows for newly marked individuals to be released after the initial release, and thus reflects the initial capture and marking process and provides estimates of abundance as well as survival. The CJS model, on the other hand, uses data only from marked animals, and so provides estimates of survival but not abundance.

Since its appearance in the 1960s, researchers have modified the Jolly-Seber model to suit their own studies. For example, Robson (1969), Pollock (1975), Otis et al. (1978), Burnham et al. (1987), Pradel, Clobert and Lebreton (1990), Lebreton et al. (1992), Lebreton and Pradel (2002), and Pledger and Schwarz (2002) extend JS models to allow for capture and survival probabilities that vary with cohort or capture history. Pollock (1981), Brownie and Robson (1983), Stokes (1984), Clobert et al. (1994), Schwarz and Arnason (2000) allow for age-dependent or breeder-dependent survival and capture probabilities. Otis et al. (1978) developed a unified approach for closed populations, including goodness-of-fit tests and tests among competing models; Burnham et al. (1987) and Pollock et al. (1990) developed an analogous approach for open populations, allowing for comparison between different treatment groups with goodness-of-fit tests and hypothesis tests. Numerous authors have modified the Jolly-Seber model to analyze tag-recovery data from exploited populations, in which tags (and animals) are recaptured only upon harvest of the animal and return of the tag from the hunter or fisherman; for examples, see Arnason (1972), Arnason (1973), Seber (1982), Brownie et al. (1985), Schwarz (1993), Schwarz, Schweigert and Arnason (1993), and Pledger and Schwarz (2002). Several authors have designed models to combine tag-recovery data with capture-recapture/resighting data; see Mardekian and McDonald (1981), Brownie and Pollock (1985), Burnham (1993), and Joe and Pollock (2002) for examples. The assumption of homogeneous capture probabilities is important in estimation of population size and recruitment, although less for estimation of survival rates (Carothers, 1973; Cormack, 1989; Lebreton et al., 1992; Kendall, Pollock and Brownie, 1995). The assumption of homogeneous capture probabilities is often not met in natural populations, however. A “robust design” using *ad hoc* estimators based in part on the Jolly-Seber design and model was developed by Pollock (1982) in an effort to offset the effects of heterogeneous capture probabilities. Kendall et al. (1995) proposed a likelihood-based approach to estimating parameters under the “robust design;” Kendall and Nichols (1995),

Kendall, Nichols and Hines (1997), and Schwarz and Stobo (1997) extended this approach to estimate temporary migration.

While the original goal of recapture studies and the Jolly-Seber model was estimation of population size, focus has since shifted to estimation of survival, and to some extent migration rates and recruitment rates to the breeding population. Model selection is also a key issue (Burnham et al., 1987; Lebreton et al., 1992). Several authors have developed models for migratory populations, focusing on either survival rates, migration rates, or both. For example, Pradel et al. (1997) address estimating survival of a resident population in the presence of transients, developing both a capture-recapture model and an *ad hoc* method of dealing with transients. Schwarz et al. (1993) estimate overall survival of a migratory population using tag-recovery data. Most authors, however, address estimating movement rates. Movement may be in and out of a single study population, as in Jackson (1939), Cameron and Williamson (1977), Zeng and Brown (1987), Nichols and Pollock (1990), and Pollock et al. (1990). Alternatively, movement may be among geographic strata or regions within a study population. If sampling and releases are always done in the same strata, then migration rates among the strata can be estimated, based on several assumptions. A key assumption is that survival is constant across strata (for examples, see Darroch, 1961; Manly and Chatterjee, 1993; Schwarz et al., 1993). Some authors have gone farther, and assumed survival to be constant across time as well (Chapman and Junge, 1956; Manly and Chatterjee, 1993). Without this assumption, only "transition" rates can be estimated, combining survival with migration. In addition to constant survival probabilities, some authors assume constant or known tag-recovery or capture probabilities (e.g., Manly and Chatterjee, 1993; Schwarz et al., 1993; Anganuzzi, Hilborn and Skalski, 1994).

Estimating movement rates with tag-recovery requires some degree of fidelity of the animals to sampling or recovery sites. Also, after an animal has migrated once during a sampling period, it is assumed not to migrate again. Schwarz, Burnham and Arnason (1988), Hilborn (1990), and Schwarz et al. (1993) all assume some degree of fidelity to sampling or recovery sites. In addition, all models using both tag-recovery and capture-recapture data assume no temporary migration out of the study area. However, Schwarz and Stobo (1997) extended the "robust design" developed by Pollock (1982), Kendall et al.

(1995), Kendall and Nichols (1995), and Kendall et al. (1997) to estimate population size, return rate to the breeding ground, survival, and recruitment in a population that returns to the breeding ground year after year but with temporary emigrants out of the study area. The resulting estimates of abundance include these temporary emigrants, and estimates of recruitment, survival, and movement rates apply to the entire population, including the temporary emigrants.

Another common assumption is that transition rates (survival and migration) depend only on the animal's current location (stratum), and are independent of past migrations. This is the assumption of Markovian transitions, and is used in the models of Arnason (1973), Schwarz et al. (1993), and Schwarz and Stobo (1997). Schwarz et al. (1993) make this assumption in their tag-recovery model, assuming that migration and survival rates are independent of the path taken between two strata; this introduces problems with estimation and identifiability of transition parameters due to convolution of the parameters and low tag-recovery rates. Hestbeck, Nichols and Malecki (1991) tested the Markovian assumption for migrating Canada geese using goodness-of-fit tests in a capture-recapture model, finding that transition probabilities depending on both the current and previous year's locations fit data better than true Markovian transition probabilities. Brownie et al. (1993) gave an alternative approach to that of Hestbeck et al. (1991), also allowing for movement that is either a first-order Markov process or dependent on locations in the previous sampling period.

Several authors have developed methods of incorporating age structure into analyses of capture-recapture data, primarily to estimate age-specific breeding probabilities or recruitment to the breeding population. Early work by Barrat, Barré and Mougin (1976) and Lebreton (1978) used recapture data and external estimates of survival to define ratio estimates of age-specific breeding probabilities. Lebreton et al. (1990) introduced a statistical model ("transversal" model) to estimate age-specific breeding probabilities from cohort-level recapture or resighting data collected through time, but without information on individual fates. For individual-level recapture data, Clobert et al. (1994) proposed a "longitudinal" model in the CJS framework that follows individuals through time. Developed originally for a single-state system, Lebreton and Pradel (2002) generalized it to a multistate model.

Clobert et al. (1994) connect capture probabilities to age-specific breeding probabilities in a population in which non-breeders have zero probability of capture. Schwarz and Arnason (2000) address the same problem, using a “super-population” model from Schwarz and Arnason (1996) and treating first-time breeders as births to the breeding population. Pradel (1996) and Pradel et al. (1997) develop a reverse capture history method that considers first-time breeders as (reverse) “deaths” from the breeding population and past breeders as “survivors.” The reverse capture history method is conditional on those animals that survive to the age at which all animals breed, whereas the methods of Clobert et al. (1994) and Schwarz and Arnason (2000) include survival parameters for all ages. Two key assumptions of Clobert et al. (1994) and Schwarz and Arnason (2000) are (1) survival rates of breeders and non-breeders are equal after the youngest breeding age, and (2) survival and capture rates among breeders are equal, regardless of age.

1.2 *Motivation of the Problem*

Six Evolutionarily Significant Units (ESUs) of anadromous salmonids from the upper Columbia River Basin and the lower Snake River Basin are listed as endangered or threatened under the Endangered Species Act, including spring/summer Chinook salmon (*Oncorhynchus tshawytscha*), fall Chinook salmon (*O. tshawytscha*), Steelhead (*O. mykiss*), and Sockeye salmon (*O. nerka*). Chinook salmon and Steelhead from the Middle Columbia River are also listed as threatened. Only wild populations are listed, but hatchery fish are studied as well, due to concern over the sustainability of hatchery populations and the relative ease of studying hatchery fish. The majority of Snake River populations spawn upstream of Lower Granite Dam, the farthest upriver of the four federally owned hydroelectric dams on the lower Snake River. Juveniles migrate downriver as weeks- or months-old fry (fall Chinook salmon) or as years-old smolts (spring/summer Chinook salmon, Steelhead), spend a variable amount of time rearing in the Columbia River estuary and then growing in the Pacific Ocean, and then mature and migrate back upriver to spawn in their natal tributaries. The age at maturity varies both among and within species and populations. Thus, the smolts in a given migration year contribute to several years of spawning adults.

Migrating salmonids from the lower Snake River must pass eight large hydroelectric

dams on the Snake and Columbia rivers; populations from the Mid-Columbia pass up to nine hydroelectric projects (Figure 1.1). Federally-owned dams are Bonneville (BON), The Dalles (TDA), John Day (JD), McNary (MCN), and Priest Rapids (PR) on the Columbia River, and Ice Harbor (IH), Lower Monumental (LMO), Little Goose (LGO), and Lower Granite (LGR) on the Snake River. Due to the listing of the populations under the ESA, managers of the federally owned hydroelectric projects on the lower Columbia and Snake rivers are required to operate these dams in such a manner that does not further deplete or harm the existing salmon populations. Researchers must monitor migrating salmonids during their migration, identifying reaches or dams where survival or passage rates are low, measuring the effect on survival of treatments such as juvenile transportation, and analyzing the effect of adult fallback over dams on subsequent survival. Additionally, rates of unaccountable loss of migrating adults are of concern, where unaccountable loss refers to adults that are not reported to have returned to hatcheries or spawning grounds, or to have been harvested in fisheries. Unaccountable loss may be due to mortality in the mainstem, illegal or unreported fishing, spawning in the mainstem, unknown turnoff to tributaries, or fallback over dams not followed by reascension.

All but one of the federally-owned dams (The Dalles) have juvenile bypass systems (JBS) that divert smolts away from the turbines and past the dam, returning bypassed smolts to the river below the dam. Smolts not bypassed in this way pass the dam via either the spillway or the turbines. Three of the Snake River dams (Lower Granite, river km [RKM] 695; Little Goose, RKM 635; and Lower Monumental, RKM 589) and one Columbia River dam (McNary, RKM 470) collect fish for the smolt transportation program. This program is run by the United States Army Corps of Engineers (USACE) together with NOAA Fisheries (National Oceanic and Atmospheric Administration, National Marine Fisheries Service). Bypassed smolts are collected at these dams and transported downriver by barge or truck to be returned to the river below Bonneville Dam, located on the Columbia at RKM 234. Transportation allows smolts to reach the Columbia River estuary earlier and without the stress and mortality risk of passing eight large dams on their downstream migration, although there are stresses involved in transportation itself (Williams, 1989). Additionally, some bypassed and collected fish are diverted to the sampling room at the

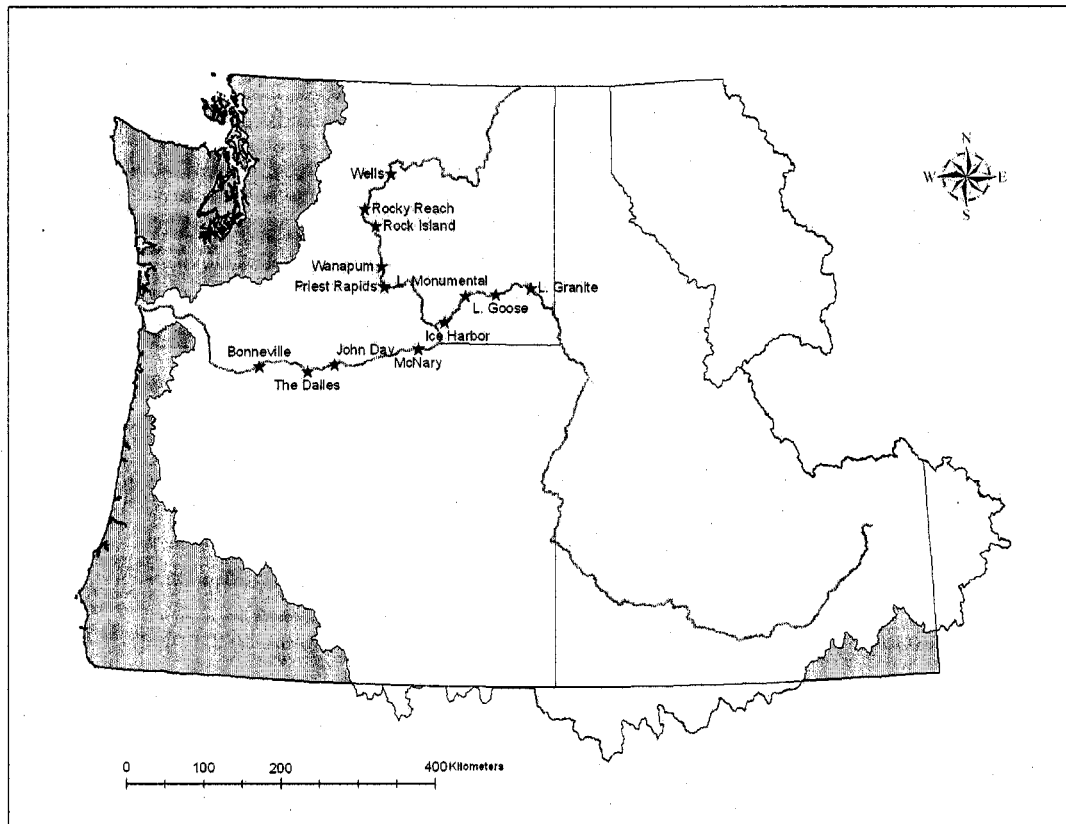


Figure 1.1: Columbia and Snake river basins, with hydroelectric dams passed by migrating salmonids. Federally-owned dams are Bonneville, The Dalles, John Day, McNary, and Priest Rapids on the Columbia River, and Ice Harbor, Lower Monumental, Little Goose, and Lower Granite on the Snake River.

dams; these fish may or may not be returned to the migrating population. Returning adults pass dams via fish ladders; some fish ladders have sampling rooms from which sampled adults may or may not be returned to the river.

In order to gauge the effects of management actions on migrating populations, tagging studies have been performed on migrating juveniles and adults. Since the early 1990s, Passive Integrated Transponder (PIT) tags (Prentice, Flagg and McCutcheon, 1990a; Prentice et al., 1990b) have been used to assess the survival of juvenile salmon migrating through the dam systems. Both hatchery and wild fish are PIT-tagged, but only a sample of the

migrating population is tagged. PIT tags are small electronic tags, 10 mm long and 2.1 mm in diameter, coded with individual codes that are automatically detected when a tagged fish swims past a detector, thereby allowing recognition of individual tags (fish) without further handling after tagging and release. PIT-tagged Snake River juveniles are detected in the JBS at LGR, LGO, and LMO on the Snake River, and at MCN, JD, and BON on the Columbia River. Previously, tagged juveniles from the upper Columbia River were also detected at Rocky Reach (RR). PIT tags are beginning to be used to assess adult survival through the hydrosystem, with detectors in adult ladders at BON, MCN, PR, Rock Island (RI), and Wells (W) on the Columbia River, and at IH and LGR on the Snake River. Detection data are collected and maintained in a database by the Pacific States Marine Fisheries Commission (PSMFC¹), and are readily available to researchers.

Release-recapture work done on salmon in freshwater is extensive, with objectives ranging from estimating survival rates of migrating juveniles (smolts) past hydroelectric projects (e.g., Burnham et al., 1987; Lowther and Skalski, 1998; Skalski et al., 1998) to estimating stream residence time of spawning adults (Lady, 1996; Lady and Skalski, 1998; Manske and Schwarz, 2000), and estimating escapement or run size (Schwarz and Dempson, 1994). Burnham et al. (1987) proposed a method of designing and analyzing release-recapture studies to assess treatment effects on survival of migrating salmon, in particular through dams. They based their method on CJS models, and provided goodness-of-fit tests and hypothesis tests to compare two or more treatment groups.

Many release-recapture studies have used PIT-tag data to assess survival of migrating juvenile salmon between and through hydroelectric projects (e.g., see Prentice et al., 1990a,b; Iwamoto et al., 1994; Muir et al., 1995, 2001a,b; Lowther and Skalski, 1998; Skalski et al., 1998), as well as their overall river survival (Skalski, 1998; Williams, Smith and Muir, 2001). Smith et al. (1994) developed a method of relating juvenile survival to individual and environmental covariates via tag detections. PIT tags have also been used to assess the effect on survival of transporting migrating juvenile salmon by barge or truck past up to eight dams

¹Pacific States Marine Fisheries Commission, PIT Tag Operations Center, 45 SE 82nd Drive, Suite 100, Gladstone, OR 97207.

(Sandford and Smith, 2002). The effect of transportation on adult return rates is commonly estimated by the Transport In-river Ratio (TIR) or equivalently Transport Benefit Ratio (TBR), the ratio of the smolt-to-adult return rate (SAR; Raymond 1988) of transported fish to that of non-transported fish (Ebel, 1980; Sandford and Smith, 2002) using the relative recovery method (Ricker, 1975). Without using detections of individually-identifiable adults, TBR and ocean survival are typically estimated by pooling tag recoveries of adults across age classes as in Sandford and Smith (2002), ignoring any effects of maturing and returning in different years.

Without using detections of PIT-tagged adults, studies of juvenile in-river survival have usually right-censored the records of those smolts that were transported, and have needed to extrapolate to estimate survival rates through the river reach ending at Bonneville Dam (e.g., Williams et al., 2001). The resulting estimators of juvenile survival may be inefficient or biased due to lack of adult data. Additionally, estimators of ocean survival and TBR based on relative recovery rates have unknown statistical properties (e.g., bias and uncertainty). The adult PIT-tag data now available allow for model-based estimation of juvenile survival through the lower reaches, as well as an opportunity to directly incorporate and estimate ocean survival and transportation effects in a release-recapture model. This in turn provides estimators with known statistical properties, i.e., maximum likelihood estimators.

Radiotelemetry tags have been used to monitor migrating adult salmonids since the late 1960s. Since the late 1990s, radio tags have been used on a large-scale basis to study the upriver migration of adult salmonids by researchers at NOAA Fisheries and the University of Idaho; the data and a further description of the study are available at <http://rtagweb.nwfsc.noaa.gov/home/index.cfm>. Migrating adults are collected at Bonneville Dam, fitted with radio transmitters, and released just downstream of Bonneville. Antenna arrays have been placed at all eight dams in the lower Columbia and Snake rivers, and single arrays are in the mouths of most tributaries. The resulting detection data include detections from these fixed-site receivers, as well as detections from mobile tracking and tag-recoveries from hatcheries and fisheries. Preliminary analysis of these data by researchers at the University of Idaho focuses on small-scale movements at the dams and rates of migration, fallback, and unaccountable loss; fallback and unaccountable loss rates are based

on ratios of observed counts at different locations (Bjornn et al., 2000; Keefer et al., 2002; Reischel and Bjornn, 2003; Boggs et al., 2004). Due to the high cost of radiotelemetry tags and the difficulty of analyzing the raw data, the federal government has plans to discontinue use of radiotelemetry tags in studying adult migration and survival, relying on the cheaper PIT tags. It is not known what information about adult migration and survival will be lost by relying on PIT tags instead of radio tags.

As with the relative recovery estimators from PIT-tag data, the estimators used with the radio-tag data have unknown statistical properties. It is not always clear what a particular measure estimates or how to measure the uncertainty associated with any particular resulting estimate. Without these two pieces of information, managers are unable to use these data to make informed policy decisions with regard to either dam operations or future tagging operations. Additionally, it is not clear what can be learned from different types of data, and whether one type is inherently more informative than another (e.g., radio tags versus PIT tags).

A modeling approach to analyzing PIT-tag and radio-tag data addresses each of these problems. A migration model that incorporates these data will provide estimators with known statistical properties with respect to bias and uncertainty (i.e., standard error). Additionally, the model parameters may be used as building blocks of precisely defined measures of treatment effects (e.g., juvenile transportation), which then have easily calculated expected values and standard errors. Also, the modeling approach provides a framework with which to analyze the benefits of one data type over another.

Release-recapture models used to analyze PIT-tag data are described above. These models (e.g., Burnham et al., 1987; Skalski, 1998; Skalski et al., 1998) are well-understood and are commonly used, but are appropriate only for juveniles and do not incorporate transportation. Thus, a new model must be developed to incorporate both juvenile and adult PIT-tag data as well as information about transported smolts.

Radiotelemetry data have been used in a variety of contexts in the wildlife field, including estimation of space use and migration corridors (e.g., Flamm et al., 2005), population size (e.g., Boulanger et al., 2004), and survival (e.g., Pollock et al., 1995). One approach to analyzing radiotelemetry data uses the nonparametric Kaplan-Meier survival model (Kaplan

and Meier, 1958) to estimate the survival function (e.g., Pollock, Winterstein and Conroy, 1989). Several researchers have developed release-recapture models using radiotelemetry data as recaptures. For example, Skalski et al. (2001) developed a model for analyzing radio-tag data from migrating juvenile salmonids. Pollock et al. (1995) used radiotelemetry data in a release-recapture model to estimate survival through time. Pollock, Jiang and Hightower (2004) combined Kaplan-Meier and Jolly-Seber approaches to modeling survival through time with radiotelemetry data. Cowen and Schwarz (2005) used a release-recapture model with radiotelemetry data to estimate survival of salmonid smolts (i.e., juveniles) in the presence of tag loss.

While the models in Pollock et al. (1995), Skalski et al. (2001), Pollock et al. (2004), and Cowen and Schwarz (2005) allow for detection rates $< 100\%$, some models assume 100% detection rates and thus avoid the problem of non-detected but extant individuals (e.g., White, 1983; Bunck and Pollock, 1993; Powell et al., 2000). The assumption of 100% detection is inappropriate here due to receiver or antenna outages at the fixed receivers, unwired passage routes at the dams (e.g., navigation locks), and imperfect mobile tracking and tag-recovery efforts (not all tagged fish are accounted for), implying that most models using radio-telemetry data are inappropriate for these data. The Pollock et al. (1995) and Pollock et al. (2004) models estimate detection rates, but focus on modeling survival through time, which is similar but not identical to modeling survival and movement through space (see below). The Skalski et al. (2001), Skalski et al. (2002), and Cowen and Schwarz (2005) models all allow for $< 100\%$ detection rates as well, but they are designed for juvenile salmon. Unlike juveniles, whose migration path is mostly linear, adult salmon engage in multi-directional migrations, falling back over dams, swimming downriver to explore tributaries, and visiting tributaries downstream of the mouth of their natal stream. Because of the non-linear nature of the adult migration and the detailed data from the adult migration available from radiotelemetry data, using a juvenile model to analyze the adult migration is tantamount to ignoring the extra information the radiotelemetry data may yield relative to PIT-tag data. Thus, the available statistical models designed for radiotelemetry data are inappropriate for this application.

It is apparent that new statistical models must be developed to appropriately analyze

both the combined juvenile and adult PIT-tag data and the adult radiotelemetry data. Because the focus of the analysis here is on migrations (juvenile and adult), the models appropriate for these data are essentially movement models, in which the main processes are movement through space and survival through space and time. Although movement models exist (see Section 1.1), existing movement models are inappropriate for these data. Most movement models track migrations over time, with repeated movements between sites (e.g., breeding grounds) on an annual or generational basis, and with detections only at the breeding grounds. Examples are the models in Schwarz et al. (1988), Schwarz et al. (1993), Brownie et al. (1993), Kendall et al. (1995), Kendall and Nichols (1995), and Kendall et al. (1997). Individuals are assumed to have some degree of site fidelity. The salmon migration data come from detections taken during the migration, rather than simply from the origin (e.g., rearing sites or hatcheries) and end (e.g., ocean) of the migration. Survival during the migration itself, rather than between migration years, is of interest here.

Although the existing movement models are inappropriate, to some degree the available models that model survival through time (see Section 1.1) may be adapted for survival and movement through space. One difference between these models and those developed here is that rather than sampling individuals at one or several breeding sites during discrete sampling periods over many years, here sampling occurs constantly through time and at many different passage points in the juvenile and adult migration route. In most cases, migrating individuals must pass each of the sampling points, conditional on survival to that point, but they need not be detected. The main difference between survival through time and survival through space is that time is linear, whereas fish movement through space may be multidirectional. Adult migrants in particular have been observed to fall back over dams, either accidentally or because they have overshot the mouth of their spawning tributary. For similar reasons, adults may swim downriver between dams. Additionally, adults may enter tributaries downstream of their natal streams, either to explore or wait out the warm temperatures of the mainstem in the cooler waters of the tributary. Such tributary "visits" may last from an hour to several days. These tributary visits are detectable, but are optional for fish directed upstream of the tributary. Thus, while the adult migration is directed and linear on a large spatial scale, it is potentially multidirectional on a smaller

scale, and the time-based release-recapture models must be suitably adapted to the space-based adult radiotelemetry data. The juvenile migration is much more linear on a small spatial scale than the adult migration, and so the available release-recapture models require fewer adaptations for the juvenile migration.

1.3 *Scope of Work*

Two types of release-recapture model are developed and presented in this dissertation. The first type is a life-cycle model that models the juvenile and adult migrations and ocean stage of Pacific salmonids using PIT-tag data from both migrations (Chapter 2). The second type models the upstream migration of adult salmonids using radiotelemetry data (Chapter 3). Both types of model estimate large-scale survival and/or movement (“transition”) rates along the migration routes. Each model is developed for a flexible number of detection sites for general applicability. The models are designed for open populations that experience death and emigration (i.e., turn-off to tributaries), but not birth and immigration. Because all marked individuals are released at approximately the same time (as juveniles for PIT-tagged animals and as adults for radio-tagged animals), a single-release, multiple-recapture multinomial likelihood model is developed for each data type, as in Skalski et al. (1998).

In order to explore the different types of information available from radio tags and PIT tags, a sequence of models is developed using different types of radiotelemetry data, ranging from simple to relatively complex. The simplest model is analogous to a linear PIT-tag model (i.e., the adult portion of the PIT-tag model presented here), while the most complex uses fallback, tributary, and censoring information from the radio-tag data. The models are compared via two “performance measures:” perceived system survival and unaccountable loss rate, described below.

1.3.1 *PIT-Tag Life-Cycle Model*

There are several objectives in developing a PIT-tag life-cycle release-recapture model. One objective is to use all of the available detection data to efficiently estimate inriver survival of juveniles and adults. A second objective is to attain model-based estimates of ocean survival

and smolt-to-adult return rates. A third objective is to use the combination of PIT-tag detections and transportation information to derive model-based estimators of transportation effects with clearly understood statistical properties (i.e., bias and precision) and interpretations. Finally, estimators for a variety of other performance measures will be developed, including adult age composition.

The PIT-tag model developed in Chapter 2 is suitable for salmonid species that migrate directly to the ocean as juveniles, and directly back to the spawning grounds as adults. Appropriate species are spring and summer Chinook salmon (*Oncorhynchus tshawytscha*), Sockeye salmon (*O. nerka*), and summer Steelhead (*O. mykiss*). Because return breeders are not considered in this model, only the first spawning migration of Steelhead is appropriate for this model. The PIT-tag model includes three main parts of the salmonid life cycle: (1) juvenile migration and detection, (2) ocean stage, including survival and maturation but no detection, and (3) adult migration and detection. The underlying model for the juvenile stage has already been developed and used to study survival of smolts as they pass through hydroelectric projects on their outmigration by Skalski et al. (1998); juvenile transportation and possible censoring due to known removals of tagged individuals at the dams must be incorporated into the model for the juvenile stage. The ocean stage can provide limited information about ocean survival and maturation, but can help identify issues in combining juvenile and adult data. The adult migration stage is similar to the juvenile migration stage, but includes age-structure stemming from the variable maturation rates among individuals from a single brood year. The multi-directional nature of the adult migration is currently poorly represented by PIT-tag data, and only the large-scale linear nature of the adult migration is modeled here. The inclusion of age-structure in the model must necessarily resemble efforts by Clobert et al. (1994), Pradel (1996), Pradel et al. (1997), and Schwarz and Arnason (2000). Each of these models a population in which animals are marked as young, released, and (mostly) non-detectable until they return to the breeding (spawning) grounds as breeders (spawners), which may occur for the first time at several ages. Unlike the populations considered by the researchers above, PIT-tagged juveniles (i.e., smolts) are detected on their outmigration, and PIT-tagged adults are detected on their immigration, rather than at the ocean and spawning grounds themselves.

More importantly, there are no return breeders; individuals mature, spawn once, and die. This means that the usual assumption of a common survival rate after the age of the youngest breeder is inappropriate, because breeders (migrating adults) and non-breeders (non-mature ocean-stage individuals) experience very different environments (river versus ocean). Also inappropriate is the assumption of common capture and survival probabilities among breeders regardless of age; although breeders (migrating adults) are all in rivers rather than the ocean, individuals maturing and migrating in different years experience different in-river conditions. Thus, the PIT-tag model will resemble existing age-structured models in some, but not all, ways.

In the past, the records of transported juveniles have been censored from PIT-tag models, precluding model-based estimation of transportation effects. Recently, Sandford and Smith (2002) used a combination of model-based, parametric estimators and non-parametric estimators from PIT-tag data to compare the smolt-to-adult return rate (SAR) of transported smolts to the SAR of non-transported smolts. The model used in Sandford and Smith (2002) was restricted to juvenile PIT-tag data, and pooled the adult data across adult return years. The PIT-tag model presented in Chapter 2 incorporates transportation as a process in the modeling of the capture histories, thus allowing for a variety of estimators of transportation effects that are wholly model-based. Various transportation effect measures are presented in Chapter 2, along with measures of adult return rates, the adult age distribution, and adult inriver survival using combined juvenile and adult PIT-tag data.

1.3.2 Adult Radio-Tag Model

The main objective in developing a release-recapture model to analyze adult radiotelemetry data is to estimate the unaccountable loss rate, which was identified by NOAA Fisheries (2000a, 2004) as an important performance measure of the adult migration. The probability of surviving and remaining in the migrating population to Lower Granite Dam or Priest Rapids Dam (i.e., “perceived system survival”) is another potentially useful performance measure. A secondary objective in developing a radio-tag model is to compare what can be learned from radio tags about the unaccountable loss rate and perceived system survival

to what can be learned from PIT tags about these quantities. With this objective in mind, a sequence of models is developed in Chapter 3, ranging from simple PIT-tag models to complex radiotelemetry models, each designed to estimate both system survival and unaccountable loss rates. Each model can be fit to radiotelemetry data that has been suitably simplified for the model; the simpler "PIT-tag models" can also be fit to adult PIT-tag data. In Chapter 3, each model is fit to radiotelemetry data from 1996 Chinook salmon that have been prepared (i.e., simplified) for the model, and estimates of system survival and unaccountable loss rate are compared among the models. On this basis, recommendations are made about the use of either radiotelemetry or PIT-tag data to estimate large-scale performance measures such as system survival and unaccountable loss rates. Additionally, a model is selected from the sequence of models and recommended for use in analyzing existing radiotelemetry data to estimate system survival and unaccountable loss rates.

The models developed in Chapter 3 are suitable for any salmonid species that migrates upstream in a single season. Thus, suitable species are spring, summer, and fall Chinook salmon (*O. tshawytscha*) and Sockeye salmon (*O. nerka*). Summer Steelhead (*O. mykiss*) that do not overwinter within the study region on their way to spawning grounds are also suitable. The assumption of homogeneous transition and capture probabilities is not appropriate for Steelhead that do overwinter during their migration, however, and so these models are inappropriate for such groups.

The more complex models developed in Chapter 3 (i.e., the "radio-tag models") use radiotelemetry data as recapture data with more flexible detection sites and individual fates than the simpler models in Chapter 3 (i.e., the PIT-tag models). Tributary turn-offs and visits are observable from radiotelemetry data, as are fallbacks that are followed by either tributary turn-offs or dam reascension. The radio-tag models incorporate both fallback and tributary detections. In general, only single detection sites are available in the tributaries, so it is impossible to estimate detection rates at these tributary sites, which are optional for fish destined to spawn upriver of these tributaries. Thus, it is assumed that the detection rate is 100% at all tributary sites. Additionally, all tributary sites between two dams are treated as single tributary sites for simplicity.

Due to imperfect detection at the dams, modeling downstream movement during fall-

back in a large-scale survival/movement model involves potential endless cycling between fallback and reascension, and is mathematically intractable. Thus, information about fallback is used in the radio-tag models, but fallback itself is not modeled. Also, the rate of fallback at a particular dam (i.e., the probability of falling back at that dam, conditional on ascending the dam) is not estimated by this radio-tag model. On the other hand, potential effects (“memory”) of either fallback or tributary visits on subsequent survival/movement parameters are incorporated, as in Hestbeck et al. (1991) and Brownie et al. (1993).

If the radio-tag models are used with known-source fish, then it is possible to estimate straying rates to tributaries downstream of the natal tributary. This is similar to estimating migration rates among strata in a study region, as in Nichols et al. (1993), Schwarz (1993), Schwarz et al. (1993), Joe and Pollock (2002), and Lebreton and Pradel (2002), with the difference that fish in the radio-tagged population are constrained to migrate in one of two directions from any point in the river: upriver to the next dam or natal spawning stream, or out of the river to a tributary downstream of the natal spawning stream (i.e., straying; downstream travel is not modeled here). Likewise, fish that have entered a tributary may either remain in the tributary, or return to the river to continue migrating upriver. Alternatively, straying may be viewed as emigrating from the study area, if the study area is considered to be the river itself. In this case, fish who enter a tributary and then return to the river are “temporary emigrants,” as in the models of Kendall et al. (1997) and Schwarz and Stobo (1997), while fish who enter a tributary and do not return to the river are “permanent emigrants.” Unlike the models of Kendall et al. (1997) and Schwarz and Stobo (1997), here it is possible to identify emigrants (strayers) as they leave the study area, because detection arrays are in tributary mouths. Additionally, whereas “temporary emigrants” in the traditional sense may be absent from the study area for several sampling periods, temporary strayers must return to the river at the same point from which they left it, and so cannot skip any sampling point in the river (i.e., dams). Without known-source fish, actual straying cannot be distinguished from legitimate turn-offs to spawning tributaries. In this case, the radio-tag models can nevertheless estimate rates of tributary entry and exit (i.e., “temporary emigration”), and the possible effect of these tributary visits on subsequent survival.

In addition to fixed-site dam and tributary detections, the radiotelemetry database includes tag-recoveries from fisheries and hatcheries, and mobile-tracking data. The mobile-tracking data are useful for studying space use, but are inappropriate for release-recapture models. Incorporating the tag-recovery (i.e., tag return) data from the hatcheries and fisheries into the model requires independent estimates of the tag-recovery and tag-reporting rates. While these data could be included in the models under the assumption of 100% recovery and reporting, it is known that the recovery and reporting rates are far less than 100%. Hatcheries often take only the early returnees to the hatcheries, so late-returning tagged fish are not examined for tags; fishermen may be reluctant to return tags at all, or may wait until the end of the season before returning tags, thus confounding information on location and date of the tag-recovery. Without estimates of tag-recovery and reporting rates, these data are not included in the radio-tag models presented here.

Two summary or performance measures are developed for each radio-tag model: perceived survival to the top of the final dam (i.e., "system survival"), and the unaccountable loss rate from the release site. Perceived survival may be considerably smaller than actual biological survival if many tagged individuals permanently leave the mainstem of the river for tributaries downstream of the final dam. The unaccountable loss rate, however, takes into account exits to tributaries and represents the probability of an unknown fate, including mortality (natural, dam-related, or harvest), fallback that is not followed by dam reascension or tributary turn-off, and spawning in the mainstem. Reducing the unaccountable loss rate is an important goal in salmon recovery in the Columbia Basin, and identifying sites of unaccountable loss and estimating its magnitude is the objective of the radiotelemetry modeling.

Chapter 2

JUVENILE-ADULT PIT-TAG MODEL

2.1 Introduction

2.1.1 Model Overview

The primary purpose of the release-recapture model developed here is to estimate survival of migrating salmonids on their migrations between their spawning grounds and the ocean. Secondly, we may estimate quantities related to ocean survival, maturity, and the effect of transportation on return rates. The model uses PIT-tag detections from the dams to estimate these quantities. While PIT-tag data are available for both hatchery and wild fish, most records are of hatchery fish, because they are more numerous and easier to tag. The model may be used on either hatchery or wild fish; ideally, hatchery and wild data sets should not be combined due to differences in physiology and migratory behavior. Smith et al. (1998) found that juvenile survival of hatchery and wild fish differs primarily in the first reach after initial release, so it may be possible to combine hatchery and wild fish in a single data set if the focus of the study is primarily juvenile in-river survival. However, Raymond (1988) and Bradford (1995) found different ocean survival rates between hatchery and wild salmon (specifically Chinook salmon), and McIsaac (1995) suggests an accelerated maturation schedule for hatchery fish relative to wild; if transportation effect or adult return rates are the focus, then hatchery and wild fish should not be combined in a single data set.

Most PIT-tag studies on the Snake River choose the initial release to be at or above LGR. The model developed here allows for any site in the Columbia/Snake River hydrosystem to be the initial detection site. While the examples used here assume the tagged fish are from the lower Snake River and use LGR as the initial juvenile detection site, the model may also be used for upper Columbia River fish, with RR or PR as the initial detection site.

Not all smolts pass a given dam via the bypass systems; some pass via the spillway or turbines, and these fish have no opportunity of being detected at the dam. It is assumed

that all tagged fish entering the JBS are detected. Adults are detected in adult fish ladders at certain dams. Due to logistical and technical issues, adult detection is not 100% at these dams, although it has improved in recent years. The model includes the detection process, which for tagged juveniles may be understood as the bypass process.

For tagged juveniles, only those bypassed (detected) may be removed for study (sampled or censored) or transported. The model allows for both processes at all juvenile detection sites (dams), and for censoring at all adult sites. While many sampled individuals are returned to the migration, we have no information on which fish are returned, and thus the detection histories of sampled fish are right-censored. Although the rate of censoring is typically low, and censoring itself may be considered a nuisance parameter, we must account for it in order to get unbiased estimates of return rates and survival between dams. Ignoring it leads to negatively biased reach survival estimates, and may also bias estimates of return rates if sampled individuals return at different rates than non-sampled individuals.

The model includes multiple transportation sites, thus allowing the user to tailor the model to fit the specifics of the transportation program as actually experienced by the fish under study, and providing flexibility in quantifying the survival effect of transportation. In general, all fish bypassed at transport dams are collected for transport, limiting the number of fish bypassed at multiple dams. There are exceptions, however. Transportation at MCN is limited to summer months in order to transport fall Chinook salmon. Also, some bypassed PIT-tagged fish are not transported, but upon detection in the bypass system are diverted by a slide gate back to the river. This practice is primarily for study purposes. Because transportation practices are different for tagged and untagged fish, careful consideration of the model's transportation results is necessary to apply them to the untagged population.

Until they reach the ocean, the tagged fish in a given release group all travel along the same route and generally at the same time, with the exception that some travel downstream by barge or truck while others migrate in-river. Once in the ocean, they disperse, although some research suggests particular migration patterns in the marine environment (e.g., see Cleaver, 1969; Netboy, 1980; Miller, Williams and Sims, 1983; Hartt and Dell, 1986; and Sandercock, 1991). Without permanent marine PIT tag detectors, we cannot make use of any particular migrations within the ocean. Individuals in a release group disperse

temporally in the ocean, as well as spatially, in that they mature at different rates and return as adults to spawn in different years. For example, some return after only one summer in the ocean, while most return after one, two, three, or more winters at sea, depending on their species, stock, and gender. All the anadromous salmonids spawning in the mid-Columbia or Snake River Basins have some degree of variation in age at maturity. Although individuals maturing in different years migrate as adults in the same regions spatially, they may be assumed to migrate in different river conditions due to temporal changes in flow, spill, and water temperature, and in different physiological states due to the effects of remaining at sea a different length of time. Thus, the model treats mature individuals returning at different ages separately, even though they come from the same release group.

In this chapter, a release-recapture model of reach survival and adult return is developed, incorporating both juvenile and adult PIT-tag detections and accounts for censoring (known removals at dams) and transportation. The age of returning adults is also incorporated. Section 2.1.2 identifies and discusses the model assumptions. The underlying model is developed via a simple example in Section 2.2, with all major biological processes incorporated as needed. The underlying model is converted to an estimable model in Section 2.3; it is generalized with respect to both juvenile and adult detection sites, censoring and transporting sites, and the number of adult age classes. Section 2.4 defines and discusses interesting biological quantities derived from the model. Section 2.5 discusses remaining conceptual issues related to the model. Section 2.6 compares the modeling approach taken here to current practices. Finally, Section 2.7 demonstrates use of the model in its entirety with a complete example.

2.1.2 Model Assumptions

The assumptions underlying the model are the typical assumptions of single-release, multiple recapture models, and are listed below. For more information on mark-recapture models and their assumptions, see Cormack (1964) or Burnham et al. (1987).

(A1) All smolts returned to the river at a given detection site have a common probability of subsequent survival, detection, censoring, and transportation, regardless of detection at

the earlier site.

(A2) All smolts diverted for transportation at a given site have a common probability of subsequent survival, detection, and (adult) censoring.

(A3) All adults at a given detection site have a common probability of upstream survival, detection, and censoring, regardless of detection at the downstream site.

(A4) The fate of each tagged individual is independent of the fate of all other tagged individuals.

(A5) Interrogation for PIT tags occurs over a negligible distance relative to the lengths of the river reaches between sampling events.

(A6) Individuals selected for PIT-tagging are representative of the population of interest.

(A7) Tagging and release have no effect on subsequent survival, detection, censoring, or transportation rates.

(A8) All tags are correctly identified, and the treatment codes at dams (censored, transported) are correctly assigned.

(A9) There is no tag loss after release.

Assumption (A1) implies no effect of juvenile detection on survival. Because juvenile detection occurs only in the juvenile bypass systems, this implies no mortality effect of the bypass system. Some literature (e.g. Muir et al., 2001b and Sandford and Smith, 2002) documents route-specific differences on juvenile survival of dam passage and adult return rates. On the other hand, Muir et al. (2001a) found no significant effect of upstream detection (bypass) on downstream survival and detection for migrating yearling Chinook salmon and Steelhead from 1993 through 1998. Assumption (A1) also implies mixing of non-bypassed smolts and smolts that are bypassed and returned to the river, immediately upon entering the tailrace of a dam. Smith et al. (1998) found violations of this mixing implication during periods of high spill, when detected (bypassed) fish arrived at downstream dams later than non-detected fish. However, there was no significant effect on downstream survival and detection. Because migration parameters vary with species, run type or race, and migration year, assumptions (A1), (A2), and (A3) imply that we should avoid combining release groups over these factors. However, some pooling of release groups may be necessary to achieve

necessary sample sizes. Pooling within species and races but across daily or weekly release groups within a migration season should be acceptable, because reach survival estimates for juveniles show little temporal variation within a season (Skalski, 1998; Skalski et al., 1998; Muir et al., 2001a).

Assumption (A4) is reasonable due to the large numbers of individuals migrating. Violations of the assumption may negatively bias standard errors, but should not affect point estimates. Assumption (A5) allows us to attribute estimated mortality to the river reaches being studied, rather than to the detection process. Because detection occurs only in dam bypass systems (juvenile or adult), which are passed relatively quickly compared to the time spent migrating, this assumption is reasonable. In addition, Skalski et al. (1998) found that pre-detection bypass mortality has no effect on point estimates or standard error estimates for survival parameters, and Muir et al. (2001a) found no significant post-detection bypass mortality for hatchery yearling Chinook salmon and hatchery Steelhead. The model developed here accounts for known removals from the bypass systems through the censoring parameters. Assumption (A6) requires that individuals not be chosen for tagging based on size or condition. We must also beware drawing conclusions for wild fish if only hatchery fish are tagged. Assumptions (A4) and (A7) together are necessary to apply results from the tagged population to the untagged population migrating at the same time. One obvious violation of this assumption is that of the bypassed smolts at transport dams, only some of the tagged smolts are transported while all of the untagged smolts are transported. This violation means that we need to carefully adjust the estimates of transportation effect derived from tagged individuals in order to apply them to untagged individuals.

2.2 Underlying Model

In order to develop a usable, meaningful model to estimate survival, the effect of transportation, and adult return rates, first consider a study design with two juvenile detection sites, two adult detection sites, and two age classes of returning adults. Assume that the younger age class (age-1 adults) is composed of fish that returned to freshwater after a single winter ("year") in the ocean, and that the older age class (age-2 adults) is composed of fish that returned after two winters in the ocean. Further, assume that the first juvenile detection

site and the second adult detection site are both LGR, and the second juvenile detection site and first adult site are both BON. It is not necessary that the juvenile sites be the same as the adult sites, but it simplifies the diagrams in Figures 2.1 and 2.2.

Figures 2.1 and 2.2 show a schematic for this study design, with migration paths indicated by directed lines. Figure 2.1 shows the migration paths for the non-transported fish, and Figure 2.2 adds migration of transported individuals. Branch points along the migration path indicate “choices” made by individuals who have survived to those points. Each path segment has a survival probability, and each detection site has a detection probability. Survival on a particular path segment is related to length of the segment, environmental conditions along the segment, and condition of the fish; these relationships are not explored here. Detection at a particular site depends on the status of the detectors, river conditions, and the route taken by the fish past the detection site (usually a dam); only the effect of the route taken is considered here. For juveniles, detection is equivalent to passing the dam via the juvenile bypass system. It is obvious that these parameters will vary for different fish, both because of their condition and because they pass points at different times. However, we make the assumption that all fish have the same parameters over the same migration path segment and at the same detection sites in a given year. If survival and detection are more constant within years than between years, then this is a reasonable assumption.

Juvenile survival between LGR and BON is represented by the parameter S_2 . Because detection takes place in the juvenile bypass systems, we can think of S_2 as survival from the middle of the JBS at LGR to the middle of the JBS at BON. Ideally, we would like to consider S_2 as survival from the tailrace of LGR to the tailrace of BON. This is appropriate if there is no bypass mortality at BON. Any pre-detection bypass mortality at BON is represented in S_2 , consistent with the tailrace-to-tailrace interpretation. Any post-detection bypass mortality at BON is represented in survival after BON, inconsistent with the tailrace-to-tailrace interpretation. However, Muir et al. (2001a) found insignificant post-detection bypass mortality, so the tailrace-to-tailrace interpretation is acceptable.

The first decision point in Figure 2.2 is transportation from LGR, for fish that are detected but not censored there. Note that the “decision” that a particular (tagged) fish be transported is generally made by researchers or dam operators, not by the fish. Fish

who are transported from LGR are assumed to have separate survival along the remaining juvenile migration and throughout the ocean distribution, relative to non-transported fish; their adult survival depends only on the year in which they return to spawn. The second decision point is at the end of the first ocean year, at which point fish who have survived that long must “decide” whether to mature and return to spawn, or to stay in the ocean another year. We may consider a third decision point to be at the end of the second ocean year, but in this study design, we assume that all fish surviving and still in the ocean at the end of the second year return then. Detection and mortality “decisions” are not shown in Figures 2.1 and 2.2. In this model, we assume that once a fish has decided to return to freshwater to spawn, there are no decisions to make during the adult migration. This is a simplification of the actual adult migration, because adults must “decide” whether or not to fallback over dams they have passed, enter tributaries, and remain in tributaries they enter. However, if we are following known-source fish from above LGR, then it is unlikely, though not impossible, that they will spawn in tributaries below LGR.

Some path segments in Figures 2.1 and 2.2 have more than one survival parameter. For example, the path from the second juvenile site (BON) to end of the first year in the ocean has two survival probabilities: σ_J denotes survival from BON to the Columbia River estuary, and σ_1 denotes survival from point of entry into the estuary to the end of the first year in the ocean, at which time individuals must decide whether to mature and return to spawn, or to remain in the ocean another year. The path from the maturation-decision point at the end of the first year, through the second year in the ocean, and on to the first adult site (BON) also has two survival parameters: σ_2 is survival from the end of the first ocean year to the end of the second ocean year (for fish who choose not to mature after one year), and σ_{A2} is survival from the end of the second ocean year (spatially, still in the ocean) to BON. Similarly, σ_{A1} is survival from the end of the first ocean year to BON. Notice that the σ_J and σ_{A_j} parameters may be viewed as representing survival over a spatial region, while the σ_j parameters are more easily thought of as being over time, with each of them representing survival through a particular ocean year. This distinction is not perfect. The starting point of a mature adult’s return migration depends on its ocean distribution, which in turn depends to some extent on species. Even within species, however, there is variation

in ocean distribution. Thus, the adult survival parameter σ_{Aj} does not relate to a well-defined spatial expanse. However, we will see that we cannot distinguish between, say, σ_J and σ_1 or σ_2 and σ_{A2} , so the distinction between spatial and temporal survival parameters and the issue of whether these are well-defined are not crucial.

There are many parameters in Figures 2.1 and 2.2. They are listed and defined in Table 2.1. Not all parameters are separately estimable, but considering survival and maturation separately allows us to develop composite parameters that are both estimable and biologically useful. This is done in the next section. Note that jacks (i.e., males who return to freshwater after one summer in the ocean) can be accommodated by redefining σ_1 , σ_2 , m_1 , and m_2 , appropriately. Also note that maturation as well as ocean survival may be affected by transportation; we will see below that this assumption affects the interpretation of the transportation benefit ratio (TBR), but does not affect the estimate of TBR.

Table 2.1: Parameters for study design with two juvenile detection sites, two adult detection sites, two adult age classes, censoring at all but last adult site, and transportation from first juvenile site. Parameters are conditional probabilities. JBS = Juvenile Bypass System.

Parameter	Definition
S_1	Survival from release point to LGR JBS;
S_2	Survival from LGR to BON JBS for in-river fish;
S_{2T}	Survival from LGR to BON JBS for transport fish;
σ_J	Survival from BON to ocean entry for in-river fish;
σ_{JT}	Survival from BON to ocean entry for transport fish;
σ_1	Survival from ocean entry through 1st winter in ocean for in-river fish;
σ_2	Survival from end of 1st winter through end of 2nd winter in ocean for in-river fish;
σ_{1T}	Survival from ocean entry through 1st winter in ocean for transport fish;
σ_{2T}	Survival from end of 1st winter through end of 2nd winter in ocean for transport fish;
m_1	Mature after 1st winter in ocean, given survival;
m_2	Mature after 2nd winter in ocean, given present and alive at end of 2nd winter; assumed = 1 here;
m_{1T}	Mature after 1st winter in ocean for transported fish, given survival;

Table 2.1 continued

Parameter	Definition
m_{2T}	Mature after 2nd winter in ocean for transported fish, given present and alive at end of 2nd winter; assumed = 1 here;
σ_{A1}	Survival from ocean distribution to BON adult fish ladder, given return after 1st winter in ocean (i.e. in year 1) for in-river fish;
σ_{A2}	Survival from ocean distribution to BON adult fish ladder, given return in year 2, for in-river fish;
σ_{A1T}	Survival from ocean distribution to BON adult fish ladder, given return in year 1, for transport fish;
σ_{A2T}	Survival from ocean distribution to BON adult fish ladder, given return in year 2, for transport fish;
S_{41}	Survival from BON to LGR for adult that matured in year 1;
S_{42}	Survival from BON to LGR for adult that matured in year 2;
p_i	Detection at Juvenile site i , given survival to site i and in-river; $i = 1, 2$; $q_i = 1 - p_i$;
p_{ij}	Detection at Adult site i in year j , given survival to site i ; $i = 3, 4$; $j = 1, 2$; $q_{ij} = 1 - p_{ij}$;
c_i	Censored at Juvenile site i , given detection at that site, $i = 1, 2$;
c_{3j}	Censored at BON for adult returning in year j , given detection there, $j = 1, 2$;
t_1	Transportation from LGR, given detection and no censoring there as a juvenile.

2.3 Estimable Model

2.3.1 Parameterization

The model shown in the schematics in Figures 2.1 and 2.2 is overparameterized and cannot be estimated. In particular, we cannot distinguish between survival parameters along a single branch in Figures 2.1 and 2.2 if there is no detection separating the two survival segments. For example, we cannot distinguish between σ_J and σ_1 in Figure 2.1 or between σ_{JT} and σ_{1T} in Figure 2.2. We must combine such non-distinguishable parameters into a single, estimable parameter. One way to combine the ocean parameters is to group all

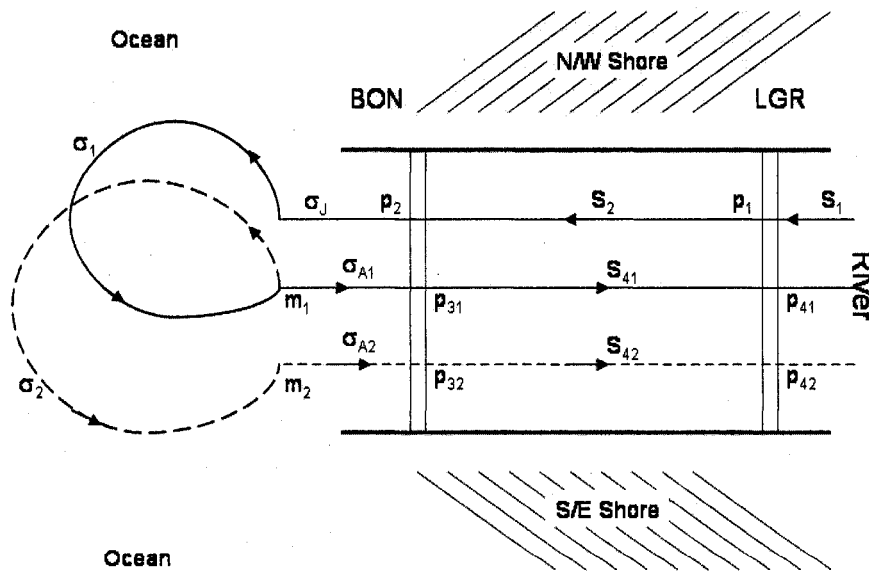


Figure 2.1: Schematic of underlying model for study design with two juvenile detection sites (LGR and BON), two adult detection sites (BON and LGR), and two adult age classes. Double vertical bars indicate a dam. Directed lines indicate migration paths. Survival, detection, and maturation processes are shown here with their parameters (S_i , σ_i ; p_i ; and m_j , respectively). The first ocean year and up-river migration of age-1 adults are in solid bold; the second ocean year and up-river migration of age-2 adults are in dashed bold. Initial release is upriver of LGR.

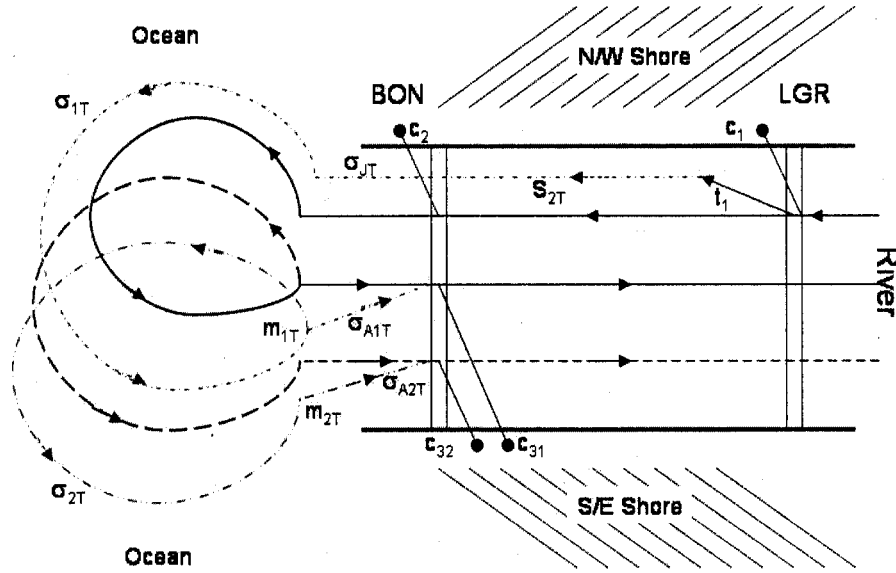


Figure 2.2: Schematic of underlying model for study design with two juvenile detection sites (LGR and BON), two adult detection sites (BON and LGR), two adult age classes, censoring at all but last adult site, and transportation from first juvenile site. We assume here that transportation does not affect adult in-river survival past BON. Censoring, transportation, and survival and maturation of transported fish are shown here with their parameters (c_i , t_i ; S_{iT} , σ_{iT} ; and m_{iT} , respectively). The first ocean year and up-river migration of age-1 adults for in-river (non-transported) individuals are in solid bold; the juvenile migration, first ocean year, and up-river migration to BON of age-1 adults for transported individuals are in dash-dot. The second ocean year and up-river migration of age-2 adults for in-river individuals are in dashed bold; the second ocean year and up-river migration to BON of age-2 adults for transported individuals are in dash-dot-dot. Initial release is above LGR.

parameters between decision points as follows (for non-transported fish):

$$\begin{aligned}
 \phi_1 &= \sigma_J \sigma_1; \\
 \phi_2 &= m_1 \sigma_{A1}; \\
 \phi_3 &= (1 - m_1) \sigma_2 m_2 \sigma_{A2}.
 \end{aligned} \tag{2.1}$$

Note that for the two-age class model, we assume $m_2 = 1$. The parameter ϕ_1 can be interpreted as the probability of surviving from the second juvenile detection site (BON) through the end of the first ocean year, or through the first winter in the ocean. The parameter ϕ_2 is the probability of maturing at the end of the first ocean year and surviving to the first adult detection site (BON), given survival through the end of the first ocean year. The parameter ϕ_3 is the probability of remaining in the ocean at the end of the first year (not maturing), surviving through the second ocean year, maturing then, and surviving to the first adult detection site, given survival through the first ocean year. If we allowed for three adult ages, we would define two new underlying σ parameters for age-3 fish (σ_3 and σ_{3A}), assume $m_2 < 1$ and the age-3 maturation parameter $m_3 = 1$, redefine ϕ_3 , and define two new ϕ parameters:

$$\begin{aligned}
 \phi_1 &= \sigma_J \sigma_1; \\
 \phi_2 &= m_1 \sigma_{A1}; \\
 \phi_3 &= (1 - m_1) \sigma_2; \\
 \phi_4 &= m_2 \sigma_{A2}; \\
 \phi_5 &= (1 - m_2) \sigma_3 m_3 \sigma_{A3}.
 \end{aligned} \tag{2.2}$$

If the model is to be used with jacks, then ϕ_1 is the probability of surviving from BON until the jacks mature and begin their return migration, and the interpretation of the remaining ϕ parameters changes similarly. Analogous parameters can be defined for transported smolts; for example, $\phi_{3T} = (1 - m_{1T}) \sigma_{2T} m_{2T} \sigma_{A2T}$ for the two-age class model. This parameterization is useful for developing the model, but because there is no detection between the

last juvenile site and the first adult site, we cannot separately estimate the ϕ parameters. Instead, we must define estimable ocean survival and maturation parameters using the ϕ parameters.

The necessary and intuitive parameterization of ocean survival and maturation for the two-age model is the following combination of the ϕ_i parameters:

$$\begin{aligned} S_{31} &= \phi_1\phi_2 = \sigma_J\sigma_1m_1\sigma_{A1}; \\ S_{32} &= \phi_1\phi_3\phi_4 = \sigma_J\sigma_1(1 - m_1)\sigma_2m_2\sigma_{A2}. \end{aligned}$$

For the three-age model, we would have:

$$\begin{aligned} S_{31} &= \phi_1\phi_2 = \sigma_J\sigma_1m_1\sigma_{A1}; \\ S_{32} &= \phi_1\phi_3\phi_4 = \sigma_J\sigma_1(1 - m_1)\sigma_2m_2\sigma_{A2}; \\ S_{33} &= \phi_1\phi_3\phi_5 = \sigma_J\sigma_1(1 - m_1)\sigma_2(1 - m_2)\sigma_3m_3\sigma_{A3}. \end{aligned} \tag{2.3}$$

The parameter S_{31} is the probability that a fish returns after one year in the ocean; S_{32} is the probability that a fish returns after two years in the ocean; S_{33} is the probability that a fish returns after three years in the ocean. Note that S_{31} , S_{32} , and S_{33} all involve both maturation and survival, so they give a “maturation and return” schedule, rather than an actual “maturation” schedule; this is discussed further in Section 2.4.3. Parameters for transported smolts are defined analogously: $S_{31T} = \phi_{1T}\phi_{2T} = \sigma_{JT}\sigma_{1T}m_{1T}\sigma_{A1T}$, etc.

Even using the combined ocean survival/maturation parameters S_{3j} and S_{3jT} , where j represents the adult age class, the survival parameters for transported smolts cannot be separately estimated; survival of transported smolts must be reparameterized. In the example, smolts detected at LGR are released from that site in one of two groups: transport (treatment) and in-river (control). “In-river fish” are returned to the river at LGR, while “transport fish” are transported downstream by barge or truck. In general, fish returned to the river at a particular dam may be transported from a lower dam, because transportation is possible from several sites. This means that fish labeled “in-river” at LGR may be labeled “transport” at LMO or MCN. Thus, “in-river” is a site-specific, rather than river-wide, label.

For this example, however, the single transport site (LGR) means that “in-river fish” are never transported.

It is common to use the “Transport Benefit Ratio” (TBR) or “Transport In-river Ratio”, to represent the effect of the transportation treatment on return rates relative to the in-river treatment: generally, the ratio of the return probabilities of transported smolts to in-river smolts is the TBR. We can use this approach to define the survival parameters for transported fish such that if θ is a survival parameter for in-river fish and θ_T is the corresponding survival parameter for transport fish, then $\theta_T = R_{1\theta}\theta$, where $R_{1\theta}$ is the reach-specific TBR for fish transported from the first juvenile detection site (LGR). For example, survival between LGR and BON for in-river fish is S_2 , so survival over this reach for fish transported from LGR is

$$S_{2T} = R_{1S_2}S_2.$$

Maturation parameters for transported fish are defined similarly. In general, define $m_{jT} = R_{1m_j}m_j$ to be the probability of a transport fish maturing after j years in the ocean, given survival through j years; in this example, j is either 1 or 2. Likewise, define the probability of a transport fish *not* maturing after j years, given survival that far, to be $1 - m_{jT} = (1 - m_j) R_{1(1-m_j)}$. Notice that $1 - m_{jT} = 1 - m_j R_{1m_j}$, yielding

$$R_{1(1-m_j)} = \frac{1 - m_j R_{1m_j}}{1 - m_j}.$$

In order to allow transportation to affect maturation, we must treat the probability of maturing and the probability of not maturing separately, but a single maturation TBR parameter is sufficient for each age class.

We cannot estimate each reach-specific parameter $R_{1\theta}$ separately, but can estimate an overall TBR for fish transported from LGR for each return age class: R_{1j} is the product of the reach-specific survival and maturation $R_{1\theta}$ parameters along the appropriate migration

path segments:

$$R_{11} = R_{1S_2} R_{1\sigma_J} R_{1\sigma_1} R_{1m_1} R_{1\sigma_{A1}} = R_{1S_2} R_{1S_{31}};$$

$$R_{12} = R_{1S_2} R_{1\sigma_J} R_{1\sigma_1} R_{1(1-m_1)} R_{1\sigma_2} R_{1m_2} R_{1\sigma_{A2}} = R_{1S_2} R_{1S_{32}}.$$

The TBR parameter R_{1j} is the ratio of the age- j return probability for LGR transport fish to the return probability that fish would experience if the river had no transportation system. This parameter R_{1j} ignores any possible downriver transportation of LGR's in-river fish. Note that the TBR R_{1j} is specific both to the site of transportation (LGR or site 1) and to the adult age class (j). Age-specific TBRs may be combined to give an overall site-specific TBR or a system-wide TBR; this will be demonstrated in Section 2.4.1 below.

For all release-recapture models with a single detection effort at each sampling occasion, it is impossible to distinguish between mortality in the final reach or time period and non-detection at the final detection site. In this case, we cannot separately estimate S_{4j} and p_{4j} , but we can estimate their product, the year- j "last reach" parameter $\lambda_j \equiv S_{4j}p_{4j}$.

In summary, we have estimable parameters for the following processes: juvenile in-river survival, adult return to BON (including ocean survival and maturation), adult in-river survival through the penultimate reach, detection at all but the final adult site, censoring, transportation, the effect of transportation on return rates, and joint survival to and detection at the final adult site. All adult parameters are specific to the year or (ocean) age of adult return. These parameters are listed in Table 2.2.

Table 2.2: Estimable parameters for the study design with two juvenile detection sites, two adult detection sites, two adult age classes, censoring at all but last adult site, and transportation from first juvenile site. JBS = Juvenile Bypass System, TBR = Transport Benefit Ratio.

Parameter	Definition
S_1	Survival from release point to LGR JBS;
S_2	Survival from LGR to BON JBS;
p_i	Detection at Juvenile site i , given survival to site i and in-river; $i = 1, 2$; $q_i = 1 - p_i$;

Table 2.2 continued

Parameter	Definition
S_{3j}	Survival from BON as a juvenile to BON as adult and returning after j years (winter) in ocean, $j = 1, 2$;
p_{3j}	Detection as an adult at BON in year j , given survival there; $j = 1, 2$; $q_{3j} = 1 - p_{3j}$;
λ_j	Conditional probability of surviving from BON to LGR for adult fish returning after j years at sea; $= S_{4j}p_{4j}$; $j = 1, 2$;
c_i	Censored at Juvenile site i , given detection at that site, $i = 1, 2$;
c_{3j}	Censored at BON for adult returning in year j , given detection there, $j = 1, 2$;
t_1	Transportation from LGR, given detection and no censoring there as a juvenile;
R_{1j}	Joint TBR for survival from LGR to adult fish ladder at BON and maturation after j years in ocean, $j = 1, 2$;
χ_i	Probability of a non-transported, non-censored juvenile not being detected after site i , conditional upon reaching site i ; $i = 1, 2$;
χ_{1T}	Probability of a juvenile transported at site 1 not being detected again;
χ_{3j}	Probability of an age- j adult not being detected after site 3, conditional upon reaching site 3 and not being censored there, $j = 1, 2$.

The parameter χ_i (Table 2.2) represents the probability of not being detected again, conditional upon reaching site i , for juvenile fish who were neither censored nor transported at site i . Likewise, the parameters χ_{1T} and χ_{3j} represent the probabilities of not being detected again for juveniles transported at site 1 and for age- j adults that reach site 3 but are not censored there, respectively. A fish that reaches a dam may have no further detections either because it dies before reaching later detection sites or because it evades detection at those sites. The χ parameters can be defined recursively:

$$\chi_1 = 1 - S_2 + S_2(1 - p_2)\chi_2;$$

$$\chi_2 = 1 - (S_{31} + S_{32}) + \{S_{31}(1 - p_{31})\chi_{31} + S_{32}(1 - p_{32})\chi_{32}\};$$

$$\chi_{1T} = 1 - S_2(S_{31}R_{11} + S_{32}R_{12}) + S_2\{S_{31}R_{11}(1 - p_{31})\chi_{31} + S_{32}R_{12}(1 - p_{32})\chi_{32}\};$$

$$\chi_{31} = 1 - \lambda_1;$$

and

$$\chi_{32} = 1 - \lambda_2.$$

2.3.2 Capture Histories and Likelihood

Data for release-recapture studies are often expressed as counts of different detection or capture histories. A detection history for a fish in this study design is a sequence of letters and numerals indicating when and where the fish is detected after release, and whether it was censored at any site or transported from LGR. Each capture history has four entries, representing the two juvenile sites and two adult sites. There are several possible records at each site, so the conventional binary indicator 0/1 for detection/no detection must be expanded to allow for censoring, transportation, and year of adult return. The codes used in the capture histories are given in Table 2.3. A typical capture history is “100B,” indicating that the fish was detected at LGR as a juvenile and returned to the river, not detected at BON as either juvenile or adult, and detected at LGR as an adult after two years in the ocean. Another capture history is “30a0,” indicating that the individual was detected as a juvenile at LGR and transported downstream from there, returned to freshwater after 1 year at sea, and was detected at BON as an adult and censored there. A third example of a capture history is “1200,” indicating that the individual was detected as a juvenile at LGR and returned to the river, and then detected as a juvenile at BON and censored there. Capture histories such as “11AB” are not allowed, because a fish that matures after 1 year at sea is assumed to complete its migration within the same year. Likewise, capture histories such as “12AA” are not allowed because any fish that is censored cannot be detected later. Table 2.4 shows the capture histories together with their probabilities.

Table 2.3: Codes used in Capture Histories

Code	Interpretation
0	Individual not detected at site (juvenile or adult site);
1	Individual detected at site and returned to river (juvenile site);
2	Individual detected at site and censored (juvenile site);
3	Individual detected at site and transported from site (juvenile site);

Table 2.3 continued

Code	Interpretation
<i>A</i>	Individual detected at site as ocean age-1 adult, and returned to river (adult site);
<i>B</i>	Individual detected at site as ocean age-2 adult, and returned to river (adult site);
<i>a</i>	Individual detected at site as ocean age-1 adult, and censored (adult site);
<i>b</i>	Individual detected at site as ocean age-2 adult, and censored (adult site).

Table 2.4: Capture histories and their probabilities for the study design with 2 juvenile detection sites, 2 adult detection sites, censoring at all but last adult site, and transportation from first juvenile site.

Capture History	Probability
0000	χ_0
000A	$S_1 q_1 S_2 q_2 S_{31} q_{31} \lambda_1$
000B	$S_1 q_1 S_2 q_2 S_{32} q_{32} \lambda_2$
00A0	$S_1 q_1 S_2 q_2 S_{31} p_{31} (1 - c_{31}) (1 - \lambda_1)$
00B0	$S_1 q_1 S_2 q_2 S_{32} p_{32} (1 - c_{32}) (1 - \lambda_2)$
00AA	$S_1 q_1 S_2 q_2 S_{31} p_{31} (1 - c_{31}) \lambda_1$
00BB	$S_1 q_1 S_2 q_2 S_{32} p_{32} (1 - c_{32}) \lambda_2$
00a0	$S_1 q_1 S_2 q_2 S_{31} p_{31} c_{31}$
00b0	$S_1 q_1 S_2 q_2 S_{32} p_{32} c_{32}$
0100	$S_1 q_1 S_2 p_2 (1 - c_2) \chi_2$
010A	$S_1 q_1 S_2 p_2 (1 - c_2) S_{31} q_{31} \lambda_1$
010B	$S_1 q_1 S_2 p_2 (1 - c_2) S_{32} q_{32} \lambda_2$
01A0	$S_1 q_1 S_2 p_2 (1 - c_2) S_{31} p_{31} (1 - c_{31}) (1 - \lambda_1)$
01B0	$S_1 q_1 S_2 p_2 (1 - c_2) S_{32} p_{32} (1 - c_{32}) (1 - \lambda_2)$
01AA	$S_1 q_1 S_2 p_2 (1 - c_2) S_{31} p_{31} (1 - c_{31}) \lambda_1$
01BB	$S_1 q_1 S_2 p_2 (1 - c_2) S_{32} p_{32} (1 - c_{32}) \lambda_2$
01a0	$S_1 q_1 S_2 p_2 (1 - c_2) S_{31} p_{31} c_{31}$
01b0	$S_1 q_1 S_2 p_2 (1 - c_2) S_{32} p_{32} c_{32}$
0200	$S_1 q_1 S_2 p_2 c_2$
1000	$S_1 p_1 (1 - c_1) (1 - t_1) \chi_1$
100A	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 q_2 S_{31} q_{31} \lambda_1$
100B	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 q_2 S_{32} q_{32} \lambda_2$
10A0	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 q_2 S_{31} p_{31} (1 - c_{31}) (1 - \lambda_1)$

Table 2.4 continued

Capture History	Probability
10B0	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 q_2 S_{32} p_{32} (1 - c_{32}) (1 - \lambda_2)$
10AA	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 q_2 S_{31} p_{31} (1 - c_{31}) \lambda_1$
10BB	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 q_2 S_{32} p_{32} (1 - c_{32}) \lambda_2$
10a0	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 q_2 S_{31} p_{31} c_{31}$
10b0	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 q_2 S_{32} p_{32} c_{32}$
1100	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) \chi_2$
110A	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) S_{31} q_{31} \lambda_1$
110B	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) S_{32} q_{32} \lambda_2$
11A0	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) S_{31} p_{31} (1 - c_{31}) (1 - \lambda_1)$
11B0	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) S_{32} p_{32} (1 - c_{32}) (1 - \lambda_2)$
11AA	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) S_{31} p_{31} (1 - c_{31}) \lambda_1$
11BB	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) S_{32} p_{32} (1 - c_{32}) \lambda_2$
11a0	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) S_{31} p_{31} c_{31}$
11b0	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 (1 - c_2) S_{32} p_{32} c_{32}$
1200	$S_1 p_1 (1 - c_1) (1 - t_1) S_2 p_2 c_2$
2000	$S_1 p_1 c_1$
3000	$S_1 p_1 (1 - c_1) t_1 \chi_{1T}$
300A	$S_1 p_1 (1 - c_1) t_1 S_2 S_{31} R_{11} q_{31} \lambda_1$
300B	$S_1 p_1 (1 - c_1) t_1 S_2 S_{32} R_{12} q_{32} \lambda_2$
30A0	$S_1 p_1 (1 - c_1) t_1 S_2 S_{31} R_{11} p_{31} (1 - c_{31}) (1 - \lambda_1)$
30B0	$S_1 p_1 (1 - c_1) t_1 S_2 S_{32} R_{12} p_{32} (1 - c_{32}) (1 - \lambda_2)$
30AA	$S_1 p_1 (1 - c_1) t_1 S_2 S_{31} R_{11} p_{31} (1 - c_{31}) \lambda_1$
30BB	$S_1 p_1 (1 - c_1) t_1 S_2 S_{32} R_{12} p_{32} (1 - c_{32}) \lambda_2$
30a0	$S_1 p_1 (1 - c_1) t_1 S_2 S_{31} R_{11} p_{31} c_{31}$
30b0	$S_1 p_1 (1 - c_1) t_1 S_2 S_{32} R_{12} p_{32} c_{32}$

The counts for each capture history are multinomial, so the likelihood has a simple structure:

$$L \propto \prod_{\omega} \pi_{\omega}^{n_{\omega}}, \quad (2.4)$$

where n_{ω} is the number of records with capture history ω and π_{ω} is the probability of having capture history ω . The product in Equation (2.4) is more usefully expressed by grouping like factors from the cell probabilities. A dot, \cdot , indicates summation over all possible codes. For example, $n_{\cdot 100} = n_{0100} + n_{1100}$ is the number of capture histories with a 1 at the second juvenile site and a 0 at both of the adult sites, and $n_{0 \cdot A} = n_{000A} + n_{00AA} + n_{100A} + n_{10AA} +$

$n_{300A} + n_{30AA}$ is the number of capture histories with no detection at the second juvenile site and detection at the second adult site after one year at sea. Using the parameters from Table 2.2, the likelihood for this example is

$$\begin{aligned}
L \propto & S_1^{N-n_{0000}} p_1^{N-n_{0...}} (1-p_1)^{n_{0...}-n_{0000}} c_1^{n_{2000}} \\
& \times (1-c_1)^{n_{1...}+n_{30...}} t_1^{n_{30...}} (1-t_1)^{n_{1...}} S_2^{N-n_{.000}} p_2^{N-n_{.0...}} \\
& \times (1-p_2)^{n_{.0...}-n_{30...}-n_{.000}+n_{3000}} c_2^{n_{.200}} (1-c_2)^{n_{.1...}} S_{31}^{n_{...A}+n_{...0A}+n_{...a0}} \\
& \times p_{31}^{n_{...A}+n_{...a0}} (1-p_{31})^{n_{...0A}} c_{31}^{n_{...a0}} (1-c_{31})^{n_{...A}} S_{32}^{n_{...B}+n_{...0B}+n_{...b0}} \\
& \times p_{32}^{n_{...B}+n_{...b0}} (1-p_{32})^{n_{...0B}} c_{32}^{n_{...b0}} (1-c_{32})^{n_{...B}} \lambda_1^{n_{...A}} \lambda_2^{n_{...B}} \\
& \times R_{11}^{n_{30A}+n_{300A}+n_{30a0}} R_{12}^{n_{30B}+n_{300B}+n_{30b0}} \\
& \times \chi_0^{n_{0000}} \chi_1^{n_{1000}} \chi_2^{n_{1100}+n_{0100}} \chi_{1T}^{n_{3000}} (1-\lambda_1)^{n_{...A0}} (1-\lambda_2)^{n_{...B0}}.
\end{aligned} \tag{2.5}$$

The exponents in the likelihood comprise a sufficient statistic, which contains the minimal sufficient statistic. Not every exponent is included in the minimal sufficient statistic due to linear dependence among the exponents. Each exponent can be expressed in terms of summary statistics, listed in Table 2.5. For example, the exponent on S_1 is $N - n_{0000}$, the number of fish detected at any site after the initial release. The exponent on S_2 is $N - n_{.000}$, the number of fish detected at any site after the first juvenile site. Analogous parameters for the juvenile sites have analogous exponents; the same is true of adult sites and their parameters. For example, every exponent of a survival parameter is the number of fish detected somewhere after the previous site, while every exponent of a detection parameter is the number of fish detected at that site. There are many ways of classifying the summary statistics, but a logical classification is given in Table 2.5. These statistics are naturally defined using the “ m -array” from Burnham et al. (1987), modified for multiple adult age classes.

Table 2.5: Summary statistics for study design with two juvenile detection sites, two adult detection sites, two adult age classes, censoring at all but last adult site, and transportation from first juvenile site.

Statistic	Formula	Definition
a_1	$N - n_{0...}$	Number detected at site 1
a_2	$N - n_{.0..}$	Number detected at site 2
a_{31}	$n_{..A.} + n_{..a0}$	Number of year-1 adults detected at site 3
a_{32}	$n_{..B.} + n_{..b0}$	Number of year-2 adults detected at site 3
a_{41}	$n_{...A}$	Number of year-1 adults detected at site 4
a_{42}	$n_{...B}$	Number of year-2 adults detected at site 4
b_0	$N - n_{0000}$	Number of fish from initial release detected at any of the sites
b_1	$n_{1...} - n_{1000}$	Number detected at site 1, re-released to the river, and detected again at a later site
b_2	$n_{.1..} - n_{.100}$	Number detected at site 2, re-released to the river, and detected again at a later site
b_{1T}	$n_{30..} - n_{3000}$	Number detected and transported from site 1 and detected again at a later (adult) site
b_{01}	$n_{00A.} + n_{000A} + n_{00a0}$	Number first detected as a year-1 adult
b_{02}	$n_{00B.} + n_{000B} + n_{00b0}$	Number first detected as a year-2 adult
b_{11}	$n_{10A.} + n_{100A} + n_{10a0}$	Number detected and re-released to the river at site 1, and next detected as a year-1 adult
b_{12}	$n_{10B.} + n_{100B} + n_{10b0}$	Number detected and re-released to the river at site 1, and next detected as a year-2 adult
b_{21}	$n_{.1A.} + n_{.10A} + n_{.1a0}$	Number detected and re-released to the river at site 2, and next detected as a year-1 adult
b_{22}	$n_{.1B.} + n_{.10B} + n_{.1b0}$	Number detected and re-released to the river at site 2, and next detected as a year-2 adult
b_{31}	$n_{..AA}$	Number detected and re-released to the river at site 3, and next detected as a year-1 adult
b_{32}	$n_{..BB}$	Number detected and re-released to the river at site 3, and next detected as a year-2 adult
b_{11T}	$n_{30A.} + n_{300A} + n_{30a0}$	Number transported from site 1 and detected again as a year-1 adult
b_{12T}	$n_{30B.} + n_{300B} + n_{30b0}$	Number transported from site 1 and detected again as a year-2 adult
d_1	n_{2000}	Number censored at site 1
d_2	$n_{.200}$	Number censored at site 2
d_{31}	$n_{..a0}$	Number of year-1 adults censored at site 3
d_{32}	$n_{..b0}$	Number of year-2 adults censored at site 3
h_1	$n_{30..}$	Number transported from site 1
g_0	b_0	Number detected after initial release

Table 2.5 continued

Statistic	Formula	Definition
g_1	$g_0 + b_1 + b_{1T} - a_1$	Number detected after site 1
g_{21}	$b_{01} + b_{11} + b_{21} + b_{11T}$	Number of year-1 adults detected after site 2
g_{22}	$b_{02} + b_{12} + b_{22} + b_{12T}$	Number of year-2 adults detected after site 2
g_{31}	$g_{21} + b_{31} - a_{31}$	Number of year-1 adults detected after site 3
g_{32}	$g_{22} + b_{32} - a_{32}$	Number of year-2 adults detected after site 3

Burnham et al. (1987) use the m -array to organize release-recapture data from fish survival studies in the same type of system as ours, i.e. migration past dams. Their monograph specifically compares treatment groups, but the m -array approach can be used for single release groups, as well. Rather than listing out the complete capture histories, the m -array is a summary of data that still enables us to fit the likelihood in Equation (2.4). The m -array is an array whose rows correspond to site-specific releases (or re-releases) and whose columns correspond to site-specific recaptures or detections. Rows may be subdivided to represent different treatment groups. For example, transport sites have two rows: one for the in-river release group and one for the transport group. Figure 2.3 shows the structure of the m -array for the study design in our example, with all adult age classes collapsed to one. The first entry in each row is the size of the release group from the site in the corresponding column. Other row entries indicate the number of that release that were *next* seen at the site corresponding to their column. These entries are of the form m_{ik} (m_{ikT}), indicating the number released to the river (transported) from site i that were next seen at site k . This m notation gives the structure its name. Thus, the initial release and its subsequent detections are in the first row of the m -array in Figure 2.3, where N is the initial release size, m_{01} is the number seen at the first juvenile site, m_{02} is the number not seen at site 1 but seen at site 2, m_{03} is the number not seen as juveniles but seen at the first adult site, etc. The row total of detections m_{0k} ($k = 1, 2, 3$, or 4) is the number of the initial release that were detected at any site. No smolts are transported from the initial release, so that release has only one row. Juvenile sites with transportation have two releases, or two rows: the first is the fish released to the river, and the second is the transported fish. Column totals of detections (m_{ik} or m_{ikT} values for column i) are the numbers detected at each

site. Any particular fish may appear in more than one row, but within a row, it appears in at most one column after the release. For example, consider a fish with detection history “3011,” where 1 in an adult column indicates detection regardless of age class. Figure 2.4 shows the contributions of this fish to the m -array; releases including the fish are circled, and detections of the fish are shaded.

Multiple adult age classes requires subdividing columns corresponding to adult sites. Figure 2.5 shows this for the two-age class example. Not all boxes in an adult release row are possible; for example, age-1 fish released from site 3 may be found in the age-1 column of site 4, but not in the age-2 column of that site. The age-structured m -array is similar to the multiple-strata m -array in Brownie et al. (1993).

Other than the m_{ik} and m_{ikT} statistics, the statistics in the m -arrays in Figures 2.3, 2.4, and 2.5 are the summary statistics listed in Table 2.5: the m -array and the summary statistics give the same information. There are several types of summary statistics. The statistic a_i is the number of fish detected at site i ; the subscript i includes age class information for adult sites. The a statistics correspond to column totals in the m -array. All b statistics indicate the number of fish detected at some site, re-released either to the river or to a transportation barge or truck, and detected again later; some involve transportation and/or age classes. In general, b statistics correspond to rows or parts of rows in the m -array. The statistic b_i is the number of fish detected at site i , re-released to the river (i.e., not transported or censored), and detected at least once at a later site; $i = 0$ indicates the initial release, so b_0 is the number of fish detected at least once in the study. Similarly, b_{iT} is the number of fish transported from site i that are detected at a later (adult) site. The statistic b_{ij} is the number of fish detected at site i , re-released to the river, and *next* detected as an age- j adult. The statistic b_{ijT} is the analogous number for fish transported from site i . The d and h statistics refer to the number of fish censored and transported, respectively, at a particular site. These statistics modify the number detected at a site (a) to give the in-river (non-transported) release size from that site. Finally, the g statistics give the number of fish detected at least once *after* a particular site, regardless of the number actually seen at the site; these statistics are defined recursively using the a and b statistics, and correspond to blocks or parts of blocks in the m -array. Figures 2.3 and 2.5 show the

Site	Release	Juvenile Sites		Adult Sites		Number recaptured
		Site 1	Site 2	Site 3	Site 4	
Initial	N	m_{01}	m_{02}	m_{03}	m_{04}	b_0
Site 1	$a_1-d_1-h_1$		m_{12}	m_{13}	m_{14}	b_1
Site 1-Tr	h_1			m_{13T}	m_{14T}	b_{1T}
Site 2	a_2-d_2			m_{23}	m_{24}	b_2
Site 3	a_3-d_3				m_{34}	b_3
Number detected		a_1	a_2	a_3	a_4	
Number censored		d_1	d_2	d_3	d_4	

Figure 2.3: The m -array for the study design with two juvenile detection sites (sites 1 and 2), two adult detection sites (sites 3 and 4), censoring possible at all but the final adult site, and transportation possible from the first juvenile site. Age class of adults is ignored. The first column identifies the release site for the row. Transport sites have two release rows: row 1 is the non-transported group, and row 2 is the transport group (labeled “-Tr”). The initial release has size N and is made at site 0. The number m_{ik} is the number of individuals released to the river at site i that are next detected at site k ; m_{ikT} is the number of individuals transported from juvenile site i that are next detected at adult site k . The statistic d_i is the number censored at site i , and h_i is the number transported from site i . Row totals (b_i , b_{iT}) and column totals (a_i) are of the m_{ik} and m_{ikT} statistics.

Site	Release	Juvenile Sites		Adult Sites	
		Site 1	Site 2	Site 3	Site 4
Initial	N	m_{01}	m_{02}	m_{03}	m_{04}
Site 1	$m_{01}-d_1-h_1$		m_{12}	m_{13}	m_{14}
Site 1-Tr	h_1			m_{13T}	m_{14T}
Site 2	a_2-d_2			m_{23}	m_{24}
Site 3	a_3-d_3				m_{34}

Figure 2.4: Contribution of capture history 3011 to m -array in Figure 2.3. Releases containing individuals with capture history 3011 are circled. Recaptures of 3011 individuals are shaded.

Site (age class)	Release	Juvenile Sites		Adult Sites (age class)				Number recaptured
		Site 1	Site 2	Site 3		Site 4		
				(1)	(2)	(1)	(2)	
Initial	N	m_{01}	m_{02}	$m_{0,31}$	$m_{0,32}$	$m_{0,41}$	$m_{0,42}$	b_0
Site 1	$a_1-d_1-h_1$		m_{12}	$m_{1,31}$	$m_{1,32}$	$m_{1,41}$	$m_{1,42}$	b_1
Site 1-Tr	h_1			$m_{1,31T}$	$m_{1,32T}$	$m_{1,41T}$	$m_{1,42T}$	b_{1T}
Site 2	a_2-d_2			$m_{2,31}$	$m_{2,32}$	$m_{2,41}$	$m_{2,42}$	b_2
Site 3 (1)	$a_{31}-d_{31}$					$m_{31,41}$		b_{31}
Site 3 (2)	$a_{32}-d_{32}$						$m_{32,42}$	b_{32}
Number detected		a_1	a_2	a_{31}	a_{32}	a_{41}	a_{42}	
Number censored		d_1	d_2	d_{31}	d_{32}	d_{41}	d_{42}	

Figure 2.5: The m -array for the study design with two juvenile detection sites (sites 1 and 2), two adult detection sites (sites 3 and 4), two adult age classes (1 and 2), censoring possible at all but the final adult site, and transportation possible from the first juvenile site. The first column identifies the release site for the row. Transport sites have two release rows: row 1 is the non-transported group, and row 2 is the transport group (labeled “-Tr”). The initial release has size N and is made at site 0. The statistic m_{ik} is the number of individuals released to the river at juvenile site i that are next detected at juvenile site k ; $m_{i,kjT}$ is the number of individuals transported from juvenile site i that are next detected at adult site k as an age- j individual; $m_{i,kj}$ ($m_{ij,kj}$) is the number of individuals released to the river at juvenile site i (adult site i in year j) that are next detected as age- j individuals at adult site k . The statistics d_i and d_{ij} are the numbers censored at juvenile site i and adult site i in year j , respectively; h_i is the number transported from site i . Row totals (b_i , b_{iT} , b_{ij}) and column totals (a_i , a_{ij}) are of the m_{ik} , $m_{i,kj}$ and $m_{i,kjT}$ statistics.

relationship between the m -array and the a , b , d , and h statistics; Figure 2.6 shows the relationship between the m -array and the g statistics.

The likelihood can be re-expressed in terms of the summary statistics:

$$\begin{aligned}
L \propto & S_1^{g_0} p_1^{a_1} (1 - p_1)^{b_0 - a_1} c_1^{d_1} (1 - c_1)^{a_1 - d_1} t_1^{h_1} (1 - t_1)^{a_1 - d_1 - h_1} \\
& \times S_2^{g_1} p_2^{a_2} (1 - p_2)^{g_1 - a_1 - b_{1T}} c_2^{d_2} (1 - c_2)^{a_2 - d_2} S_{31}^{g_{21}} p_{31}^{a_{31}} \\
& \times (1 - p_{31})^{g_{21} - a_{31}} c_{31}^{d_{31}} (1 - c_{31})^{a_{31} - d_{31}} S_{32}^{g_{22}} p_{32}^{a_{32}} \\
& \times (1 - p_{32})^{g_{22} - a_{32}} c_{32}^{d_{32}} (1 - c_{32})^{a_{32} - d_{32}} \lambda_1^{g_{31}} \lambda_2^{g_{32}} \\
& \times R_{11}^{b_{11T}} R_{12}^{b_{12T}} \chi_0^{N - b_0} \chi_1^{a_1 - d_1 - h_1 - b_1} \chi_2^{a_2 - d_2 - b_2} \chi_{1T}^{h_1 - b_{1T}} \\
& \times (1 - \lambda_1)^{a_{31} - d_{31} - b_{31}} (1 - \lambda_2)^{a_{32} - d_{32} - b_{32}}.
\end{aligned} \tag{2.6}$$

The set of summary statistics in Table 2.5 contains the minimal sufficient statistics, as well as some extraneous statistics. We see from Equation (2.6) and Table 2.5 that we do not need the separate b_{i1} and b_{i2} statistics for $i = 0, 1$, and 2 ; rather, we need their sums $b_{01} + b_{11} + b_{21}$ and $b_{02} + b_{12} + b_{22}$, together with b_{31} and b_{32} . Also, the g statistics can be written in terms of the a and b statistics. This leaves us with 17 sufficient statistics, comprising the minimal sufficient statistic and given in Table 2.6.

Table 2.6: Minimal sufficient statistics for study design with two juvenile detection sites, two adult detection sites, two adult age classes, censoring at all but last adult site, and transportation from first juvenile site.

Statistic	Formula	Definition
a_1	$N - n_{0..}$	Number detected at site 1
a_2	$N - n_{0..}$	Number detected at site 2
a_{31}	$n_{..A.} + n_{..a0}$	Number of year-1 adults detected at site 3
a_{32}	$n_{..B.} + n_{..b0}$	Number of year-2 adults detected at site 3
b_0	$N - n_{0000}$	Number of fish from initial release detected at any of the sites
b_1	$n_{1...} - n_{1000}$	Number detected at site 1, re-released to the river, and detected again at a later site
b_2	$n_{.1..} - n_{.100}$	Number detected at site 2, re-released to the river, and detected again at a later site

Table 2.6 continued

Statistic	Formula	Definition
$\sum_{i=0}^2 b_{i1}$	$n_{\dots A} + n_{\dots 0A} + n_{\dots a0}$	Number of in-river fish detected as adults in year 1
b_{31}	$n_{\dots AA}$	Number detected and re-released to the river at site 3, and next detected as a year-1 adult
b_{32}	$n_{\dots BB}$	Number detected and re-released to the river at site 3, and next detected as a year-2 adult
b_{11T}	$n_{30A} + n_{300A} + n_{30a0}$	Number transported from site 1 and detected again as a year-1 adult
b_{12T}	$n_{30B} + n_{300B} + n_{30b0}$	Number transported from site 1 and detected again as a year-2 adult
d_1	n_{2000}	Number censored at site 1
d_2	$n_{\dots 200}$	Number censored at site 2
d_{31}	$n_{\dots a0}$	Number of year-1 adults censored at site 3
d_{32}	$n_{\dots b0}$	Number of year-2 adults censored at site 3
h_1	$n_{30\dots}$	Number transported from site 1

2.3.3 Generalization

It is straightforward to generalize the parameters, statistics, and likelihood of the specific example above to develop a general model for any number of juvenile detection sites, adult detection sites, censoring and transporting sites, and adult age classes. Let there be v juvenile detection sites, with censoring and transportation possible at each juvenile site; note that the final juvenile site may not be BON, so transportation is possible from that site. Also, let there be u adult detection sites and w adult age classes, with censoring possible at all but the final adult site. The estimable parameters are given in Table 2.7.

Site (age class)	Release	Juvenile Sites		Adult Sites (age class)			
		Site 1	Site 2	Site 3		Site 4	
				(1)	(2)	(1)	(2)
Initial	N	$m_{0,1}$	$m_{0,2}$	$m_{0,31}$	$m_{0,32}$	$m_{0,41}$	$m_{0,42}$
Site 1	$a_1-d_1-h_1$		m_{12}	$m_{1,31}$	$m_{1,32}$	$m_{1,41}$	$m_{1,42}$
Site 1-Tr	h1			$m_{1,31T}$	$m_{1,32T}$	$m_{1,41T}$	$m_{1,42T}$
Site 2	a_2-d_2			$m_{2,31}$	$m_{2,32}$	$m_{2,41}$	$m_{2,42}$
Site 3 (1)	$a_{31}-d_{31}$					$m_{3,41}$	
Site 3 (2)	$a_{32}-d_{32}$						$m_{32,42}$

Figure 2.6: Relationship between m -array and g statistics. The m -array shown here is for a study design with two juvenile detection sites (sites 1 and 2), two adult detection sites (sites 3 and 4), two adult age classes (1 and 2), censoring possible at all but the final adult site, and transportation possible from the first juvenile site. The statistics g_0 and g_{21} are indicated as examples. Recaptures contributing to g_0 are shaded from lower left to upper right. Recaptures contributing to g_{21} are shaded from upper left to lower right. Recaptures contributing to both g_0 and g_{21} are cross-hatched.

The “last detection” parameters χ_i and χ_{ij} are defined as follows:

$$\chi_i = \begin{cases} 1 - S_{i+1} + S_{i+1}q_{i+1}\chi_{i+1} & \text{for } i = 0, \dots, v-1; \\ 1 - \sum_{j=1}^w S_{v+1,j} + \sum_{j=1}^w S_{v+1,j}q_{v+1,j}\chi_{v+1,j} & \text{for } i = v; \end{cases}$$

$$\chi_{iT} = 1 - S_{i+1} \cdots S_v \sum_{j=1}^w S_{v+1,j} R_{ij} + S_{i+1} \cdots S_v \sum_{j=1}^w S_{v+1,j} R_{ij} q_{v+1,j} \chi_{v+1,j} \quad \text{for } i = 1, \dots, v;$$

$$\chi_{ij} = \begin{cases} 1 - S_{i+1,j} + S_{i+1,j}q_{i+1,j}\chi_{i+1,j} & \text{for } i = v+1, \dots, v+u-2; \\ 1 - \lambda_j & \text{for } i = v+u-1; \end{cases}$$

where

$$q_i = 1 - p_i, \text{ for } i = 1, \dots, v;$$

$$q_{ij} = 1 - p_{ij}, \text{ for } i = v+1, \dots, v+u-1; j = 1, \dots, w.$$

Table 2.7: Estimable parameters for generalized model.

Parameter	Definition
S_1	Probability of survival from release point to first detection site;
S_i	Conditional probability of survival from detection site $i-1$ to detection site i , $i = 2, \dots, v$ for in-river fish;
$S_{v+1,j}$	Conditional joint probability of surviving from site v to site $v+1$ and returning to site $v+1$ after j years in the ocean; $j = 1, \dots, w$;
S_{ij}	Conditional probability of surviving from site $i-1$ to site i for adult fish that matured after j years in the ocean; $i = v+2, \dots, v+u-1$; $j = 1, \dots, w$;
p_i	Conditional probability of detection at detection site i , given survival to site i inriver; $i = 1, \dots, v$; $q_i = 1 - p_i$;
p_{ij}	Conditional probability of detection at site i in year j , given survival to site i ; $i = v+1, \dots, v+u-1$; $j = 1, \dots, w$; $q_{ij} = 1 - p_{ij}$;
λ_j	Conditional probability of surviving from site $v+u-1$ to site $v+u$ for adult fish returning after j years in the ocean; $j = 1, \dots, w$;
c_i	Conditional probability of being censored at site i , given detection at that site, $i = 1, \dots, v$;
c_{ij}	Conditional probability of being censored at site i for adult returning after j years in the ocean, given detection at site i ,

Table 2.7 continued

Parameter	Definition
t_i	$i = v + 1, \dots, v + u - 1; j = 1, \dots, w;$ Conditional probability of being transported from site i , given detection at that site, and no censoring, $i = 1, \dots, v;$
R_{ij}	Transport-Benefit-Ratio (TBR) for fish transported from site i and detected as an adult after j years in the ocean; $j = 1, \dots, w;$
χ_i	Probability of a non-transported, non-censored juvenile not being detected after site i , conditional upon reaching site i ; $i = 1, \dots, v;$
χ_{iT}	Probability of a juvenile transported at site i not being detected after site i ; $i = 1, \dots, v;$
χ_{ij}	Probability of an age- j adult not being detected after site i , conditional upon reaching site i and not being censored there; $i = v + 1, \dots, v + u - 1; j = 1, \dots, w.$

Summary statistics and minimal sufficient statistics are given in Tables 2.8 and 2.9, respectively. The g_i and g_{ij} statistics can be expressed in terms of the other summary statistics as follows:

$$g_i = \begin{cases} b_0 & \text{for } i = 0; \\ g_{i-1} + b_i + b_{iT} - a_i & \text{for } i = 1, \dots, v - 1; \end{cases} \quad (2.7)$$

$$g_{ij} = \begin{cases} \sum_{k=0}^v b_{kj} + \sum_{k=1}^v b_{kjT} & \text{for } i = v; j = 1, \dots, w; \\ g_{i-1,j} + b_{ij} - a_{ij} & \text{for } i = v + 1, \dots, v + u - 1; j = 1, \dots, w. \end{cases} \quad (2.8)$$

The generalized likelihood is given in Equation (2.9). Although censoring and transportation are allowed at all suitable sites, the number of minimal sufficient statistics and the number of estimable parameters depend on the number of sites for which there actually is censoring or transportation. The model is full rank, with an equal number of parameters and minimal sufficient statistics: $2v + v_c + v_t + (2u - 1)w + \sum_{i=1}^v I_{iT}w_{iT} + \sum_{i=v+1}^{v+u-1} I_{ic}w_{ic}$, where v_c is the number of juvenile detection sites with censoring; v_t is the number of juvenile sites with transportation ($0 < t_i < 1$), I_{iT} is an indicator function that is 1 if and only if site i is a transportation site; w_{iT} is the number of age classes of adults returning from the transport group from site i ; I_{ic} is an indication function that is 1 if and only if site i has censoring (of

adults); and w_{ic} is the number of age classes that are censored at site i . Because the number of parameters equals the number of minimal sufficient statistics, the maximum likelihood estimators can be found either analytically or numerically. If two or more parameters are constrained to be equal, the maximum likelihood estimators must be found numerically. The generalized likelihood is

$$\begin{aligned}
L \propto & \chi_0^{N-b_0} \prod_{i=1}^v \left\{ S_i^{g_{i-1}} p_i^{a_i} q_i^{g_{i-1}-a_i-\sum_{k=1}^{i-1} b_{kT}} c_i^{d_i} (1-c_i)^{a_i-d_i} t_i^{h_i} \right. \\
& \times (1-t_i)^{a_i-d_i-h_i} \left(\prod_{j=1}^w R_{ij}^{b_{ijT}} \right) \chi_i^{a_i-d_i-h_i-b_i} \chi_{iT}^{h_i-b_{iT}} \left. \right\} \prod_{j=1}^w \lambda_j^{g_{v+u-1,j}} \\
& \times \prod_{j=1}^w \left[\prod_{i=v+1}^{v+u-1} \left\{ S_{ij}^{g_{i-1,j}} p_{ij}^{a_{ij}} q_{ij}^{g_{i-1,j}-a_{ij}} c_{ij}^{d_{ij}} (1-c_{ij})^{a_{ij}-d_{ij}} \chi_{ij}^{a_{ij}-d_{ij}-b_{ij}} \right\} \right]. \quad (2.9)
\end{aligned}$$

Throughout this work, interpret as 1 any product of the form $\prod_{i=v+1}^v \theta_i$, whose lower index limit is greater than its upper index limit.

Table 2.8: Summary statistics for generalized model.

Statistic	Definition
a_i	Number detected at site i , $i = 1, \dots, v$;
a_{ij}	Number of (ocean) age j adults detected at site i ; $i = v+1, \dots, v+u$; $j = 1, \dots, w$;
b_i	Number detected at site i , re-released to the river, and detected again at a later site; $i = 0, \dots, v$;
b_{iT}	Number detected and transported from site i and detected again at a later (adult) site; $i = 1, \dots, v$;
b_{ij}	Number detected and re-released to the river at site i , and detected again at a later site for the first time in year (or ocean age) j ; $i = 0, \dots, v+u-1$; $j = 1, \dots, w$;
b_{ijT}	Number transported from site i and detected at an adult site for the first time in year j ; $i = 1, \dots, v$; $j = 1, \dots, w$;
d_i	Number censored at site i ; $i = 1, \dots, v$
d_{ij}	Number of ocean-age j fish censored at site i ; $i = v+1, \dots, v+u-1$; $j = 1, \dots, w$;
h_i	Number transported from site i ; $i = 1, \dots, v$;
g_i	Number detected after site i ; $i = 0, \dots, v-1$;
g_{ij}	Number detected after site i in year (or ocean age) j ; $i = v, \dots, v+u-1$; $j = 1, \dots, w$.

Table 2.9: Minimal sufficient statistics for generalized model.

Statistic	Definition
a_i	Number detected at site i , $i = 1, \dots, v$
a_{ij}	Number of (ocean) age j adults detected at site i ; $i = v + 1, \dots, v + u - 1$; $j = 1, \dots, w$
b_i	Number detected at site i , re-released to the river, and detected again at a later site; $i = 0, \dots, v$
$\sum_{i=0}^v b_{ij}$	Number detected as adults in year j ; $j = 1, \dots, w - 1$
b_{ij}	Number detected and re-released to the river at site i , and detected again at a later site for the first time in year (or ocean age) j ; $i = v + 1, \dots, v + u - 1$; $j = 1, \dots, w$
b_{ijT}	Number transported from site i and next detected at an adult site in year j ; $i = 1, \dots, v$; $j = 1, \dots, w$
d_i	Number censored at site i ; $i = 1, \dots, v$
d_{ij}	Number of ocean-age j fish censored at site i ; $i = v + 1, \dots, v + u - 1$; $j = 1, \dots, w$
h_i	Number transported from site i ; $i = 1, \dots, v$

For the full model, it is possible to use the method of moments to find the maximum likelihood estimators (MLEs), or to find initial values or seeds for parameters maximized numerically in a reduced model. Formulas for the MLEs for the generalized model are in Table 2.10. For data sets whose summary statistics have large values, it may be necessary to rewrite the MLE formulas to avoid multiplying very large numbers. Also, note that the MLEs for survival can be written in terms of the MLEs for detection. For example, if \hat{S}_i and \hat{p}_i are the MLEs for S_i and p_i ($i = 2, \dots, v$), respectively, then

$$\begin{aligned}
\hat{S}_i &= \frac{b_{i-1} \left\{ \left(\sum_{k=0}^{i-1} b_k - \sum_{k=1}^i a_k \right) (a_i - d_i - h_i) + a_i b_i \right\}}{b_i \left(\sum_{k=0}^{i-1} b_k - \sum_{k=1}^{i-1} a_k \right) (a_{i-1} - d_{i-1} - h_{i-1})} \\
&= \frac{b_{i-1} a_i}{\hat{p}_i \left(\sum_{k=0}^{i-1} b_k - \sum_{k=1}^{i-1} a_k \right) (a_{i-1} - d_{i-1} - h_{i-1})}.
\end{aligned}$$

Table 2.10: Maximum likelihood estimators (MLEs) for parameters in general study design with v juvenile detection sites, u adult detection sites, w adult ages, censoring at all but the last site, and transportation from all juvenile sites. The “ \hat{S}_k ” notation indicates the MLE of S_k .

Parameter	MLE	Appropriate Sites
S_1	$\frac{(b_{i-1}-a_i)(a_i-d_i-h_i)+a_i b_i}{N b_i}$	$i = 1$
S_i	$\frac{b_{i-1}}{b_i} \frac{(\sum_{k=0}^{i-1} b_k - \sum_{k=1}^i a_k)(a_i-d_i-h_i)+a_i b_i}{(\sum_{k=0}^{i-1} b_k - \sum_{k=1}^{i-1} a_k)(a_{i-1}-d_{i-1}-h_{i-1})}$	$i = 2, \dots, v$
p_i	$\frac{a_i b_i}{(\sum_{k=0}^{i-1} b_k - \sum_{k=1}^i a_k)(a_i-d_i-h_i)+a_i b_i}$	$i = 1, \dots, v$
c_i	d_i/a_i	$i = 1, \dots, v$
t_i	$h_i/(a_i - d_i)$	$i = 1, \dots, v$
R_{ij}	$\frac{b_{ij} T(a_v - d_v - h_v)(\sum_{k=0}^v b_k - \sum_{k=1}^v a_k)}{h_i b_v (\prod_{k=i+1}^v \hat{S}_k) (\sum_{k=0}^v b_{kj})}$	$i = 1, \dots, v$
$S_{v+1,j}$	$\frac{b_{i-1} \sum_{k=0}^{i-1} b_{kj}}{b_{i,j} g_{i-1,j}} \frac{(g_{i-1,j} - a_{i,j})(a_{i,j} - d_{i,j}) + a_{i,j} b_{i,j}}{(a_{i-1} - d_{i-1} - h_{i-1})(\sum_{k=0}^{i-1} b_k - \sum_{k=1}^{i-1} a_k)}$	$i = v + 1$
S_{ij}	$\frac{b_{i-1,j}}{b_{i,j}} \frac{(g_{i-1,j} - a_{i,j})(a_{i,j} - d_{i,j}) + a_{i,j} b_{i,j}}{g_{i-1,j} (a_{i-1,j} - d_{i-1,j})}$	$i = v + 2, \dots, v + u - 1$
p_{ij}	$\frac{a_{i,j} b_{i,j}}{(g_{i-1,j} - a_{i,j})(a_{i,j} - d_{i,j}) + a_{i,j} b_{i,j}}$	$i = v + 1, \dots, v + u - 1$
c_{ij}	$d_{i,j}/a_{i,j}$	$i = v + 1, \dots, v + u - 1$
λ_j	$\frac{b_{v+u-1,j}}{a_{v+u-1,j} - d_{v+u-1,j}}$	$i = v + u$

2.4 Quantities of Interest

The model presented here is useful for estimating survival over specific reaches. It also provides model-based methods of estimating certain derived quantities, such as transportation effect, adult return rates, and return age distribution. These quantities describe the life history of the stock being studied, and aid in management. Although the model must take into account censoring rates at dams as nuisance parameters, it is unnecessary to adjust for

these in defining derived quantities, unless the sampling program is of special interest. In general, interest is in the effect of the river and the hydrosystem on the fish; sampling is a temporary process that is not inherent to either the river or the hydrosystem, and can be ignored. In this section, I discuss model-based definitions of transportation effect, ocean survival or adult return rates, and the age distribution of returning adults. Estimators of these quantities can be found by replacing each parameter with its maximum likelihood estimator, and approximate standard errors can be found with the delta method (Seber, 1982, pp. 7-9).

One issue that arises in developing the performance measures listed above is in applying them to untagged fish. Researchers are typically interested in learning about the untagged population. One of the main assumptions of this model and all tagging studies is that tagged and untagged individuals act the same. Under this assumption, it is possible to apply to the untagged population the results of the tagging study, which are inherently for tagged individuals. Tagging smolts with PIT tags has been shown to have no significant effect on survival, assuming proper handling during tagging and release (Prentice et al., 1987, 1990a; Prentice, 1990; also see Skalski et al., 1998). Under the assumption of equal mixing, untagged smolts enter dam bypass systems and sampling rooms at the same rates as tagged smolts of a similar size. However, the transportation system works differently for tagged and untagged smolts, and the two groups are transported at different rates. Whereas tagged smolts in the bypass system are collected for transport at the rate t_i (typically < 1 for study purposes), generally all untagged smolts in the bypass system are collected for transport. This difference between transportation practices for tagged and untagged smolts prevents direct application of TBR and other transportation-related measures developed for tagged smolts to untagged smolts. Nevertheless, as long as it can be assumed that the basic model parameters other than t_i apply to untagged as well as tagged smolts, then it is possible to derive performance measures for the untagged population. In particular, the site- and age-specific model TBR parameters R_{ij} must be valid for both tagged and untagged smolts.

Let t_i^U represent the conditional transportation rate for untagged smolts at site i , i.e., the probability of transportation for an untagged smolt, given it has entered the bypass system of dam i . Tagging data cannot be used to estimate t_i^U , so it must be obtained

from independent information sources. Typically, with transportation operations running continuously throughout the migration season, all untagged bypassed smolts are transported at transport sites, so t_i^U is either 1 (i is a transport site) or 0 (i is not a transport site). Alternatively, transportation operations may be active only on alternate days, allowing some bypassed fish to be intentionally returned to the river at transport dams to provide alternative survival options. In such cases, the conditional transportation rate for untagged smolts, t_i^U , may be fixed to 0.5 at transport dams, or to another value depending on actual operations. In general, researchers must use records of dam and transportation operations to determine the appropriate value of t_i^U ; it cannot be estimated from tagging data.

Several of the performance measures for tagged smolts (defined below) depend on detection probabilities p_i . Untagged smolts are not detected. However, detection rates of tagged smolts within the bypass systems are typically assumed to be 100%, meaning that detection for tagged smolts is equivalent to entering the bypass system. Because tagged and untagged smolts use the bypass systems at the same rate, p_i may be considered to be the probability of a smolt (tagged or untagged) passing dam i via the bypass system, and $1 - p_i = q_i$ as the probability of a smolt passing via turbines or spillway. Using this interpretation of p_i and q_i , performance measures for untagged fish are derived from corresponding measures for tagged fish by replacing the conditional transportation rate parameters, t_i , for tagged fish with the analogous parameters, t_i^U , for untagged fish. Some measures (i.e., R_{ij} and R_i) do not depend on t_i , and so are valid for both tagged and untagged fish. The remaining measures are developed first for tagged fish and then for untagged fish. The direct inference of the “untagged” measures is to fish in the release group, had they been treated as untagged. Further inference to other fish is subjective, and is left to the individual researcher.

Measures of transportation effects are presented below, followed by measures of adult return rates, estimates of return age distributions, and estimates of inriver adult survival rates.

2.4.1 *Transportation Effects*

Transporting migrating smolts past dams is one of the primary strategies used to mitigate the negative effect of dams on smolt survival and adult return rates. Managers need to know if the transportation system actually improves adult return rates, and if so, by how much. Two reasonable management questions are (1) Is it worth transporting smolts from a particular dam? and (2) Is it worth transporting smolts from any dam? Generally, the main interest is in comparing adult return rates of fish with transportation to those without it.

Several issues arise in defining measures of transportation effects. The first issue is whether to treat a transport dam in isolation from the rest of the transportation system or in the context of that system. The Columbia River Basin includes multiple transport dams, so a fish that is not transported at one site (i) may be transported at a downriver site ($k > i$). If transportation from the downriver site (k) affects adult returns, then the effect of transportation at site i is confounded with the effect of transportation at site k , unless site i is viewed as if it were the only transport site in the hydrosystem. This “isolated” viewpoint is useful for assessing the effect of transportation from site i relative to no transportation system whatsoever. The “contextual” viewpoint, on the other hand, treats transport site i in the context of the entire transportation system, including possible transportation from downriver dams. This viewpoint is useful for dam managers who must decide whether or not to transport smolts who are in their bypass system. In general, the isolated and contextual viewpoints are the same for the final transport site, but differ for upriver sites. Both isolated and contextual site-specific measures of transportation effects are presented below.

The second issue in defining measures of transportation effects is whether to measure effects of transportation at individual sites, or to measure the overall effects of the entire transportation system. The site-specific viewpoint is useful for dam managers, and is used in the measures in Ward et al. (1997) and Sandford and Smith (2002). However, that viewpoint largely ignores the importance of the proportion of smolts that are transported at the various transport dams. It might be suspected that the overall efficacy of the entire transportation system depends on the proportion of smolts entering the transportation

system and the relative effect when it occurs. Therefore, a system-wide expression of TBR is needed to convey the overall effects of transportation on smolt-to-adult returns.

In summary, six alternative measures of transportation effects are presented: (1) Isolated Site- and Age-specific TBR for Tagged and Untagged Fish (R_{ij}), (2) Isolated Site-specific TBR for Tagged and Untagged Fish (R_i), (3) Contextual Site-specific TBR for Tagged Fish (RC_i), (4) Contextual Site-specific TBR for Untagged Fish (RC_i^U), (5) System-wide TBR for Tagged Fish (R_{sys}), and (6) System-wide TBR for Untagged Fish (R_{sys}^U). Additionally, an alternative system-wide estimator (R_{cond}) is presented for consideration.

2.4.1.1 Isolated Site- and Age-specific TBR for Tagged and Untagged Fish (R_{ij})

Transportation effects are incorporated into the model via the age- and site-specific TBR parameters, R_{ij} . The parameter R_{ij} is a relative measure of the effect of transportation from site i on rates of returns to the first adult site (site $v + 1$) for age- j adults. This parameter allows us to express the probability of a fish, transported at site i , returning to freshwater as an age- j adult in terms of the inriver survival parameters S_{i+1}, \dots, S_v and the ocean return probabilities $S_{v+1,j}$:

$$Pr[\text{Adult return in year } j \mid \text{Transported from site } i] = \left(\prod_{k=i+1}^v S_k \right) S_{v+1,j} R_{ij}. \quad (2.10)$$

In general, there are multiple transport sites in the Snake and Columbia rivers, with transportation possible at LGR, LGO and LMO on the Snake River, and at MCN on the Columbia River. Each fish is transported from at most one dam, and fish that are not transported from an upriver dam may be transported at a downriver dam. The model parameter R_{ij} , however, reflects the effect of transportation from only a single dam (i), ignoring the rest of the transportation system. Because R_{ij} compares the age- j return rates of site- i transport fish to the age- j return rates that would be experienced if there were no downstream transportation sites, R_{ij} isolates the effects of site- i transportation in the hydrosystem, and measures site- i transportation effects unconfounded by any actual downstream transportation. Thus, R_{ij} is an “isolated age- and site-specific TBR” parameter. The model assumptions imply that R_{ij} applies to both tagged and untagged individuals.

The maximum likelihood estimate (MLE) of R_{ij} , \hat{R}_{ij} , is found by fitting the likelihood in Equation (2.9) to data, or from the formulas in Table 2.10. An asymptotically consistent estimate of the variance of \hat{R}_{ij} comes directly from the variance-covariance matrix estimated in the numerical maximum likelihood routine.

2.4.1.2 Isolated Site-specific TBR for Tagged and Untagged Fish (R_i)

The TBR parameter R_{ij} is specific to age- j adults. The age-specific TBRs for site i may be combined to give an isolated, site-specific TBR, regardless of age at return. Call this isolated, site-specific value R_i . Define the event “Return(i, j)” as “return from site i to site $v + 1$ in age class j .” Then, R_i is defined as follows:

$$\begin{aligned}
 R_i &= \frac{\Pr[\text{Return from site } i \mid T_i]}{\Pr[\text{Return from site } i \mid \text{No transportation possible}]} \\
 &= \frac{\sum_{j=1}^w \Pr[\text{Return}(i, j) \mid T_i]}{\sum_{j=1}^w \Pr[\text{Return}(i, j) \mid \text{No transportation possible}]} \\
 &= \frac{S_{i+1} \cdots S_v \sum_{j=1}^w S_{v+1,j} R_{ij}}{S_{i+1} \cdots S_v \sum_{j=1}^w S_{v+1,j}} \\
 &= \frac{\sum_{j=1}^w S_{v+1,j} R_{ij}}{\sum_{j=1}^w S_{v+1,j}}. \tag{2.11}
 \end{aligned}$$

This measure of transportation effects accounts only for the effects of site- i transportation on adult return rates, ignoring the effects of any downstream transportation; thus, R_i is an isolated measure of transportation effects. The measure R_i is a weighted average of the age-specific R_{ij} , with weights equal to the year-specific ocean return probabilities. The model assumes that transportation does not affect adult inriver survival upstream of the first adult site (typically Bonneville Dam). Because R_i does not depend on the conditional transportation rate at site i , it applies to both tagged and untagged individuals.

The TBR R_i is a function of the model parameters $S_{v+1,1}, \dots, S_{v+1,w}$, and R_{i1}, \dots, R_{iw} . The MLE of R_i , \hat{R}_i , is found by replacing the parameters used in Equation (2.11) with their

MLEs, i.e.:

$$\hat{R}_i = \frac{\sum_{j=1}^w \hat{S}_{v+1,j} \hat{R}_{ij}}{\sum_{j=1}^w \hat{S}_{v+1,j}}. \quad (2.12)$$

Using the delta method (Seber 1982, pp. 7-9) of estimating variances, together with the estimated variance-covariance matrix from the numerical likelihood maximization routine, the asymptotic variance estimator of \hat{R}_i is expressible as

$$\begin{aligned} \widehat{Var}(\hat{R}_i) &= \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial R_i}{\partial S_{v+1,j}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial R_i}{\partial S_{v+1,m}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,j}, \hat{S}_{v+1,m}) \\ &\quad + \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial R_i}{\partial R_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial R_i}{\partial R_{im}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{ij}, \hat{R}_{im}) \\ &\quad + 2 \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial R_i}{\partial S_{v+1,j}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial R_i}{\partial R_{im}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,j}, \hat{R}_{im}), \end{aligned} \quad (2.13)$$

where $\hat{\theta}$ is the MLE of the vector of model parameters used in calculating \hat{R}_i , and where the partial derivatives are:

$$\begin{aligned} \frac{\partial R_i}{\partial S_{v+1,j}} &= \frac{R_{ij} - R_i}{\sum_{m=1}^w S_{v+1,m}}; \\ \frac{\partial R_i}{\partial R_{ij}} &= \frac{S_{v+1,j}}{\sum_{m=1}^w S_{v+1,m}}. \end{aligned} \quad (2.14)$$

This gives the estimated variance of \hat{R}_i as

$$\widehat{Var}(\hat{R}_i) = \frac{\sum_{j=1}^w \sum_{m=1}^w \Psi_{im}}{\left(\sum_{m=1}^w \hat{S}_{v+1,m} \right)^2},$$

where

$$\begin{aligned} \Psi_{im} &= (\hat{R}_{ij} - \hat{R}_i)(\hat{R}_{im} - \hat{R}_i) \widehat{Cov}(\hat{S}_{v+1,j}, \hat{S}_{v+1,m}) + \hat{S}_{v+1,j} \hat{S}_{v+1,m} \widehat{Cov}(\hat{R}_{ij}, \hat{R}_{im}) \\ &\quad + 2(\hat{R}_{ij} - \hat{R}_i) \hat{S}_{v+1,m} \widehat{Cov}(\hat{S}_{v+1,j}, \hat{R}_{im}). \end{aligned}$$

Recall that the covariance a random variable, X , with itself is simply its variance:

$$\text{Cov}(X, X) = \text{Var}(X).$$

2.4.1.3 Contextual Site-specific TBR for Tagged Fish (RC_i)

The measures R_{ij} and R_i are isolated TBRs, viewing site i as if it were the only transportation site in the hydrosystem. They are useful for assessing the effect of transportation from site i relative to no transportation whatsoever. However, because the transportation system generally includes transportation from multiple sites, fish that are not transported from site i may be transported from a downriver site. A measure of site i 's transportation effects that takes into account downstream transport sites may be useful for dam managers who need to know if they should transport a fish entrained in their bypass system. Let RC_i be such a contextual site-specific TBR for site i , where

$$RC_i = \frac{\text{Pr}[\text{Adult return} \mid \text{Transported from site } i]}{\text{Pr}[\text{Adult return} \mid \text{Pass site } i \text{ inriver}]}$$

The measure RC_i is the ratio of the adult return rate (to site $v + 1$) of site- i transport fish (treatment group) to that of fish who survive to site i , but who are not transported there (control group). Fish in the control group for RC_i may be transported downriver, or they may migrate wholly inriver. Before deriving an expression for RC_i , let us define some notation. The event T_i is “transported from site i ,” and the event “not T_i ” is “pass site i inriver,” both conditional on surviving to site i . Fish who pass a site inriver pass either via the turbines or spillway (so are undetected), or are bypassed (detected) but not transported. Recall that detection is equivalent to being bypassed. Then the numerator of RC_i can be expressed using the isolated TBR, R_i :

$$\begin{aligned} \text{Pr}[\text{Adult return} \mid \text{Transported from site } i] &= \sum_{j=1}^w \text{Pr}[\text{Return}(i, j) \mid T_i] \\ &= \prod_{k=i+1}^v S_k R_i \sum_{j=1}^w S_{v+1, j}. \end{aligned} \quad (2.15)$$

The denominator of RC_{ij} is

$$\begin{aligned}
& \sum_{j=1}^w Pr[\text{Return}(i, j) \mid \text{not } T_i] \\
&= \sum_{j=1}^w \left(Pr[T_{k>i}, \text{Return}(i, j) \mid \text{not } T_i] + Pr[\text{Never transp.}, \text{Return}(i, j) \mid \text{not } T_i] \right) \\
&= \sum_{j=1}^w \left(\sum_{k=i+1}^v [S_k p_k t_k S_{k+1} \cdots S_v S_{v+1,j} R_{kj} \prod_{l=i+1}^{k-1} S_l z_l] + S_{i+1} z_{i+1} \cdots S_v z_v S_{v+1,j} \right) \\
&= \sum_{j=1}^w \left(S_{i+1} \cdots S_v S_{v+1,j} \left[\sum_{k=i+1}^v (p_k t_k R_{kj} \prod_{l=i+1}^{k-1} z_l) + z_{i+1} \cdots z_v \right] \right),
\end{aligned}$$

where $z_k = 1 - p_k t_k$ is the probability of passing site k without being transported at that site, conditional upon reaching it. Interpret as 1 any product whose upper limit is greater than its lower limit. For example, $\prod_{l=i+1}^i z_l = 1$. Then RC_i is

$$\begin{aligned}
RC_i &= \frac{S_{i+1} \cdots S_v R_i \sum_{j=1}^w S_{v+1,j}}{\sum_{j=1}^w \left[S_{i+1} \cdots S_v S_{v+1,j} \left\{ \sum_{k=i+1}^v (p_k t_k R_{kj} \prod_{l=i+1}^{k-1} z_l) + (\prod_{l=i+1}^v z_l) \right\} \right]} \\
&= \frac{R_i \sum_{j=1}^w S_{v+1,j}}{\sum_{k=i+1}^v (p_k t_k R_k \sum_{j=1}^w S_{v+1,j} \prod_{l=i+1}^{k-1} z_l) + (\prod_{l=i+1}^v z_l) \sum_{j=1}^w S_{v+1,j}} \\
&= \frac{R_i}{\sum_{k=i+1}^v (p_k t_k R_k \prod_{l=i+1}^{k-1} z_l) + \prod_{l=i+1}^v z_l}. \tag{2.16}
\end{aligned}$$

The TBR measure RC_i is the isolated site-specific TBR for site i , R_i , divided by the overall effect of the downriver transportation system on return rates from site i (c.f. R_{sys} below).

Replacing the numerator of Equation (2.16) and the R_k in the denominator of Equation (2.16) with Equation (2.11), it is apparent that RC_i is a function of the parameters $S_{v+1,j}$ ($j = 1, \dots, w$), R_{kj} , ($k = i, \dots, v$; $j = 1, \dots, w$), p_k ($k = i + 1, \dots, v$), and t_k ($k = i + 1, \dots, v$). Because RC_i depends on the conditional transportation rates t_k , it is valid only for tagged individuals. The estimated variance, based on the delta method, is a sum of the covariances of the MLEs of these parameters. From Equation (2.9), it is apparent that \hat{t}_i is independent of the other MLEs, i.e., $Cov(\hat{t}_i, \hat{\alpha}) = 0$ for any other parameter α .

Thus, the estimator of the variance of \widehat{RC}_i is

$$\begin{aligned}
\widehat{Var}(\widehat{RC}_i) = & \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial RC_i}{\partial S_{v+1,j}} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial RC_i}{\partial S_{v+1,m}} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{S}_{v+1,m}) \\
& + \sum_{k=i}^v \sum_{y=i}^v \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial RC_i}{\partial R_{kj}} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial RC_i}{\partial R_{ym}} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{R}_{kj}, \widehat{R}_{ym}) \\
& + \sum_{k=i+1}^v \sum_{y=i+1}^v \left(\frac{\partial RC_i}{\partial p_k} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial RC_i}{\partial p_y} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{p}_k, \widehat{p}_y) \\
& + \sum_{k=i+1}^v \left(\frac{\partial RC_i}{\partial t_k} \Big|_{\widehat{\theta}} \right)^2 \widehat{Var}(\widehat{t}_k) \\
& + 2 \sum_{j=1}^w \sum_{k=i}^v \sum_{m=1}^w \left(\frac{\partial RC_i}{\partial S_{v+1,j}} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial RC_i}{\partial R_{km}} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{R}_{km}) \\
& + 2 \sum_{j=1}^w \sum_{y=i+1}^v \left(\frac{\partial RC_i}{\partial S_{v+1,j}} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial RC_i}{\partial p_y} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{p}_y) \\
& + 2 \sum_{k=i}^v \sum_{j=1}^w \sum_{y=i+1}^v \left(\frac{\partial RC_i}{\partial R_{kj}} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial RC_i}{\partial p_y} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{R}_{kj}, \widehat{p}_y), \tag{2.17}
\end{aligned}$$

where $\widehat{\theta}$ is the MLE of the vector of model parameters used in calculating \widehat{RC}_i . The necessary partial derivatives are

$$\begin{aligned}
\frac{\partial RC_i}{\partial S_{v+1,j}} &= \frac{RC_i}{R_i \sum_{m=1}^w S_{v+1,m}} \gamma_{ij}, & j = 1, \dots, w; \\
\frac{\partial RC_i}{\partial R_{ij}} &= \frac{RC_i S_{v+1,j}}{R_i \sum_{m=1}^w S_{v+1,m}}, & j = 1, \dots, w; \\
\frac{\partial RC_i}{\partial R_{kj}} &= \frac{-RC_i^2 p_k t_k \left\{ \prod_{l=i+1}^{k-1} (1 - p_l t_l) \right\} S_{v+1,j}}{R_i \sum_{m=1}^w S_{v+1,m}}, & k = i+1, \dots, v; j = 1, \dots, w; \\
\frac{\partial RC_i}{\partial p_k} &= \frac{t_k R_k (1 - RC_k) RC_i^2 \prod_{l=i+1}^{k-1} (1 - p_l t_l)}{RC_k R_i}, & k = i+1, \dots, v; \\
\frac{\partial RC_i}{\partial t_k} &= \frac{p_k R_k (1 - RC_k) RC_i^2 \prod_{l=i+1}^{k-1} (1 - p_l t_l)}{RC_k R_i}, & k = i+1, \dots, v; \tag{2.18}
\end{aligned}$$

where, for $i = 1, \dots, v$ and $j = 1, \dots, w$,

$$\gamma_{ij} = R_{ij} - R_i - RC_i \sum_{s=i+1}^v \left\{ p_s t_s (R_{sj} - R_s) \prod_{l=i+1}^{s-1} (1 - p_l t_l) \right\}.$$

Thus, the estimated variance of \widehat{RC}_i is

$$\widehat{Var}(\widehat{RC}_i) = \frac{RC_i^2}{R_i^2 \left(\sum_{x=1}^w S_{v+1,x} \right)^2} \sum_{j=1}^w \sum_{m=1}^v \Psi_{jm} + 2 \sum_{j=1}^w \sum_{y=i+1}^v \Omega_{jy} + \sum_{k=i+1}^v \sum_{y=i+1}^v \Gamma_{ky},$$

where

$$\begin{aligned} \Psi_{jm} &= \gamma_{ij} \gamma_{im} \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{S}_{v+1,m}) + S_{v+1,j} S_{v+1,m} \widehat{Cov}(\widehat{R}_{ij}, \widehat{R}_{im}) \\ &\quad + 2\gamma_{ij} S_{v+1,m} \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{R}_{im}) - 2\gamma_{ij} S_{v+1,m} \sum_{k=i+1}^v \left\{ RC_i p_k t_k \delta_k \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{R}_{km}) \right\} + \\ &\quad \sum_{y=i+1}^v \left[RC_i S_{v+1,j} S_{v+1,m} p_y t_y \delta_y \left\{ \sum_{k=i+1}^y [RC_i p_k t_k \delta_k \widehat{Cov}(\widehat{R}_{kj}, \widehat{R}_{ym})] - 2\widehat{Cov}(\widehat{R}_{ij}, \widehat{R}_{ym}) \right\} \right], \\ \Omega_{jy} &= \frac{RC_i^3 R_y (1 - RC_y) \delta_y}{RC_y R_i^2 \sum_{x=1}^w S_{v+1,x}} \times \\ &\quad \left[\gamma_{ij} t_y \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{p}_y) + S_{v+1,j} \left\{ t_y \widehat{Cov}(\widehat{R}_{ij}, \widehat{p}_y) - \sum_{k=i+1}^v RC_i p_k t_k \delta_k t_y \widehat{Cov}(\widehat{R}_{kj}, \widehat{p}_y) \right\} \right], \\ \Gamma_{ky} &= \frac{R_k R_y (1 - RC_k) (1 - RC_y) RC_i^4 \delta_k \delta_y}{RC_k RC_y R_i^2} \left\{ t_k t_y \widehat{Cov}(\widehat{p}_k, \widehat{p}_y) + p_k p_y \widehat{Cov}(\widehat{t}_k, \widehat{t}_y) \right\}, \end{aligned}$$

and

$$\delta_k = \prod_{l=i+1}^{k-1} (1 - p_l t_l).$$

2.4.1.4 Contextual Site-specific TBR for Untagged Fish (RC_i^U)

The TBR measure RC_i depends on the conditional transportation rates t_k , and so is valid only for tagged individuals. The analogous measure for fish in the release group, had they been treated as untagged, is RC_i^U , found by replacing the t_k parameters in Equation (2.16)

with the conditional transportation rates for untagged fish, t_k^U :

$$RC_i^U = \frac{R_i}{\sum_{k=i+1}^v (p_k t_k^U R_k \prod_{l=i+1}^{k-1} z_l^U) + z_{i+1}^U \cdots z_v^U}, \quad (2.19)$$

where $z_l^U = 1 - p_l t_l^U$ is the probability of an untagged fish passing site i without being transported there, conditional upon reaching site i . The variance of \widehat{RC}_i^U is of the same form as the variance of \widehat{RC}_i , but with t_i^U replacing t_i in Equation (2.17) and in the partial derivatives in Equation (2.18). If the researcher has an estimate of $Var(\widehat{t}_i^U)$, then that quantity may be used in estimating $\widehat{Var}(\widehat{RC}_i^U)$; otherwise, the terms involving $Var(\widehat{t}_i^U)$ will be zero.

2.4.1.5 System-wide TBR for Tagged Fish (R_{sys})

The TBR measures R_i and RC_i represent the contributions of individual dams to the overall effect of the transportation system on adult return rates. We also need to estimate the overall, or system-wide, transportation effect. A system-wide transportation effect can be approached in two ways. One way is to compare the conditional return rate of transported smolts to the conditional return rate of non-transported smolts, as done on a site-specific level for RC_i . The conditions in this approach describe the two treatment groups, “transported” and “non-transported.” The second approach is to compare the return rate of smolts under the transportation system to the return rate of smolts without the transportation system. The two approaches are different in two ways. First, the former approach compares only transported smolts to in-river smolts, all of whom migrate in the presence of the transportation system, but only some of whom are transported. The latter approach compares the return rate of *all* smolts, transported or not, under one system (transportation possible) to that under another system (no transportation possible). Secondly, the former approach compares conditional return rates, in which the conditions define the treatment group; the latter approach uses non-conditional return rates. This may seem a minor difference, but using conditional return rates is problematic for a system-wide TBR, as discussed below. For now, consider the latter, unconditional approach. Define R_{sys} to be the system-wide

TBR:

$$R_{sys} = \frac{Pr[\text{Return} \mid \text{Transportation system}]}{Pr[\text{Return} \mid \text{No transportation system}]} \quad (2.20)$$

Note that the conditions in Equation (2.20) define the river system and probability distribution used, rather than the groups of fish in different treatment groups. There is only one juvenile migration path smolts can follow if they are to return as adults in a system without transportation: they must survive in-river from the release point to the final juvenile site, and return from that site to the first adult site. This means that the probability of returning in the denominator is simply $S_1 \cdots S_v \sum S_{v+1,j}$. Smolts who migrate in a system with transportation, on the other hand, have multiple migration routes, depending on the number of transportation sites. They may migrate wholly in-river, or they may be transported from any one of the transport sites. Similar to the denominator of RC_i , we have

$$\begin{aligned} & Pr[\text{Return} \mid \text{Transportation system}] \\ &= \sum_{i=1}^v \left(\prod_{k=1}^{i-1} S_k z_k \right) S_i p_i t_i \left(\prod_{k=i+1}^v S_k \right) \sum_{j=1}^w S_{v+1,j} R_{ij} + \left(\sum_{j=1}^w S_{v+1,j} \right) \left(\prod_{i=1}^v S_i z_i \right) \\ &= \left(\prod_{i=1}^v S_i \right) \sum_{j=1}^w S_{v+1,j} \left\{ \sum_{i=1}^v \left(\prod_{k=1}^{i-1} z_k \right) p_i t_i R_i + \prod_{i=1}^v z_i \right\}. \end{aligned}$$

Combining this probability of adult return under the transportation system with the probability of adult return without the transportation system gives

$$R_{sys} = \sum_{i=1}^v \left\{ \left(\prod_{k=1}^{i-1} z_k \right) p_i t_i R_i \right\} + \prod_{i=1}^v z_i \quad (2.21)$$

The TBR measure R_{sys} is simply the weighted average of the individual isolated site-specific TBRs (R_i), with weights equal to the probabilities of the different migration paths (using $R_i = 1$ for the non-transportation path).

The measure R_{sys} is a function of the parameters $S_{v+1,j}$ ($j = 1, \dots, w$), R_{ij} ($i = 1, \dots, v$; $j = 1, \dots, w$), p_i ($i = 1, \dots, v$), and t_i ($i = 1, \dots, v$). The variance of \hat{R}_{sys} can be estimated

by

$$\begin{aligned}
\widehat{Var}(\widehat{R}_{sys}) = & \sum_{j=1}^w \sum_{m=1}^w \left(\left. \frac{\partial R_{sys}}{\partial S_{v+1,j}} \right|_{\widehat{\theta}} \right) \left(\left. \frac{\partial R_{sys}}{\partial S_{v+1,m}} \right|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{S}_{v+1,m}) \\
& + \sum_{k=1}^v \sum_{y=1}^v \sum_{j=1}^w \sum_{m=1}^w \left(\left. \frac{\partial R_{sys}}{\partial R_{kj}} \right|_{\widehat{\theta}} \right) \left(\left. \frac{\partial R_{sys}}{\partial R_{ym}} \right|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{R}_{kj}, \widehat{R}_{ym}) \\
& + \sum_{k=1}^v \sum_{y=1}^v \left(\left. \frac{\partial R_{sys}}{\partial p_k} \right|_{\widehat{\theta}} \right) \left(\left. \frac{\partial R_{sys}}{\partial p_y} \right|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{p}_k, \widehat{p}_y) \\
& + \sum_{k=1}^v \left(\left. \frac{\partial R_{sys}}{\partial t_k} \right|_{\widehat{\theta}} \right)^2 \widehat{Var}(\widehat{t}_k) \\
& + 2 \sum_{j=1}^w \sum_{k=1}^v \sum_{m=1}^w \left(\left. \frac{\partial R_{sys}}{\partial S_{v+1,j}} \right|_{\widehat{\theta}} \right) \left(\left. \frac{\partial R_{sys}}{\partial R_{km}} \right|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{R}_{km}) \\
& + 2 \sum_{j=1}^w \sum_{k=1}^v \left(\left. \frac{\partial R_{sys}}{\partial S_{v+1,j}} \right|_{\widehat{\theta}} \right) \left(\left. \frac{\partial R_{sys}}{\partial p_k} \right|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_{v+1,j}, \widehat{p}_k) \\
& + 2 \sum_{k=1}^v \sum_{j=1}^w \sum_{y=1}^v \left(\left. \frac{\partial R_{sys}}{\partial R_{kj}} \right|_{\widehat{\theta}} \right) \left(\left. \frac{\partial R_{sys}}{\partial p_y} \right|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{R}_{kj}, \widehat{p}_y), \tag{2.22}
\end{aligned}$$

where $\widehat{\theta}$ is the MLE of the vector of model parameters used in calculating \widehat{R}_{sys} . The necessary partial derivatives are

$$\begin{aligned}
\frac{\partial R_{sys}}{\partial S_{v+1,j}} &= \frac{\sum_{s=1}^v \left\{ p_s t_s (R_{sj} - R_s) \prod_{l=1}^{s-1} (1 - p_l t_l) \right\}}{\sum_{m=1}^w S_{v+1,m}}, & j = 1, \dots, w; \\
\frac{\partial R_{sys}}{\partial R_{ij}} &= \frac{p_i t_i S_{v+1,j} \prod_{l=1}^{i-1} (1 - p_l t_l)}{\sum_{m=1}^w S_{v+1,m}}, & i = 1, \dots, v; \\
\frac{\partial R_{sys}}{\partial p_i} &= \frac{t_i R_i (RC_i - 1) \prod_{s=1}^{i-1} (1 - p_s t_s)}{RC_i}, & i = 1, \dots, v; \\
\frac{\partial R_{sys}}{\partial t_i} &= \frac{p_i R_i (RC_i - 1) \prod_{s=1}^{i-1} (1 - p_s t_s)}{RC_i}, & i = 1, \dots, v.
\end{aligned}$$

2.4.1.6 System-wide TBR for Untagged Fish (R_{sys}^U)

The system-wide TBR R_{sys} is applicable only to tagged individuals, because it depends on the conditional transportation rates t_i . An analogous measure for the fish in the release

group, had they been treated as untagged, is R_{sys}^U :

$$R_{sys}^U = \sum_{i=1}^v \left\{ \left(\prod_{k=1}^{i-1} z_k^U \right) p_i t_i^U R_i \right\} + \prod_{i=1}^v z_i^U. \quad (2.23)$$

The variance of \hat{R}_{sys}^U is estimated by Equation (2.22), but with t_i^U replacing t_i .

2.4.1.7 Conditional System-wide TBR for Tagged Fish (R_{cond})

The measure R_{sys} is an unconditional system-wide TBR value, where the transport group includes non-transported fish. The site-specific TBR values are all based on conditional definitions, in which the transport group is only those fish transported. Consider developing a conditional system-wide TBR that parallels the site-specific values, as suggested above. Ideally, the conditional definition of a system-wide TBR takes the general form

$$R_{cond} = \frac{Pr[\text{Return} \mid \text{Transported somewhere}]}{Pr[\text{Return} \mid \text{Never transported}]}.$$

The main difficulty with this approach is defining the treatment groups. Simply making them “transported” and “never transported” is inappropriate, because the “transported” group is known to have survived in-river to at least the first transport site, while fish in the “never transported” group may not be transported because they died before reaching a transport site. We may condition on reaching the first transport site, but this simply moves the difficulty downstream: fish transported from site 2 are known to have survived that far, while fish not transported from site 2 may have died before reaching that site. Following this reasoning leads to conditioning on survival to the final transport site, for both transport and non-transport fish. Let site t be the final transport site, with $t \leq v$. Using this approach, the conditional definition of a system-wide TBR is

$$\begin{aligned} R_{cond} &= \frac{Pr[\text{Return} \mid \text{Transported somewhere, survive to site } t]}{Pr[\text{Return} \mid \text{Not transported, survive to site } t]} \\ &= \frac{\sum_{i=1}^t Pr[T_i, \text{return}] / \sum_{i=1}^t Pr[T_i, \text{survive to site } t]}{Pr[\text{Not transp., return}] / Pr[\text{Not transp., survive to site } t]}. \end{aligned}$$

The probability of survival in the barge is typically assumed to be approximately 1 (0.98; USACE, 1993). Under this assumption, R_{cond} is approximately

$$R_{cond} \approx \frac{\sum_{i=1}^t \left\{ S_i p_i t_i R_i \left(\prod_{k=i+1}^v S_k \right) \sum_{j=1}^w S_{v+1,j} \prod_{k=1}^{i-1} S_k z_k \right\} / \sum_{i=1}^t \left(S_i p_i t_i \prod_{k=1}^{i-1} S_k z_k \right)}{\left(\prod_{k=1}^v S_k \right) \left(\prod_{k=1}^t z_k \right) \sum_{j=1}^w S_{v+1,j} / \left(\prod_{k=1}^t S_k z_k \right)}$$

$$\approx \frac{\sum_{i=1}^t \left(p_i t_i R_i \prod_{k=1}^{i-1} z_k \right)}{\sum_{i=1}^t \left\{ p_i t_i \left(\prod_{k=1}^{i-1} z_k \right) / \left(\prod_{k=i+1}^t S_k \right) \right\}} \quad (2.24)$$

If there is only a single transport site (t), then $R_{cond} = R_t$. Otherwise, R_{cond} is a combination of the site-specific TBR values and juvenile reach survival rates through the final transport site. The factor $1/(\prod_{k=i+1}^t S_k)$ represents the effect of transportation from site i on survival past the last transport site, and is based on the assumption that survival in the barge is approximately 100%, at least in the early stages past the remaining transport sites. Without this factor, R_{cond} is the same as the combined-site TBR reported in Sandford and Smith (2002), but allowing for multiple juvenile detections at transport sites. Including the factor $1/(\prod_{k=i+1}^t S_k)$ is unsatisfactory, because it requires an assumption about barge survival that cannot be adequately tested or estimated. Also, it prevents R_{cond} from being a simple weighted average of the site-specific R_i values, which is appealing mathematically. However, omitting the factor $1/(\prod_{k=i+1}^t S_k)$ is equivalent to making another assumption, namely that barge survival between each transport site and the final transport site is the same as in-river survival between these points, or that in-river survival is approximately 100%. This assumption is unwarranted. Due to the dependence of R_{cond} on potentially faulty and untestable assumptions, it is recommended that the more defensible R_{sys} be used rather than R_{cond} as a system-wide measure of the effectiveness of the transportation system.

2.4.1.8 Scenarios

Several measures of transportation effect have been defined, varying on assumptions about the viewpoint taken (isolated or contextual) and whether or not the fish are tagged, and on the level of specificity desired (site or system-wide). To better understand the differences among these various quantities, consider the two scenarios shown in Figure 2.7. For both

scenarios, the expressions for the alternative TBRs are presented and compared.

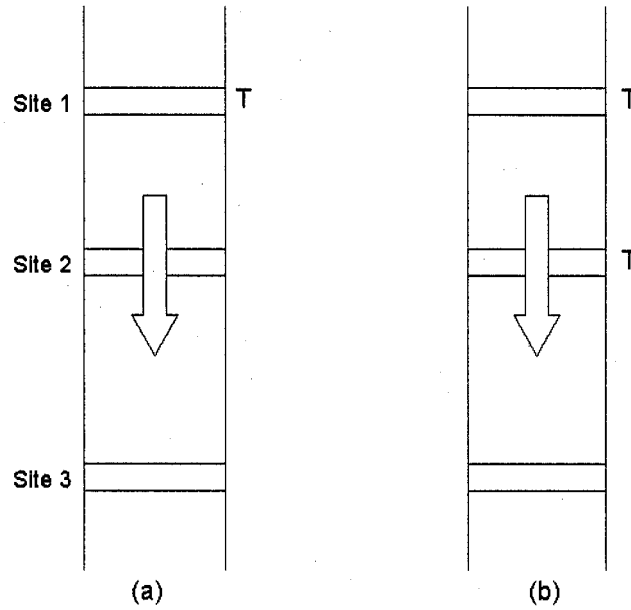


Figure 2.7: Scenarios for TBR examples. Each scenario shows the river with three dams (detection sites), with the arrow indicating direction of flow. Transportation (T) is possible either at (a) dam 1 only or (b) both dam 1 and dam 2.

2.4.1.8.1 Scenario A Consider the study design shown in Figure 2.7(a). Only juvenile detection sites are shown, because the configuration of adult sites does not affect TBR as long as there are enough adult sites to estimate adult return rates to BON (i.e., at least two). In Figure 2.7(a), there are three juvenile detection sites, with transportation possible only at the first site. Site 4 (not shown) is the first adult site. With a single transportation site, there are five alternative measures of transportation effect: R_1 , RC_1 , RC_i^U , R_{sys} , and R_{sys}^U . Note that z_1 and z_1^U are both < 1 while $z_2 = z_3 = z_2^U = z_3^U = 1$. Consider the site-specific TBRs first. The R_{1j} values are estimated directly from the model. The other

site-specific values are:

$$R_1 = \frac{\sum_{j=1}^w S_{4j} R_{1j}}{\sum_{j=1}^w S_{4j}}; \quad RC_1 = \frac{R_1}{z_2 z_3} = R_1; \quad RC_1^U = \frac{R_1}{z_2^U z_3^U} = R_1.$$

With only a single transportation site, the river downstream from that site appears the same whether or not transportation practices at other dams are considered; thus, $R_1 = RC_1 = RC_1^U$. The system-wide TBR values are:

$$R_{sys} = 1 - p_1 t_1 (1 - R_1); \quad R_{sys}^U = 1 - p_1 t_1^U (1 - R_1).$$

If $R_1 > 1$ (transportation from site 1 increases adult return rates), then both R_{sys} and R_{sys}^U are > 1 as expected, with $R_{sys}^U > R_{sys}$ if $t_1^U > t_1$. If $R_1 < 1$ (transportation from site 1 decreases adult return rates) and $t_1^U > t_1$, then $R_{sys}^U < R_{sys}$.

2.4.1.8.2 Scenario B Figure 2.7(b) shows a second scenario, again with three juvenile detection sites and with transportation possible at the first two sites but not at the third. In this case, it should be expected that the site-specific TBRs for site 2 will be equal, regardless of tagging or the viewpoint used, because there is no transportation downstream of site 2. On the other hand, it should be expected that the site-specific TBRs for site 1 will be unequal, due to transportation at site 2. The parameters z_1 , z_2 , z_1^U , and z_2^U are each < 1 , and $z_3 = z_3^U = 1$. The site-specific TBRs for tagged and untagged fish are:

$$\begin{aligned} R_1 &= \frac{\sum_{j=1}^w S_{4j} R_{1j}}{\sum_{j=1}^w S_{4j}}; & R_2 &= \frac{\sum_{j=1}^w S_{4j} R_{2j}}{\sum_{j=1}^w S_{4j}}; \\ RC_1 &= \frac{R_1}{z_2 z_3 + p_2 t_2 R_2} = \frac{R_1}{1 - p_2 t_2 (1 - R_2)}; & RC_2 &= \frac{R_2}{z_3} = R_2; \\ RC_1^U &= \frac{R_1}{z_2^U z_3^U + p_2 t_2^U R_2} = \frac{R_1}{1 - p_2 t_2^U (1 - R_2)}; & RC_2^U &= \frac{R_2}{z_3^U} = R_2; \end{aligned}$$

As expected, the isolated and contextual TBRs are the same for both tagged and untagged smolts for site 2, but differ for site 1. In general, the site-specific TBRs (i.e., R_i , RC_i ,

and RC_i^U) will be equal for the final transport site, but not for upriver transport sites. If transportation from site 2 increases adult return rates (i.e., $R_2 > 1$), then $RC_1 < R_1$ and $RC_1^U < R_1$, because return rates of site 1 control fish are augmented by transportation from site 2. Also, if $R_2 > 1$ and $t_1^U > t_1$, then $RC_1 > RC_1^U$ because a larger proportion of the untagged controls than the tagged controls from site 1 are transported at site 2.

The system-wide TBR values for tagged and untagged smolts are:

$$\begin{aligned} R_{sys} &= p_1 t_1 R_1 + (1 - p_1 t_1) \{1 - p_2 t_2 (1 - R_2)\}; \\ R_{sys}^U &= p_1 t_1^U R_1 + (1 - p_1 t_1^U) \{1 - p_2 t_2^U (1 - R_2)\}. \end{aligned}$$

With more transport sites, the system-wide TBR values become more convoluted. Which of R_{sys} and R_{sys}^U is larger depends on the values of the isolated site-specific TBRs (R_i) and on the transportation fractions for tagged and untagged smolts ($p_i t_i$ and $p_i t_i^U$, respectively).

2.4.1.9 Which TBR to Use

Several alternative Transport Benefit Ratios have been presented as measures of transportation effect. They vary in level of specificity (age and site, site alone, or system-wide), viewpoint taken (isolated or contextual with respect to the remainder of the transportation system), and tagging status of the applicable population (tagged or untagged). Under what circumstances is one more appropriate than the others?

First, note that managers and scientists are primarily interested in the effect of transportation on the larger untagged population, rather than the smaller tagged population. Second, note that the control groups for the isolated TBRs (R_{ij} and R_i) and the system-wide TBRs (R_{sys} and R_{sys}^U) represent migration through the hydrosystem with dams but without transportation. Third, the age- and site-specific TBR values R_{ij} are useful primarily for model parameterization and for defining the site-specific and system-wide TBRs; unless the focus is the interaction between transportation and age of return, we should consider only either the site-specific values R_i or RC_i^U , or the system-wide value R_{sys}^U .

Managers of specific dams are interested primarily in the effect of their dam operations on survival and return rates, and thus should use the site-specific TBR values. If they are

interested only in the effect of transportation operations at their own dam on adult return rates, then they should use R_i , which separates the effects of transportation at dam i from the effect of transportation at downstream dams. On the other hand, dam managers may want to know whether it is better to transport fish that are in their bypass system, or better to return them to the river. The contextual TBR measure RC_i^U can help them answer that question, because it takes into account actual transportation operations at downstream dams.

Hatchery managers and tribal leaders are interested in the return rates of their fish, and so are interested in survival throughout the entire hydrosystem rather than past any one dam. Similarly, they are interested in the overall effect of the transportation system on return rates, rather than the effect of transportation from one site. Thus, hatchery managers and tribes should use R_{sys}^U , rather than site-specific values.

NOAA Fisheries, state fish and wildlife agencies, and conservation scientists are also interested in the overall effect of the transportation system, so should use R_{sys}^U . As a measure of the efficacy of transportation throughout the hydrosystem, and as a function of both conditional bypass (detection) and transportation rates (p_i and t_i , respectively), the measure R_{sys}^U may be used to optimally allocate transportation effort across dams. Fisheries managers may also be interested in the effect of transportation from a single site, either alone (R_i) or in the context of the entire transportation program (RC_i^U).

It is important that all parties involved understand the different types of TBR available, and know which value is being used in any given situation. In general, R_i , RC_i^U , and R_{sys}^U are unequal, so miscommunication and misunderstandings may arise without clearly identifying the type of TBR being used. Whatever measure of transportation effect is considered should be analyzed in terms of a modeling context as presented here. This practice clarifies what is being estimated by the various TBR values, and may help avoid unnecessary confusion and miscommunication.

2.4.2 Adult Return Rates

2.4.2.1 Ocean Return Rate for Non-transported Fish (O_{NT})

The age-specific parameter $S_{v+1,j}$ represents the probability of returning to the first adult site after j years (or winters) in the ocean, conditional on reaching the final juvenile site without having been transported. Because the permanent detection site for both juveniles and adults closest to the ocean is Bonneville Dam, 234 kilometers from the mouth of the Columbia River, $S_{v+1,j}$ necessarily includes some inriver survival, as well as ocean survival and maturation rates. Ocean survival cannot be estimated unless we make precise assumptions about maturation rates and inriver survival. Although we cannot separate ocean survival from inriver survival and maturation rates, we can estimate the ocean return rate from the last juvenile site to the first adult site, regardless of age at return, by summing the age-specific ocean return rates. Let O_{NT} be the ocean return rate for non-transported fish:

$$O_{NT} = \sum_{j=1}^w S_{v+1,j}. \quad (2.25)$$

The measure O_{NT} is valid for both tagged and untagged fish because it does not depend on the conditional transportation rates. The MLE of O_{NT} , denoted \hat{O}_{NT} , is found by replacing the model parameters in Equation (2.25) with their maximum likelihood estimates, i.e.:

$$\hat{O}_{NT} = \sum_{j=1}^w \hat{S}_{v+1,j}. \quad (2.26)$$

The variance of \hat{O}_{NT} is estimated by

$$\begin{aligned} \widehat{Var}(\hat{O}_{NT}) &= \sum_{j=1}^w \sum_{m=1}^w \widehat{Cov}(\hat{S}_{v+1,j}, \hat{S}_{v+1,m}) \\ &= \sum_{j=1}^w \widehat{Var}(\hat{S}_{v+1,j}) + 2 \sum_{j=1}^w \sum_{m=j+1}^w \widehat{Cov}(\hat{S}_{v+1,j}, \hat{S}_{v+1,m}). \end{aligned} \quad (2.27)$$

2.4.2.2 Site-specific Ocean Return Rate for Transported Fish (O_{T_i})

The ocean return rate O_{NT} is valid only for non-transported fish, because ocean survival is assumed to be affected by transportation. For fish transported from site i , the probability of returning from the transport site to the first adult site is O_{T_i} :

$$\begin{aligned}
 O_{T_i} &= Pr(\text{Return to } v+1 \mid \text{Transported at } i) \\
 &= S_{i+1} \cdots S_v \sum_{j=1}^w S_{v+1,j} R_{ij} \\
 &= S_{i+1} \cdots S_v R_i \sum_{j=1}^w S_{v+1,j}.
 \end{aligned} \tag{2.28}$$

The measure O_{T_i} is valid for both tagged and untagged fish because it does not depend on the conditional transportation rates. The MLE of O_{T_i} , denoted \hat{O}_{T_i} , is

$$\hat{O}_{T_i} = \hat{S}_{i+1} \cdots \hat{S}_v \hat{R}_i \sum_{j=1}^w \hat{S}_{v+1,j}. \tag{2.29}$$

The variance estimator for \hat{O}_{T_i} is

$$\begin{aligned}
 \widehat{Var}(\hat{O}_{T_i}) &= \sum_{k=i+1}^v \sum_{y=i+1}^v \left(\frac{\partial O_{T_i}}{\partial S_k} \Big|_{\hat{\theta}} \right) \left(\frac{\partial O_{T_i}}{\partial S_y} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_k, \hat{S}_y) \\
 &+ \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial O_{T_i}}{\partial S_{v+1,j}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial O_{T_i}}{\partial S_{v+1,m}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,j}, \hat{S}_{v+1,m}) \\
 &+ \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial O_{T_i}}{\partial R_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial O_{T_i}}{\partial R_{im}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{ij}, \hat{R}_{im}) \\
 &+ 2 \sum_{k=i+1}^v \sum_{j=1}^w \left(\frac{\partial O_{T_i}}{\partial S_k} \Big|_{\hat{\theta}} \right) \left(\frac{\partial O_{T_i}}{\partial S_{v+1,j}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_k, \hat{S}_{v+1,j}) \\
 &+ 2 \sum_{k=i+1}^v \sum_{j=1}^w \left(\frac{\partial O_{T_i}}{\partial S_k} \Big|_{\hat{\theta}} \right) \left(\frac{\partial O_{T_i}}{\partial R_{ij}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_k, \hat{R}_{ij}) \\
 &+ 2 \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial O_{T_i}}{\partial S_{v+1,j}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial O_{T_i}}{\partial R_{im}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,j}, \hat{R}_{im}),
 \end{aligned}$$

where $\hat{\theta}$ is the MLE of the parameters used in Equation (2.28). The necessary partial derivatives are:

$$\begin{aligned} \frac{\partial O_{T_i}}{\partial S_y} &= \frac{O_{T_i}}{S_y}, & y &= i + 1, \dots, v; \\ \frac{\partial O_{T_i}}{\partial S_{v+1,j}} &= S_{i+1} \cdots S_v R_{ij}, & j &= 1, \dots, w; \\ \frac{\partial O_{T_i}}{\partial R_{ij}} &= S_{i+1} \cdots S_v S_{v+1,j}, & j &= 1, \dots, w. \end{aligned} \quad (2.30)$$

The age- and site-specific parameters R_{ij} reflect transportation effects on inriver survival below the transportation site as well as on ocean survival, so we cannot estimate the probability of transport fish returning from site $v + 1$ to site v unless we make assumptions about TBRs and inriver survival. For example, survival of transported smolts in the barge is often assumed to be 0.98 (USACE, 1993). This assumption allows us to express the effect of transportation on ocean return rates as $R_{i,ocean_j} = R_{ij} S_{i+1} \cdots S_v / 0.98$, and the ocean return rate of site- i transport fish as $(S_{i+1} \cdots S_v / 0.98) \sum_{j=1}^w S_{v+1,j} R_{ij}$. It should be noted that the barge survival value of 0.98 is an estimate from past studies, which may be inappropriate for any particular transport group and whose standard error is unknown; thus, the most defensible ocean return rate for transport fish is that from the transport site (O_{T_i}), rather than from the final juvenile site.

2.4.2.3 Site-specific Smolt-to-Adult Return Rate for Tagged Fish ($SAR_{(K)}$)

Researchers are typically interested in return rates from the release site or transport site to spawning grounds or back to the release site. Without independent estimates of detection rates at those sites, we cannot estimate adult return rates there. However, it is often assumed that adult detection at the final detection site (typically LGR) is 100%, implying that we can estimate return rates to that site (i.e., site $v + u$), which may be downriver of the release site. If detection at the final site is not assumed to be 100%, then we may estimate return rates only to the penultimate site (i.e., site $v + u - 1$). On the other hand, it may be of interest to estimate the return rate to the first adult site. Each of these

return rates may be considered a smolt-to-adult return rate (SAR). Here, SAR is labeled with a subscript, K , denoting the site to which return rates are estimated, typically either $K = v + u$ or $K = v + u - 1$. Define $SAR_{(K)}$ to be the probability of returning to site K ($K = v + 1, \dots, v + u$) as an adult, conditional only on the initial release:

$$SAR_{(K)} = \prod_{i=1}^v S_i \sum_{j=1}^w \left[\prod_{i=v+1}^K S_{ij} \left\{ \sum_{i=1}^v \left(p_i t_i R_{ij} \prod_{l=1}^{i-1} z_l \right) + \prod_{i=1}^v z_i \right\} \right]. \quad (2.31)$$

The measure $SAR_{(K)}$ depends on the conditional transportation rates, and so is valid only for tagged individuals. The MLE of $SAR_{(K)}$ is:

$$\widehat{SAR}_{(K)} = \prod_{i=1}^v \widehat{S}_i \sum_{j=1}^w \left[\prod_{i=v+1}^K \widehat{S}_{ij} \left\{ \sum_{i=1}^v \left(\widehat{p}_i \widehat{t}_i \widehat{R}_{ij} \prod_{l=1}^{i-1} \widehat{z}_l \right) + \prod_{i=1}^v \widehat{z}_i \right\} \right]. \quad (2.32)$$

The variance of $\widehat{SAR}_{(K)}$ is estimated by

$$\begin{aligned} \widehat{Var}(\widehat{SAR}_{(K)}) = & \sum_{i=1}^v \sum_{k=1}^v \left(\frac{\partial SAR_{(K)}}{\partial S_i} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial S_k} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_i, \widehat{S}_k) \\ & + \sum_{i=v+1}^K \sum_{k=v+1}^K \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial SAR_{(K)}}{\partial S_{ij}} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial S_{km}} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_{ij}, \widehat{S}_{km}) \\ & + \sum_{i=1}^v \sum_{k=1}^v \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial SAR_{(K)}}{\partial R_{ij}} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial R_{km}} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{R}_{ij}, \widehat{R}_{km}) \\ & + \sum_{i=1}^v \sum_{k=1}^v \left(\frac{\partial SAR_{(K)}}{\partial p_i} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial p_k} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{p}_i, \widehat{p}_k) \\ & + \sum_{i=1}^v \left(\frac{\partial SAR_{(K)}}{\partial t_i} \Big|_{\widehat{\theta}} \right)^2 \widehat{Var}(\widehat{t}_i) \\ & + 2 \sum_{i=1}^v \sum_{k=v+1}^K \sum_{j=1}^w \left(\frac{\partial SAR_{(K)}}{\partial S_i} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial S_{kj}} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_i, \widehat{S}_{kj}) \\ & + 2 \sum_{i=1}^v \sum_{k=1}^v \sum_{j=1}^w \left(\frac{\partial SAR_{(K)}}{\partial S_i} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial R_{kj}} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_i, \widehat{R}_{kj}) \\ & + 2 \sum_{i=1}^v \sum_{k=1}^v \left(\frac{\partial SAR_{(K)}}{\partial S_i} \Big|_{\widehat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial p_k} \Big|_{\widehat{\theta}} \right) \widehat{Cov}(\widehat{S}_i, \widehat{p}_k) \end{aligned}$$

$$\begin{aligned}
& + 2 \sum_{i=v+1}^K \sum_{k=1}^v \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial SAR_{(K)}}{\partial S_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial R_{km}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{ij}, \hat{R}_{km}) \\
& + 2 \sum_{i=v+1}^K \sum_{k=1}^v \sum_{j=1}^w \left(\frac{\partial SAR_{(K)}}{\partial S_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial p_k} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{ij}, \hat{p}_k) \\
& + 2 \sum_{i=1}^v \sum_{k=1}^v \sum_{j=1}^w \left(\frac{\partial SAR_{(K)}}{\partial R_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial SAR_{(K)}}{\partial p_k} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{ij}, \hat{p}_k), \quad (2.33)
\end{aligned}$$

where $\hat{\theta}$ is the MLE of the vector of model parameters used in calculating $\widehat{SAR}_{(K)}$. The partial derivatives are (for $i = 1, \dots, v$ unless otherwise specified, and for $j = 1, \dots, w$):

$$\begin{aligned}
\frac{\partial SAR_{(K)}}{\partial S_i} &= \frac{SAR_{(K)}}{S_i}; \\
\frac{\partial SAR_{(K)}}{\partial S_{ij}} &= \frac{(\prod_{k=1}^v S_k)(\prod_{k=v+1}^K S_{kj})}{S_{ij}} \left\{ \sum_{k=1}^v (p_k t_k R_{kj} \prod_{l=1}^{k-1} z_l) + \prod_{k=1}^v z_k \right\}, \\
&\text{for } i = v+1, \dots, K; \\
\frac{\partial SAR_{(K)}}{\partial R_{ij}} &= \left(\prod_{k=1}^v S_k \right) \left(\prod_{k=v+1}^K S_{kj} \right) p_i t_i \prod_{k=1}^{i-1} z_k; \\
\frac{\partial SAR_{(K)}}{\partial p_i} &= \frac{t_i}{z_i} \prod_{k=1}^v S_k \sum_{j=1}^w \prod_{k=v+1}^K S_{kj} \left\{ R_{ij} \prod_{l=1}^i z_l - \sum_{s=i+1}^v (p_s t_s R_{sj} \prod_{l=1}^{s-1} z_l) - \prod_{l=1}^v z_l \right\}; \\
\frac{\partial SAR_{(K)}}{\partial t_i} &= \frac{p_i}{z_i} \prod_{k=1}^v S_k \sum_{j=1}^w \prod_{k=v+1}^K S_{kj} \left\{ R_{ij} \prod_{l=1}^i z_l - \sum_{s=i+1}^v (p_s t_s R_{sj} \prod_{l=1}^{s-1} z_l) - \prod_{l=1}^v z_l \right\}. \quad (2.34)
\end{aligned}$$

2.4.2.4 Site-specific Smolt-to-Adult Return Rate for Untagged Fish ($SAR_{(K)}^U$)

The smolt-to-adult return rate to site K for untagged fish, $SAR_{(K)}^U$, is estimated by replacing the parameters t_i in Equation(2.31) with the corresponding values t_i^U . The variance estimator of $\widehat{SAR}_{(K)}^U$ is simply Equation (2.33) with t_i^U replacing t_i , allowing for a non-zero $\widehat{Var}(t_i^U)$ input by the user.

2.4.3 Return Age Distributions

Recall from the underlying model that the probability of returning as an adult in age class j is a product of inriver and ocean survival and maturation proclivities:

$$S_{v+1,j} = \sigma_J \sigma_1 m_j \sigma_{A_j} \prod_{k=1}^{j-1} (1 - m_k) \sigma_{k+1}.$$

Maturation is confounded with ocean survival and the inriver survival contained in σ_J and σ_{A_j} , so the maturation rates m_j are not separately estimable. Instead, we can estimate two sets of probabilities: the return age distribution, and the conditional maturation and return probabilities. First consider the return age distribution. The entry for age j is the probability of returning after j years in the ocean, conditional on returning as an adult:

$$\begin{aligned} S_{v+1,j} / \sum_{k=1}^w S_{v+1,k} & \quad \text{for inriver fish, and} \\ (S_{v+1,j} R_{ij}) / \left(\sum_{k=1}^w S_{v+1,k} R_{ik} \right) & \quad \text{for site-}i \text{ transport fish.} \end{aligned}$$

The terms in each distribution add to 1.

2.4.3.1 Return Age Distribution for Tagged Fish (A_j)

It is possible to combine the inriver fish with the transport groups to derive a return age distribution for all fish in the study, regardless of migration route. The entries in this overall distribution are the same as those for inriver fish, weighted by the age-specific probabilities of the different migration routes. The weights are similar to those used in R_{sys} , the effect of the transportation system on ocean return rates (Equation (2.21)). The age- j entry for this overall return age distribution is:

$$\begin{aligned}
A_j &= \frac{S_{v+1,j}}{\sum_{k=1}^w S_{v+1,k}} \frac{\left\{ \sum_{i=1}^v \left(p_i t_i R_{ij} \prod_{y=1}^{i-1} z_y \right) + \prod_{i=1}^v z_i \right\}}{\left[\sum_{i=1}^v \left(p_i t_i R_i \prod_{y=1}^{i-1} z_y \right) + \prod_{i=1}^v z_i \right]} \\
&= \frac{S_{v+1,j}}{\sum_{k=1}^w S_{v+1,k}} \frac{\left\{ \sum_{i=1}^v \left(p_i t_i R_{ij} \prod_{y=1}^{i-1} z_y \right) + \prod_{i=1}^v z_i \right\}}{R_{sys}}.
\end{aligned} \tag{2.35}$$

The variance estimator for \hat{A}_j , derived using the delta method, is

$$\begin{aligned}
\widehat{Var}(\hat{A}_j) &= \sum_{m=1}^w \sum_{n=1}^w \left(\frac{\partial A_j}{\partial S_{v+1,m}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial A_j}{\partial S_{v+1,n}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,m}, \hat{S}_{v+1,n}) \\
&\quad + \sum_{m=1}^w \sum_{n=1}^w \left(\frac{\partial A_j}{\partial R_{im}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial A_j}{\partial R_{in}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{im}, \hat{R}_{in}) \\
&\quad + \sum_{k=1}^v \sum_{y=1}^v \left(\frac{\partial A_j}{\partial p_k} \Big|_{\hat{\theta}} \right) \left(\frac{\partial A_j}{\partial p_y} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{p}_k, \hat{p}_y) \\
&\quad + \sum_{k=1}^v \left(\frac{\partial A_j}{\partial t_k} \Big|_{\hat{\theta}} \right)^2 \widehat{Var}(\hat{t}_k) \\
&\quad + 2 \sum_{m=1}^w \sum_{n=1}^w \left(\frac{\partial A_j}{\partial S_{v+1,m}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial A_j}{\partial R_{in}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,m}, \hat{R}_{in}) \\
&\quad + 2 \sum_{m=1}^w \sum_{k=1}^v \left(\frac{\partial A_j}{\partial S_{v+1,m}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial A_j}{\partial p_k} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,m}, \hat{p}_k) \\
&\quad + 2 \sum_{m=1}^w \sum_{k=1}^v \left(\frac{\partial A_j}{\partial R_{im}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial A_j}{\partial p_k} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{im}, \hat{p}_k),
\end{aligned} \tag{2.36}$$

where $\hat{\theta}$ is the MLE of the vector of model parameters used to calculate \hat{A}_j . The necessary partial derivatives are ($i = 1, \dots, v; j = 1, \dots, w$):

$$\begin{aligned}
\frac{\partial A_j}{\partial S_{v+1,j}} &= \frac{A_j}{S_{v+1,j}} - \frac{A_j}{R_{sys}} \frac{\partial R_{sys}}{\partial S_{v+1,j}} - \frac{A_j}{\sum_{m=1}^w S_{v+1,m}} \\
&\quad + \frac{S_{v+1,j}}{\sum_{m=1}^w S_{v+1,m}} \frac{1}{R_{sys}} \sum_{s=1}^v \left\{ p_s t_s \frac{\partial R_{sj}}{\partial S_{v+1,j}} \prod_{y=1}^{s-1} (1 - p_y t_y) \right\}; \\
\frac{\partial A_j}{\partial S_{v+1,n}} &= -A_j \left(\frac{1}{\sum_{m=1}^w S_{v+1,m}} + \frac{1}{R_{sys}} \frac{\partial R_{sys}}{\partial S_{v+1,n}} \right), \quad n = 1, \dots, w; n \neq j;
\end{aligned}$$

$$\begin{aligned}
\frac{\partial A_j}{\partial R_{ij}} &= \frac{S_{v+1,j}}{\sum_{m=1}^w S_{v+1,m}} \frac{1}{R_{sys}} (1 - A_j) p_i t_i \prod_{y=1}^{i-1} (1 - p_y t_y); \\
\frac{\partial A_j}{\partial R_{im}} &= \frac{-A_j}{R_{sys}} \frac{\partial R_{sys}}{\partial R_{im}}, & m = 1, \dots, w; m \neq j; \\
\frac{\partial A_j}{\partial p_i} &= \frac{-A_j}{R_{sys}} \frac{\partial R_{sys}}{\partial p_i} + \frac{S_{v+1,j}}{\sum_{m=1}^w S_{v+1,m}} \frac{t_i \prod_{y=1}^{i-1} (1 - p_y t_y)}{R_{sys}} \gamma_{ij};
\end{aligned}$$

and

$$\frac{\partial A_j}{\partial t_i} = \frac{-A_j}{R_{sys}} \frac{\partial R_{sys}}{\partial t_i} + \frac{S_{v+1,j}}{\sum_{m=1}^w S_{v+1,m}} \frac{p_i \prod_{y=1}^{i-1} (1 - p_y t_y)}{R_{sys}} \gamma_{ij}; \quad (2.37)$$

where

$$\gamma_{ij} = R_{ij} - \sum_{s=i+1}^v \left\{ p_s t_s R_{sj} \prod_{y=i+1}^{s-1} (1 - p_y t_y) \right\} - \prod_{y=i+1}^v (1 - p_y t_y).$$

2.4.3.2 Return Age Distribution for Untagged Fish (A_j^U)

The overall return age distribution in Equation (2.35) is valid only for tagged fish; for untagged fish, the conditional transportation rates for tagged fish (t_i) are replaced with the analogous rates for untagged fish (t_i^U) to give A_j^U . As usual, the variance of \hat{A}_j^U is estimated by Equation (2.36) but with t_i^U replacing t_i , and allowing for (but not requiring) a non-zero $\widehat{Var}(t_i^U)$ input by the user.

2.4.3.3 Conditional Adult Return Rate for Tagged Fish (μ_j)

Now consider the conditional maturation and return probabilities. The age- j conditional maturation and return probability is the probability of returning after j years in the ocean, conditional on surviving to the final juvenile site and not returning earlier. For inriver fish, the final juvenile site is site v , and the age- j conditional maturation and return probability is $S_{v+1,j} / (1 - \sum_{k=1}^{j-1} S_{v+1,k})$, the ratio of the age- j ocean return probability to the probability of *not* returning earlier. Notice that the denominator includes the possibility of dying in the ocean before year j , so that this quantity involves ocean survival parameters

$\sigma_1, \dots, \sigma_j$ as well as the maturation parameters m_j . For fish transported from site i , the “last” juvenile site is site i , and the conditional age- j maturation and return probability is $\left\{ \left(\prod_{k=i+1}^v S_k \right) S_{v+1,j} R_{ij} \right\} / \left\{ 1 - \left(\prod_{k=i+1}^v S_k \right) \sum_{k=1}^{j-1} S_{v+1,k} R_{ik} \right\}$. Note that the conditional age-specific maturation and return probabilities for any treatment group (inriver or transported from site i) do not sum to 1.

The conditional maturation and return probabilities for all fish, regardless of migration method (transportation or inriver) is more complicated, because the “last” juvenile site varies with migration group. However, we can express the probability of returning to the first adult site in year j , conditional both on surviving to the “last” juvenile site and on not returning before year j , by:

$$\mu_j = \frac{\left(\prod_{i=1}^v S_i \right) S_{v+1,j} \left\{ \sum_{i=1}^v (p_i t_i R_{ij} \prod_{y=1}^{i-1} z_y) + \prod_{i=1}^v z_i \right\}}{\delta_j}, \quad (2.38)$$

where

$$\begin{aligned} \delta_j = & \left(\prod_{i=1}^v S_i z_i \right) \left(1 - \sum_{k=1}^{j-1} S_{v+1,k} \right) \\ & + \sum_{i=1}^v \left\{ \prod_{y=1}^{i-1} (S_y z_y) S_i p_i t_i \left(1 - \prod_{l=i+1}^v S_l \sum_{k=1}^{j-1} S_{v+1,k} R_{lk} \right) \right\}. \end{aligned}$$

Ocean return probabilities in Equation (2.38) are weighted by the probabilities of the different migration paths and by the TBR parameters R_{ij} . The estimated variance of $\hat{\mu}_j$ is

$$\begin{aligned} \widehat{Var}(\hat{\mu}_j) = & \sum_{i=1}^v \sum_{y=1}^v \left(\frac{\partial \mu_j}{\partial S_i} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial S_y} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_i, \hat{S}_y) \\ & + \sum_{k=v+1}^j \sum_{m=v+1}^j \left(\frac{\partial \mu_j}{\partial S_{v+1,k}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial S_{v+1,m}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,k}, \hat{S}_{v+1,m}) \\ & + \sum_{i=1}^v \sum_{y=1}^v \sum_{k=1}^j \sum_{m=1}^j \left(\frac{\partial \mu_j}{\partial R_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial R_{ym}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{ik}, \hat{R}_{ym}) \end{aligned}$$

$$\begin{aligned}
& + \sum_{i=1}^v \sum_{y=1}^v \left(\frac{\partial \mu_j}{\partial p_i} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial p_y} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{p}_i, \hat{p}_y) \\
& + \sum_{i=1}^v \left(\frac{\partial \mu_j}{\partial t_i} \Big|_{\hat{\theta}} \right)^2 \widehat{Var}(\hat{t}_i) \\
& + 2 \sum_{i=1}^v \sum_{k=1}^j \left(\frac{\partial \mu_j}{\partial S_i} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial S_{v+1,k}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_i, \hat{S}_{v+1,k}) \\
& + 2 \sum_{i=1}^v \sum_{y=1}^v \sum_{k=1}^j \left(\frac{\partial \mu_j}{\partial S_i} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial R_{yk}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_i, \hat{R}_{yk}) \\
& + 2 \sum_{i=1}^v \sum_{y=1}^v \left(\frac{\partial \mu_j}{\partial S_i} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial p_y} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_i, \hat{p}_y) \\
& + 2 \sum_{k=1}^j \sum_{i=1}^v \sum_{m=1}^j \left(\frac{\partial \mu_j}{\partial S_{v+1,k}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial R_{im}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,k}, \hat{R}_{im}) \\
& + 2 \sum_{k=1}^j \sum_{i=1}^v \left(\frac{\partial \mu_j}{\partial S_{v+1,k}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial p_i} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{v+1,k}, \hat{p}_i) \\
& + 2 \sum_{i=1}^v \sum_{k=1}^j \sum_{y=1}^v \left(\frac{\partial \mu_j}{\partial R_{ik}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial \mu_j}{\partial p_y} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{ik}, \hat{p}_y), \tag{2.39}
\end{aligned}$$

where $\hat{\theta}$ is the MLE of the vector of model parameters used in calculating $\hat{\mu}_j$. The necessary partial derivatives are given below (Equation (2.40)). Interpret as 0 any sum whose upper limit is smaller than its lower limit. For example, $\sum_{m=1}^0 S_{v+1,m} = 0$.

$$\begin{aligned}
\frac{\partial \mu_j}{\partial S_i} &= \frac{\mu_j}{S_i \delta_j} \sum_{m=1}^{i-1} \left\{ \prod_{y=1}^{m-1} (S_y z_y) S_m p_m t_m \right\}, & i = 1, \dots, v; \\
\frac{\partial \mu_j}{\partial S_{v+1,j}} &= \frac{\mu_j}{S_{v+1,j}}; \\
\frac{\partial \mu_j}{\partial S_{v+1,k}} &= \frac{\mu_j \mu_k \delta_k}{\delta_j S_{v+1,k}}, & k = 1, \dots, j-1; \\
\frac{\partial \mu_j}{\partial R_{ij}} &= \frac{\mu_j (1 - \mu_j) S_{v+1,j} p_i t_i \prod_{y=1}^{i-1} z_y}{A_j R_{sys} \sum_{m=1}^w S_{v+1,m}}, & i = 1, \dots, v; \\
\frac{\partial \mu_j}{\partial R_{ik}} &= \frac{\mu_j^2 S_{v+1,k} p_i t_i \prod_{y=1}^{i-1} z_y}{A_j R_{sys} \sum_{m=1}^w S_{v+1,m}}, & k = 1, \dots, j-1;
\end{aligned}$$

$$\begin{aligned}\frac{\partial \mu_j}{\partial p_i} &= \frac{\mu_j t_i \prod_{y=1}^{i-1} z_y}{A_j R_{s_y s} \sum_{m=1}^w S_{v+1,m}} \left\{ S_{v+1,j} \gamma_{ij} - \frac{\mu_j \alpha_{ij}}{\prod_{y=i+1}^v S_y} \right\}, & i = 1, \dots, v; \\ \frac{\partial \mu_j}{\partial t_i} &= \frac{\mu_j p_i \prod_{y=1}^{i-1} z_y}{A_j R_{s_y s} \sum_{m=1}^w S_{v+1,m}} \left\{ S_{v+1,j} \gamma_{ij} - \frac{\mu_j \alpha_{ij}}{\prod_{y=i+1}^v S_y} \right\}, & i = 1, \dots, v;\end{aligned} \quad (2.40)$$

where

$$\begin{aligned}\gamma_{ij} &= R_{ij} - \sum_{s=i+1}^v \left(p_s t_s R_{sj} \prod_{y=i+1}^{s-1} z_y \right) - \prod_{y=i+1}^v z_y; \\ \alpha_{ij} &= 1 - \prod_{y=i+1}^v S_y \sum_{k=1}^{j-1} S_{v+1,k} R_{ik} \\ &\quad - \sum_{s=i+1}^v \left\{ \left(\prod_{y=i+1}^{s-1} S_y z_y \right) S_s p_s t_s \left(1 - \prod_{y=s+1}^v S_y \sum_{k=1}^{j-1} S_{v+1,k} R_{sk} \right) \right\}.\end{aligned}$$

2.4.3.4 Conditional Adult Return Rate for Untagged Fish (μ_j^U)

The age- j conditional maturation and return probability, μ_j , in Equation (2.38) is for tagged fish; it can be modified for untagged fish by replacing the t_i parameters with the appropriate values of t_i^U to find μ_j^U . The variance estimator of $\hat{\mu}_j^U$ is simply Equation (2.39), but with t_i^U replacing t_i and allowing for a non-zero $\widehat{Var}(\hat{t}_i^U)$ input by the user.

2.4.4 Inriver Adult Survival

Yearly inriver adult survival from the first adult site (i.e., site $v+1$) to the penultimate adult site (i.e., site $v+u-1$) can be estimated directly from the model parameters. If detection at the final adult site (i.e., site $v+u$) is known, so that $S_{v+u,j}$ is separable from $p_{v+u,j}$, then we can estimate yearly adult survival from site $v+1$ to site $v+u$. It may be of interest to measure the overall inriver survival, S_A , of adults from a particular brood year or outmigration, with all adult age classes combined.

2.4.4.1 Inriver Adult Survival for Tagged Fish (S_A)

Overall adult inriver survival from a particular juvenile release group is the weighted sum of year-specific adult inriver survival probabilities, with weights equal to the entries of the

return age distribution, A_1, \dots, A_w . With detection estimated separately at the final adult site (or assumed to be 100%), we have:

$$S_A = Pr[\text{Survive from } v+1 \text{ to } v+u \mid \text{Reach } v+1] \\ = \sum_{j=1}^w A_j \prod_{k=v+2}^{v+u} S_{kj}. \quad (2.41)$$

If detection is not known at the final adult detection site, then Equation (2.41) may be modified to give the overall adult survival through site $v+u-1$. The estimated variance of \hat{S}_A is:

$$\begin{aligned} \widehat{Var}(\hat{S}_A) &= \sum_{i=v+1}^{v+u} \sum_{k=v+1}^{v+u} \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial S_A}{\partial S_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial S_A}{\partial S_{km}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{ij}, \hat{S}_{km}) \\ &+ \sum_{i=1}^v \sum_{k=1}^v \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial S_A}{\partial R_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial S_A}{\partial R_{km}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{ij}, \hat{R}_{km}) \\ &+ \sum_{i=1}^v \sum_{k=1}^v \left(\frac{\partial S_A}{\partial p_i} \Big|_{\hat{\theta}} \right) \left(\frac{\partial S_A}{\partial p_k} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{p}_i, \hat{p}_k) \\ &+ \sum_{i=1}^v \left(\frac{\partial S_A}{\partial t_i} \Big|_{\hat{\theta}} \right)^2 \widehat{Var}(\hat{t}_i) \\ &+ 2 \sum_{i=v+1}^{v+u} \sum_{k=1}^v \sum_{j=1}^w \sum_{m=1}^w \left(\frac{\partial S_A}{\partial S_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial S_A}{\partial R_{km}} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{ij}, \hat{R}_{km}) \\ &+ 2 \sum_{i=v+1}^{v+u} \sum_{k=1}^v \sum_{j=1}^w \left(\frac{\partial S_A}{\partial S_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial S_A}{\partial p_k} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{S}_{ij}, \hat{p}_k) \\ &+ 2 \sum_{i=1}^v \sum_{k=1}^v \sum_{j=1}^w \left(\frac{\partial S_A}{\partial R_{ij}} \Big|_{\hat{\theta}} \right) \left(\frac{\partial S_A}{\partial p_k} \Big|_{\hat{\theta}} \right) \widehat{Cov}(\hat{R}_{ij}, \hat{p}_k), \end{aligned} \quad (2.42)$$

where $\hat{\theta}$ is the MLE of the vector of model parameters used to calculate \hat{S}_A . The necessary partial derivatives for Equation (2.42) are ($i = 1, \dots, v$ unless otherwise specified):

$$\begin{aligned}
\frac{\partial S_A}{\partial S_{v+1,j}} &= \frac{A_j S_{v+2,j} \cdots S_{v+u,j}}{S_{v+1,j}} \\
&\quad - \sum_{k=1}^w \left(\frac{A_k S_{v+2,k} \cdots S_{v+u,k}}{\sum_{m=1}^w S_{v+1,m}} \left[1 + \frac{\sum_{s=1}^v \{p_s t_s (R_{sj} - R_s) \prod_{l=1}^{s-1} z_l\}}{R_{sys}} \right] \right); \\
\frac{\partial S_A}{\partial S_{ij}} &= \frac{A_j S_{v+2,j} \cdots S_{v+u,j}}{S_{ij}}, \quad \text{for } i = v+2, \dots, v+u; \\
\frac{\partial S_A}{\partial R_{ij}} &= \frac{S_{v+1,j} p_i t_i \prod_{y=1}^{i-1} z_y}{R_{sys} \sum_{m=1}^w S_{v+1,m}} \left(S_{v+2,j} \cdots S_{v+u,j} - \sum_{k=1}^w A_k S_{v+2,k} \cdots S_{v+u,k} \right); \\
\frac{\partial S_A}{\partial p_i} &= \sum_{j=1}^w \frac{\partial A_j}{\partial p_i} S_{v+2,j} \cdots S_{v+u,j}; \\
\frac{\partial S_A}{\partial t_i} &= \sum_{j=1}^w \frac{\partial A_j}{\partial t_i} S_{v+2,j} \cdots S_{v+u,j}.
\end{aligned} \tag{2.43}$$

2.4.4.2 Inriver Adult Survival for Untagged Fish (S_A^U)

The inriver adult survival measure S_A is valid only for tagged fish; to find the comparable measure for untagged fish (S_A^U), replace A_j in Equation (2.41) with A_j^U . The variance of \hat{S}_A^U is estimated by Equation (2.42), but with t_i replaced by t_i^U and allowing for a non-zero $\widehat{Var}(t_i^U)$ input by the user.

2.5 Conceptual Issues

There are several conceptual issues relating to this model that have not been discussed. One deals with fixed parameters that need not be estimated. A second issue is identifying the detection sites to include in analysis. A third issue is that of collapsing across age classes; when is it appropriate and what are the ramifications? These issues are discussed here.

2.5.1 Fixing Parameters

Equation (2.9) is a generalized likelihood that accommodates any number of juvenile and adult detection sites, with censoring and transportation possible at all juvenile sites and

censoring possible at all but the final adult site. For a particular study design or data set, however, it is likely that some detection sites will have neither censoring nor transportation. Additionally, some transportation sites may have no transported smolts returning to BON as adults. In these cases, it is necessary for the user to modify Equation (2.9) by removing the appropriate processes from the model.

For example, there is currently no sampling program at BON, so both the censoring parameter and the censoring statistic at BON are zero: $c_{BON} = 0$ and $d_{BON} = 0$. Similarly, there is no transportation from BON, so $t_{BON} = h_{BON} = 0$. The likelihood in Equation (2.9) is valid with these zero-valued parameters under the interpretation that $0^0 = 1$. For practical purposes, however, all factors involving the parameters c_{BON} and t_{BON} and any other zero-valued parameters should be removed from the likelihood. First, they are extraneous nuisance parameters whose values are already known. Second, any software program used to maximize the likelihood in Equation (2.9) will not interpret 0^0 as 1, and will be unable to fit the model. Also, with no transportation at BON, the TBR parameters for BON, $R_{BON,j}$, are undefined, and factors involving these parameters should be removed from the likelihood. Thus, it is necessary for the user to modify Equation (2.9) to suit the state of the censoring and transportation operations at the time of data collection. The summary statistics identify zero-valued nuisance parameters to be removed; however, these statistics are not included in the minimal sufficient statistics.

It may be that no transported smolts from a particular transportation site return as adults, or that they return in some adult age classes but not in others. For example, consider the case in which no smolts transported at MCN return as adults. This may be due to the small size of the transport group rather than to any negative effect of transportation at MCN. The user must fix the pertinent age- and site-specific TBR values $R_{MCN,j}$ in order to fit the model; equivalently, any factors involving the $R_{MCN,j}$ parameters must be removed from the likelihood in Equation (2.9). If the user has independent estimates of some or all of the $R_{MCN,j}$ parameters, the appropriate parameters may be fixed to these estimates, along with the appropriate standard errors. Without independent estimates and insufficient power to detect a positive $R_{MCN,j}$ value, $R_{MCN,j}$ should be fixed to 1 for use in calculating derived quantities, implying the null hypothesis of no transportation effect. Note that in

this case, $R_{MCN,j}$ are not estimated to be 1, but are rather assumed to be 1 in the absence of sufficient information indicating otherwise.

A related problem is that of transport sites with 100% transportation of detected smolts, i.e., sites with $t_i = 1$. This practice was used in the early and mid-1990s, and is problematic because it leads to an overparameterized model, even with the t_i parameters fixed. In general, changing t_i to 1 from some value between 0 and 1 removes one estimable parameter (t_i , now fixed to 1), and two minimal sufficient statistics: b_i , because no detected fish are released to the river at site i , and h_i , because now $h_i = a_i - d_i$. With $t_i < 1$ for all juvenile detection sites, the model is full rank, so fixing t_i to 1 for any site i makes the model overparameterized. Thus, transportation rates should not be 100% at any transport site. If any sites have 100% transportation, methods such as those developed in Sandford and Smith (2002) should be used to estimate transportation effects.

2.5.2 Identifying Detection Sites

This model is sufficiently flexible to analyze data sets with any number of juvenile and adult detection sites. However, it requires at least one juvenile site and at least two adult sites. Including only a single juvenile site gives little information about the juvenile migration and the effect of any transportation, however, and it is recommended that more sites be used. The second adult site is required to estimate return rates, unless we have independent estimates of detection at the first adult detection site for every year of adult detections. More adult detection sites tell us more about the adult migration. Because adult data comes from several years, there may be adult detection data from a dam for some years but not for others. In this case, the appropriate p_{ij} parameters should be fixed to 0. In general, the more detection sites we include (with high detection rates), the more detailed our data, and the more unbiased and precise our parameter estimates. The model allows for censoring and transportation, but does not require them if they do not occur; however, they and the appropriate detection sites should be included if they do occur. The number of age classes used does not affect the validity of the model, and should be determined based on the biology of the fish and the observed returns; this is discussed in the next subsection.

Ideally, the last juvenile site and first adult site should be as close to the ocean as possible to get as much information about ocean survival as possible. This means that these sites should both be BON. Even in this case, what may be termed “ocean survival” includes maturation and survival through significant inriver reaches; see Section 2.4.2.

2.5.3 *Collapsing age classes*

With no defined upper limit to return age, the oldest age class may potentially include returns over several ages. Additionally, it may be necessary or desirable to combine the jack age class with the youngest adult age class. Current practice is to ignore adult age when estimating return parameters, TBR, and up-river adult parameters. What are the ramifications of this?

If adult age may be legitimately ignored, then we must be able to express the probability of any age-independent adult capture history as the sum of the probabilities of the corresponding age-dependent capture histories. For example, with three adult ages and two adult detection sites, the probability of being detected at both sites for non-transported fish, conditional on survival past the last juvenile site (v), is $\sum_{j=1}^3 S_{v+1,j} p_{v+1,j} \lambda_j$ using age-dependent parameters, and is $S_{v+1} p_{v+1} \lambda$ using age-independent parameters. If adult age classes may be legitimately pooled, then:

$$S_{v+1} p_{v+1} \lambda = S_{v+1,1} p_{v+1,1} \lambda_1 + S_{v+1,2} p_{v+1,2} \lambda_2 + S_{v+1,3} p_{v+1,3} \lambda_3. \quad (2.44)$$

Solutions to Equation (2.44) require that at least two of the three types of parameters $S_{v+1,j}$, $p_{v+1,j}$, and λ_j be constant across age classes. Otherwise, the resulting survival and detection parameters in the collapsed (age-independent) model are functions of all adult parameters from the uncollapsed (age-dependent) model. For example, one solution to Equation (2.44) is:

$$\begin{aligned}
S_{v+1} &= S_{v+1,1} + S_{v+1,2} + S_{v+1,3}; \\
p_{v+1} &= \frac{S_{v+1,1}p_{v+1,1} + S_{v+1,2}p_{v+1,2} + S_{v+1,3}p_{v+1,3}}{S_{v+1,1} + S_{v+1,2} + S_{v+1,3}}; \\
\lambda &= \frac{S_{v+1,1}p_{v+1,1}\lambda_1 + S_{v+1,2}p_{v+1,2}\lambda_2 + S_{v+1,3}p_{v+1,3}\lambda_3}{S_{v+1,1}p_{v+1,1} + S_{v+1,2}p_{v+1,2} + S_{v+1,3}p_{v+1,3}}.
\end{aligned} \tag{2.45}$$

The parameter S_{v+1} is the ocean return probability for non-transported fish, and p_{v+1} and λ are weighted sums of the $p_{v+1,j}$ and λ_j parameters, respectively. Alternatively, p_{v+1} and λ may be defined as:

$$\begin{aligned}
p_{v+1} &= \frac{S_{v+1,1}p_{v+1,1}\lambda_1 + S_{v+1,2}p_{v+1,2}\lambda_2 + S_{v+1,3}p_{v+1,3}\lambda_3}{S_{v+1,1}\lambda_1 + S_{v+1,2}\lambda_2 + S_{v+1,3}\lambda_3}; \\
\lambda &= \frac{S_{v+1,1}\lambda_1 + S_{v+1,2}\lambda_2 + S_{v+1,3}\lambda_3}{S_{v+1,1} + S_{v+1,2} + S_{v+1,3}}.
\end{aligned} \tag{2.46}$$

In either case, S_{v+1} is biologically meaningful, but p_{v+1} and λ are not, because they both involve parameters other than their age-specific counterparts. Detection and the last reach parameter (λ) are typically nuisance parameters, so if the focus is on return probabilities, then collapsing age classes is reasonable. However, it is obvious that there are two consistent solutions to Equation (2.44), and in fact, there are more. For instance, p_{v+1} may be defined as $p_{v+1,1} + p_{v+1,2} + p_{v+1,3}$, and S_{v+1} and λ as weighted sums of $S_{v+1,j}$ and λ_j , respectively. With more adult detection sites, the parameters in the collapsed-age model will be yet more convoluted, including biologically interesting adult reach survival parameters.

The above discussion ignores transportation. If there is transportation from site 1, then collapsing the three adult age classes would give:

$$S_{v+1}R_1p_{v+1}\lambda = S_{v+1,1}R_{11}p_{v+1,1}\lambda_1 + S_{v+1,2}R_{12}p_{v+1,2}\lambda_2 + S_{v+1,3}R_{13}p_{v+1,3}\lambda_3, \tag{2.47}$$

in addition to Equation (2.44). Following the inriver case above, a possible solution to Equation (2.47) is:

$$\begin{aligned}
S_{v+1} &= S_{v+1,1} + S_{v+1,2} + S_{v+1,3}; \\
R_1 &= \frac{S_{v+1,1}R_{11} + S_{v+1,2}R_{12} + S_{v+1,3}R_{13}}{S_{v+1,1} + S_{v+1,2} + S_{v+1,3}}; \\
p_{v+1} &= \frac{S_{v+1,1}R_{11}p_{v+1,1} + S_{v+1,2}R_{12}p_{v+1,2} + S_{v+1,3}R_{13}p_{v+1,3}}{S_{v+1,1}R_{11} + S_{v+1,2}R_{12} + S_{v+1,3}R_{13}}; \\
\lambda &= \frac{S_{v+1,1}R_{11}p_{v+1,1}\lambda_1 + S_{v+1,2}R_{12}p_{v+1,2}\lambda_2 + S_{v+1,3}R_{13}p_{v+1,3}\lambda_3}{S_{v+1,1}R_{11}p_{v+1,1} + S_{v+1,2}R_{12}p_{v+1,2} + S_{v+1,3}R_{13}p_{v+1,3}}.
\end{aligned} \tag{2.48}$$

The parameter S_{v+1} is the ocean return probability for non-transported fish, R_1 is the isolated site-specific TBR derived in Section 2.4.1.2, and p_{v+1} and λ are weighted sums of the $p_{v+1,j}$ and λ_j , respectively. Note that the solution in Equation (2.48) is not consistent with the solutions from the non-transport case above (Equations (2.45) and (2.46)), because p_{v+1} and λ both depend on the R_{1j} parameters here. To make the transport and non-transport cases consistent, the TBR, detection, and λ parameters in Equation (2.48) must be redefined:

$$\begin{aligned}
S_{v+1} &= S_{v+1,1} + S_{v+1,2} + S_{v+1,3}; \\
R_1 &= \frac{S_{v+1,1}R_{11}p_{v+1,1}\lambda_1 + S_{v+1,2}R_{12}p_{v+1,2}\lambda_2 + S_{v+1,3}R_{13}p_{v+1,3}\lambda_3}{S_{v+1,1}p_{v+1,1}\lambda_1 + S_{v+1,2}p_{v+1,2}\lambda_2 + S_{v+1,3}p_{v+1,3}\lambda_3}; \\
p_{v+1} &= \frac{S_{v+1,1}p_{v+1,1} + S_{v+1,2}p_{v+1,2} + S_{v+1,3}p_{v+1,3}}{S_{31} + S_{v+1,2} + S_{v+1,3}}; \\
\lambda &= \frac{S_{v+1,1}p_{v+1,1}\lambda_1 + S_{v+1,2}p_{v+1,2}\lambda_2 + S_{v+1,3}p_{v+1,3}\lambda_3}{S_{v+1,1}p_{v+1,1} + S_{v+1,2}p_{v+1,2} + S_{v+1,3}p_{v+1,3}}.
\end{aligned} \tag{2.49}$$

This solution to Equation (2.47) is consistent with the solution to Equation (2.44), but it is inconsistent with the derivation of the site-specific TBR, R_1 , from Section 2.4.1.2. In fact, any solution to Equation (2.47) that does not involve the R_{1j} parameters in the definitions of S_{v+1} , p_{v+1} , and λ will be inconsistent with the derivation of R_1 in Section 2.4.1.2, unless the adult parameters are constant over age class (i.e., over years). With only two adult detection sites, S_{v+1} and R_i are the only biologically interesting adult parameters; however, with more adult detection sites, parameters in the collapsed-age model will be more

convoluted, including biologically useful adult upriver survival parameters. Thus, if there is transportation in the model, collapsing the age classes is invalid, unless the age-specific adult parameters are constant over years.

Adult detection data should not be pooled across return years unless adult parameters are constant across years. However, it may be necessary to combine some age classes due to low adult return rates or detection rates. In such cases, it should be acknowledged that the resulting survival, detection, and TBR parameters have no biological interpretation unless at most one of them varies across age classes. This is especially important if adult upriver survival is a focus on the investigation, though less important if adult return rates to freshwater or TBR is the focus, because neither depends on upriver adult parameters.

The common practice of estimating smolt-to-adult return rates (SARs) by the ratio of fish recovered at the release site to those released, regardless of return year, gives a valid return rate estimate despite collapsing adult age classes, as long as detection at the final site is accounted for. It is not the pooling of returns over adult age classes that is problematic in this case, but rather the estimation of detection and potential overlooking of censoring.

2.6 Comparison with Current Practices

2.6.1 Juvenile Survival

PIT-tagging of juvenile migrating salmonids is standard practice in the Snake and Columbia Rivers. Until the early 1990s, detection of PIT-tagged smolts in juvenile bypass systems was possible only at LGR, LGO, LMO, and MCN for Snake River salmon, and at Rocky Reach and MCN for upper Columbia River salmon; since then, detection of juveniles is also possible at JD and BON. Researchers currently use Cormack-Jolly-Seber (CJS; Cormack, 1964, Seber, 1965, and Jolly, 1965) methods with juvenile detection data to estimate reach survival of juveniles as they migrate through the hydrosystem; for examples, see Iwamoto et al. (1994), Muir et al. (1995), Muir et al. (1996), Muir et al. (2001a), Skalski et al. (1998), and Smith et al. (1998). Before detections at JD and BON were possible, survival could be estimated only to LMO using CJS methods; with detections at JD and BON, survival can be estimated to MCN and JD. In the absence of lower reach detection data, researchers ex-

trapolated survival on a per-project or per-km basis to estimate survival through the lower reaches. Extrapolations on a per-km basis are typically, but not always, closer to empirical estimates based on CJS methods than are per-project-based extrapolations (NOAA Fisheries, 2000c), but both methods ignore additional mortality risks in lower reaches due to slower moving water, increased densities of predators, and different configuration of juvenile bypass outlets (Bouwes et al., 1999).

PIT-tag detection of adults has recently become available at several dams along the lower Columbia and Snake rivers (BON, MCN, IH, and LGR), as well as at Priest Rapids, Rock Island, and Wells on the upper Columbia. The approach described in this chapter incorporates adult detections into the CJS methods previously used, and provides empirical model-based estimation of juvenile survival to BON, rather than extrapolation-based estimates. Current practice is to estimate reach survival estimates for daily release groups. Daily release groups may not provide enough adult detections to use CJS methods to estimate daily survival through the JD-BON reach, but release groups may be pooled suitably to provide sufficient return data. A drawback of using adult data to estimate juvenile survival is the need to wait several years for adult detections.

2.6.2 Adult Return Rates

The current practice of estimating adult return rates is to estimate the smolt-to-adult return rate, or SAR. The parameter SAR is the ratio of the number of adult returns to the number of juveniles released, typically counting both at LGR for Snake River fish (NOAA Fisheries, 2000c). The measure SAR is estimated using counts of juveniles and adults, with adjustments for detection rates when possible. Adults are typically pooled over return years. Because estimates of SAR are not model-based, bootstrapping is used to find variance estimates (Sandford and Smith, 2002). Often, different SAR estimates are computed for fish with different juvenile detection histories; for example, only those fish undetected at any transport site may be included, to mimic the passage history of untagged fish (Sandford and Smith, 2002).

The approach taken in this chapter is model-based, and very flexible. Return rates may

be derived from BON to BON, or from LGR to LGR, as demonstrated in Section 2.4.2. Thus, it is possible to derive model-based estimates of SAR to and from any site desired and for any detection history. The exception is that because we cannot separate survival and detection at the final adult site, we cannot estimate survival or return rates to that site. On the other hand, we have model-based estimates of precision, and estimators (MLEs) with well-known properties. The model parameter return rates are year-specific, but may be combined to give the overall return rate for fish from a given outmigration year, as shown in Section 2.4.2.

2.6.3 *Transportation Effect*

Transportation effect is typically estimated by two groups: dam operators, interested primarily in the effects of operations at their own dam, and organizations such as hatcheries, tribes, and NOAA Fisheries, interested in the overall effect of the entire hydrosystem on survival and return rates. There are multiple ways to define or quantify a transportation effect, but all essentially compare the SAR of transported fish to the SAR of non-transported (control) fish. Historically, batch marks such as coded wire tags, freeze brands, or fin clips have been used, with both treatment (transport) and control (inriver) groups released at a transport dam. The effect of transportation from a particular dam on adult returns was estimated using Ricker's relative recovery rate method (Ricker, 1975; Burnham et al., 1987), producing a quantity variably referred to as the transport-control ratio T/C or T:C, transport benefit ratio TBR, and transport-inriver ratio T/I. This value is simply the ratio of relative recoveries:

$$\frac{n_T/N_T}{n_C/N_C}, \quad (2.50)$$

where N_T (N_C) is the number of transport (control) fish released at a dam and n_T (n_C) is the number of subsequent recoveries, adjusted for detection efficiency. In some cases, it was acknowledged that T/I as defined in (2.50) needed to be adjusted due to possible downstream transportation of control fish, but possible adjustments were not suggested until Ward et al. (1997). The general assumption was that any downstream transportation

would increase adult returns of control fish, so the unadjusted T/I value from (2.50) is a minimal value. Ward et al. (1997) suggested dividing T/I by the fraction of the control fish reaching the transport release site that reached it wholly inriver, in order to account for downstream transportation of control fish.

Because individuals in the control (inriver) group may be transported downstream, the quantity in Expression (2.50) is similar to the site-specific TBR RC_i developed in Section 2.4.1.3. However, RC_i ignores censoring of control fish, whereas individuals in N_C and n_C may be sampled (censored) downstream, and either removed permanently or allowed to continue migrating. If all sampled fish continue migrating and then return as adults at the same rate as those not sampled, then RC_i is the first-order Taylor Series approximation of the expected value of the ratio in Expression (2.50). However, if sampling affects adult return rates, then Expression (2.50) is a biased estimator of RC_i . We can include censoring in RC_i , but we cannot account for the effect of censoring on return rates. Censoring is a nuisance parameter, and we would like to ignore it. Unfortunately, Expression (2.50) incorporates censoring's effects on return rates. On the other hand, the model presented in this chapter accounts for censoring in fitting the data, and so both R_i and RC_i give valid TBRs in which censoring is appropriately ignored. Further, Expression (2.50) is estimated from tagged fish, and so is valid for untagged fish only if transportation operations are the same for both tagged and untagged fish. Thus, Expression (2.50) may be applied to untagged fish if it is estimated from batch-marked fish, but not if it is estimated from PIT-tagged fish. On the other hand, the measure RC_i^U is a valid TBR for fish in the release group, if treated as untagged, in the presence of downstream censoring and transportation. The measures R_i and RC_i^U are preferable to Expression (2.50), given enough adult detections to make them estimable. Dam operators should use R_i if they are interested only in the effect of transportation from their dam, regardless of transportation at other dams; if they choose to view the effect of their transportation program in the context of the entire hydrosystem, they should use RC_i^U .

With the advent of PIT tags, individual capture histories at juvenile dams became available, and it became possible to identify the control fish from a particular transportation study that were transported from a downstream site. In addition, PIT tags allow trans-

portation to be assessed without deliberate paired treatment-control releases at each of the transport dams. Instead, transport and control (inriver) fish may be identified from the capture histories, and then SARs from each group may be compared (Sandford and Smith, 2002). Sandford and Smith (2002) use only the capture histories of tagged fish that mimic valid passage histories of untagged fish, namely those with at most one detection at any of the transport dams, including the dam at which they are transported (if any).

One issue raised by using PIT tags to estimate a transportation effect is how to estimate the size of the release groups, N_T and N_C . The capture histories tell us the size of the transport group from a particular dam, but without using a deliberate paired release at each dam, we do not know the size of the control group at the dam. This is because the control group includes those fish not detected (bypassed) at the dam, because they are inriver fish by definition; we cannot identify all these fish from the capture histories. The number N_C must be estimated. Sandford and Smith (2002) provide a method of estimating the size of the control group for each dam using estimates of detection (bypass) rates. They effectively condition on survival to the final transport site by using “LGR equivalents” in estimating the size of the release groups (transport as well as control). The “LGR equivalent” for a particular release group (transport or inriver at dam i) is the number of study fish that were alive at LGR (the first transport site on the Snake River) that were “destined” for that particular release group, had they survived to dam i . Because survival between LGR and any downriver transport site i is assumed to be the same for those fish destined to be transported at i as for those destined to pass i inriver, the resulting site-specific estimator in Sandford and Smith (2002) estimates R_i , developed in Section 2.4.1.2. Sandford and Smith (2002)’s estimator is designed for daily release groups, uses adult data pooled across return years, and is not model-based, thus requiring the bootstrap to estimate standard errors.

The current practice of quantifying a system-wide transportation effect is to compare the SAR of transported smolts to the SAR of non-transported smolts for a given outmigration year, species, and run type; often only part of the outmigration season is considered, because SAR values tend to vary seasonally. However, most literature (e.g., Ward et al., 1997; Sandford and Smith, 2002) describes how to define and measure dam-specific T/I values, rather than system-wide values. Nevertheless, often a single value is reported that combines

several or all dams, and it is not clear how that value is found. For example, Sandford and Smith (2002) use LGR equivalents to combine transport groups from different dams, but do not explain how. Their multiple-site estimator appears to estimate a quantity similar to R_{cond} , without adjustment by the survival rates between the transport site and the final transport site (see Section 2.4.1.7).

Another commonly used measure of transportation effect is D , or differential delayed mortality. The measure D is the ratio of post-BON survival for the transport group relative to the control (inriver) group, and is related to T/I :

$$T/I = \frac{SAR_T}{SAR_I} = \frac{S_{BON,T}}{S_{BON,I}} \times D, \quad (2.51)$$

where SAR_x is the smolt-to-adult return rate for fish in treatment group x (either transport [$x = T$] or inriver [$x = I$]), and $S_{BON,x}$ is survival from the point of transportation (typically LGR) to the release point below BON for fish in treatment group x . The value $D < 1$ implies lowered survival of transported smolts after release from BON compared to inriver smolts, or delayed mortality for transported smolts. Typically, $D < 1$, possibly due to delayed onset of disease relative to passage through the hydrosystem, lack of previous culling of weak individuals, or disease due to the stress of transportation (NOAA Fisheries, 2000c). It is traditionally assumed that survival of transported smolts during transportation ($S_{BON,T}$) is approximately 1 (0.98; USACE, 1993). Thus, if differential delayed mortality (D) is greater than the survival of non-transported smolts through the hydrosystem, then $T/I > 1$; otherwise, $T/I \leq 1$.

There have been disagreements over how to estimate both T/I and D (e.g., Bouwes et al., 1999), most of which were alluded to above: Should the capture histories used mimic those of untagged fish? How should the size of the control group be estimated? How should multiple sites be combined without inappropriately including survival between the sites? A further issue is that the transport group used does not always include transported fish from all transport sites. For example, it may include only sites LGR and LGO, ignoring transports from LMO and MCN (Bouwes et al., 1999). Estimates of D are based on the assumption that barge survival is 0.98, regardless of transportation site, migration year,

species, or run. Even if 0.98 is a valid assumption, estimates of D depend on the method of estimating survival to BON for non-transport fish; often, this has been extrapolation on a per-km or per-project basis.

Part of the confusion in estimating a transportation effect stems from poorly explained or poorly conceived definitions of T/I , which in turn arise from the tradition of using the relative recovery method and having to estimate release numbers N_T and N_C . In the past, with only batch marks or juvenile detections of PIT tags available, it was necessary to use the relative recovery method or some modification of it, such as that proposed by Sandford and Smith (2002). With improved detection of adults at several dams, however, it is no longer necessary to rely on Ricker's relative recovery method and the necessary modifications; instead, a model-based approach is available to estimate transportation effect, as developed in this chapter. Extrapolation is no longer required to estimate survival to BON for inriver fish; instead, survival to BON can be estimated directly, along with standard errors of model parameters. While the common method of quantifying transportation effects ignores the year or age class of adult return, the method devised here is age-class specific, and provides ways of combining age-specific TBR values to find a value specific to a given transport site. The model also demonstrates that pooling across adult age classes is generally invalid. Variances of model-based, derived TBR values may be approximated using the delta method (Seber, 1982, pp. 7-9). This model assumes that transportation affects only juvenile outmigration and ocean survival, as well as maturation rates and survival back to BON as an adult, rather than affecting up-river adult survival and straying rates; thus, unlike T/I , the TBR values consider return rates only to BON rather than to the transport site or to LGR. However, the model may easily be expanded to estimate transportation effects on return rates to LGR, as long as there is adult detection above LGR or an independent estimate of adult detection rates at LGR.

Without a model-based approach, it is necessary to estimate the sizes of groups with different capture histories, including those with no detections, in order to estimate the SAR values necessary for T/I and D estimation. Estimators become complicated and difficult to understand, and focus is diverted from definitions of desirable quantities. The model-based approach both allows and requires us to focus on definitions of quantities to estimate.

Once a precise, reasonable, and estimable definition is formed, it can be expressed using model parameters, even if it involves undetected or untagged individuals. The model-based approach suggests avoiding a conditional definition of system-wide TBR such as R_{cond} or T/I , and instead suggests using a comparison of unconditional return rates with and without transportation. The model-based approach also makes this comparison possible.

Model parameters may be used to express and estimate D , assuming barge survival is known. From Equation (2.51) and replacing T/I with a model-based TBR, we have

$$D = \frac{TBR \times S_{BON,I}}{0.98}.$$

Using a site-specific TBR such as R_i or RC_i^U gives a site-specific D . Expressing a system-wide D is more difficult, due to the difficulties with expressing a conditional system-wide TBR value. Using R_{sys} or R_{sys}^U is inappropriate, because the treatment fish in those quantities include inriver fish whose survival to BON is not 0.98. Nevertheless, an expression for delayed differential mortality due to the transportation system could be derived using the model parameters and the assumption that all barge survival is 0.98, or some other accepted value.

2.6.4 Adult Survival

The usual method of estimating survival of adults during the upriver migration is to compare counts of adults at upper dams with counts at lower dams. Counts are adjusted for known removals, including removals at dams, known catches in downriver fisheries, and known turn-offs to tributaries and spawning grounds. It is unlikely that all fish caught in every fishery or reaching every spawning ground are reported, so the number of known removals is problematic. Also, fallbacks positively bias counts at downstream dams, and negatively bias estimates of adult reach survival. In the last decade, some studies have used radio telemetry to better identify removals and fallbacks; e.g., see Bjornn, Keefer and Stuehrenburg (1999), NOAA Fisheries (2000b), and Keefer et al. (2002). These studies also use dam counts to estimate survival, assuming 100% detection of radio-tagged fish at the dams. In addition to adjusting for known removals, the radio telemetry studies also adjust

for fallback. Estimating the precision of survival estimates is still a problem. In addition, study fish are tagged with radio tags as they pass BON as adults. Typically, the hatcheries or natal tributaries of these fish are unknown (see Ross and Domingue, 2004, however). Tracking non-known-source fish prevents researchers from distinguishing among mortality, straying, and turn-offs to natal tributaries, and so only perceived survival between dams can be estimated.

The approach taken here is model-based using adult PIT-tag data. Adults return to the Columbia River hydrosystem with PIT tags they received as juveniles. To some extent, these tagged adults are known-source fish: although their spawning grounds may be unknown, the hatchery or trap at which they were tagged as juveniles is known. Also, if the juveniles were tagged and released at a dam (e.g., LGR), they are known to have originated upstream of that dam. Thus, apparent mortality estimated by the model includes straying and harvesting, but does not include loss due to valid exit to tributaries and spawning grounds below LGR. Because survival is based on individual-specific detection histories rather than counts of batch-marked (or unmarked) individuals, fallback does not directly bias the survival estimates as in the count-based method. On the other hand, this model is not designed to address fallback specifically; fish that fallback over a dam and do not reascend will negatively bias survival in the reach above the dam. The model depends on efficient PIT-tag detection in the adult ladders, and is not feasible without it.

2.7 1999 Summer Chinook Salmon Example

In this section, I present an example of using the life-cycle PIT-tag model to estimate reach survival probabilities, transportation effect measures, and other performance measures. The data presented here were downloaded in May, 2004 from PTAGIS, the PIT-tag database maintained by PSMFC. These data represent all PIT-tag detection records for $N = 51,318$ summer Chinook salmon from the McCall and Pahsimeroi hatcheries, released as smolts in the Snake River or its tributaries upstream of Lower Granite Dam (LGR) in 1999. These fish were released in multiple release groups in multiple locations, but are treated in this model as being in a single release group. Thus, the survival parameter to the first detection site, Lower Granite Dam, is not biologically meaningful for any given release group, but

rather is a weighted average of the survival rates experienced by each release group. Other parameters are biologically meaningful for all fish, with the caveat that we are ignoring within-year temporal variations in survival, detection, censoring, and transportation rates.

Figure 2.8 shows a schematic of the detection sites for this data set. There were six juvenile detection sites (1=LGR, 2=LGO, 3=LMO, 4=MCN, 5=JD, and 6=BON) and two adult detection sites (7=BON and 8=LGR). Transportation was possible at LGR, LGO, LMO, and MCN. Only five summer Chinook salmon were transported from MCN in 1999. Returning adults were detected at BON and LGR in 1999 (“jacks”), 2000, 2001, and 2002. There were very few jacks, so adult detections in 1999 and 2000 were combined to form age class 1, with adults in 2001 and 2002 forming age classes 2 and 3, respectively. The modified m -array for these data is given in Table 2.11. Of the 51,318 tagged smolts released, 26,274 were detected during the juvenile migration at one or more of the six juvenile detection sites, and 1,007 adults were detected during the spawning migration at either BON or LGR dams. Of those detected as juveniles, 10,538 were transported, 14,526 were returned to the river after each detection, and the remaining 1,210 were censored due to sampling at the dams. Of the detected adults, 472 had been transported as juveniles, and 535 had not been transported (Table 2.11.) No adult censoring occurred.

No fish transported from LMO returned in the first age class, i.e., in years 1999 or 2000. The MLE of the age-1 TBR parameter for LMO (R_{31}) is therefore 0, but because of the small size of the transport group at LMO, and the low ocean return rate for age class 1, R_{31} would need to be > 1.5 in order for the expected number of adult returns from that group to be > 1 in the age class 1. Because we did not have sufficient power to detect an age-1 transportation effect from LMO, we fixed R_{31} at 1 in order to fit the model. This is consistent with the null hypothesis of no effect of transportation at LMO on age-1 return rates.

Only five summer Chinook salmon were transported from MCN in 1999. It was impossible to detect a transportation effect from so small a transport group, so these fish were treated as if censored at MCN in order to fit the model. In calculating the TBR measures and other performance measures, R_{4j} was fixed to 1 (i.e., no effect of transportation at MCN) for $j = 1, 2, 3$, although no derived TBR measures are reported for MCN. The con-

ditional transportation rate at MCN for untagged fish, t_4^U , was fixed to 0 for calculating performance measures. The conditional transportation rates for the other transport sites were fixed to 1: $t_1^U = t_2^U = t_3^U = 1$.

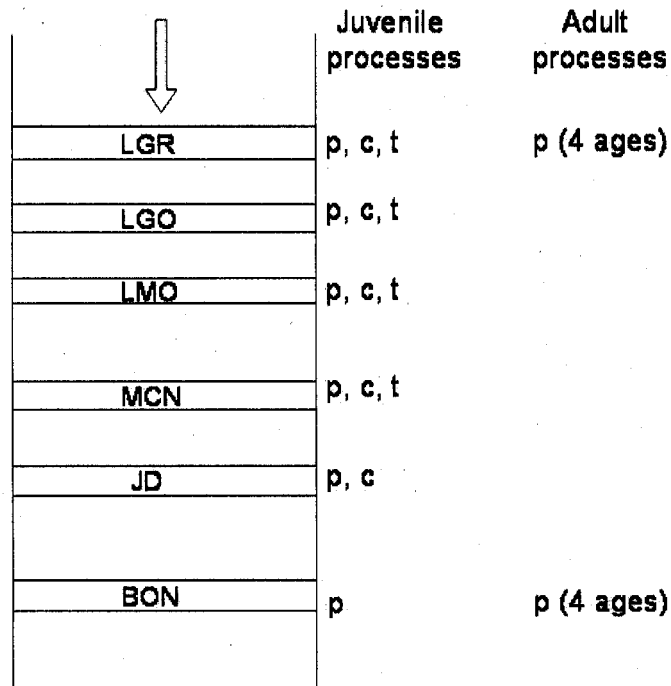


Figure 2.8: Schematic for 1999 summer Chinook salmon data set. A schematic of the hydrosystem with six dams (LGR, LGO, LMO, MCN, JD, and BON) is shown, with the arrow indicating direction of flow. The processes available at each dam as a juvenile site and as an adult site are indicated: p = detection, c = censoring, t = transportation. Adult sites with detection indicate the number of age classes for which detection occurs.

Maximum likelihood estimates were found using the formulas in Table 2.10, and used as seeds in a numerical estimation routine used to estimate standard errors. The resulting MLEs and standard errors are given in Table 2.12. In general, standard errors on survival estimates increased going downriver: $\widehat{SE}(\hat{S}_1) = 0.008$, $\widehat{SE}(\hat{S}_4) = 0.012$, and $\widehat{SE}(\hat{S}_6) = 0.054$. This is logical because there is less information about the immediate fate of fish

passing downriver sites than of those passing upriver sites. Also, with so few smolts returning as adults, it is primarily the downriver juvenile sites that provide information about upriver smolt survival, implying that improved adult detection cannot replace downriver juvenile detection requirements when estimating juvenile survival.

Table 2.13 lists the estimated TBR measures for this release of summer Chinook salmon in 1999. Values of estimated TBR measures ranged from $\hat{R}_{32} = 0.768$ ($\widehat{SE} = 0.412$) to $\hat{R}_{33} = 3.003$ ($\widehat{SE} = 1.993$). Site-specific values of the isolated TBR measures R_i were highest at LGR ($\hat{R}_1 = 2.015$, $\widehat{SE} = 0.152$), intermediate at LGO ($\hat{R}_2 = 1.396$, $\widehat{SE} = 0.112$) and lowest at LMO ($\hat{R}_3 = 1.098$, $\widehat{SE} = 0.403$) (Table 2.13). It makes sense that isolated TBR values were higher for upriver sites if transportation was beneficial, because smolts transported from upriver sites avoided passage through more dams than smolts transported from downriver sites. Thus, R_i reflects the relative location of site i in the hydrosystem, as well as the effectiveness of the transportation operations at site i . The difference between the isolated and contextual site-specific TBR values was greatest at LGR, with an isolated value of $\hat{R}_1 = 2.105$ and a contextual value of $\widehat{RC}_1 = 1.857$ ($\widehat{SE} = 0.134$) (Table 2.13). The contextual TBR value at LGR was smaller than the isolated value there due to substantial smolt transportation downriver at LGO ($\hat{t}_2 = 0.4413$, $\widehat{SE} = 0.0045$) with a TBR > 1 (i.e. $\hat{R}_2 = 1.396$, $\widehat{SE} = 0.112$). The isolated and contextual TBR values at LGO were nearly identical because downriver transportation was inconsequential ($\hat{t}_3 = 0.0271$, $\widehat{SE} = 0.0020$) with a TBR of approximately 1 (i.e. $\hat{R}_3 = 1.098$, $\widehat{SE} = 0.403$) at LMO (Tables 2.12, 2.13). The contextual TBR values for tagged and untagged fish, RC_i and RC_i^U , were slightly different for both LGR and LGO. For both LGR and LGO, $\widehat{RC}_i^U < \widehat{RC}_i$ because a larger proportion of the untagged control fish benefited from downriver transportation than of the tagged control fish. The difference between the tagged and untagged values was greater at LGR than for LGO because transportation at LGO appeared more beneficial (for LGR control fish) than transportation at LMO (for LGO control fish).

Table 2.11: Modified m-array for summer Chinook salmon released in the Snake River above LGR in 1999. Adult age classes are: 1 = 1999 and 2000 adults; 2 = 2001 adults; 3 = 2002 adults. The first column identifies the release site for the row. Transport sites have 2 release rows: row 1 is the non-transported group, and row 2 is the transport group (labeled “-Tr”).

Site (age class)	Juvenile Detection Sites						Adult Detection Sites (age class)									Number recaptured
	Release	LGR	LGO	LMO	MCN	JD	BON	BON			LGR					
								(1	2	3)	(1	2	3)			
Initial	51,318	7,311	11,495	4,142	1,964	552	810	2	30	8	19	65	16	26,414		
LGR	1,896		835	285	156	46	57	0	3	0	0	5	2	1,389		
LGR-Tr	5,007							5	75	7	26	126	19	258		
LGO	6,772			2,415	1,087	295	348	0	9	3	3	28	3	4,191		
LGO-Tr	5,350							6	58	8	20	98	19	209		
LMO	6,317				1,718	574	546	1	22	4	8	40	6	2,919		
LMO-Tr	176							0	1	1	0	2	1	5		
MCN	4,739					712	628	2	21	2	15	37	7	1,424		
MCN-Tr	5							0	0	0	0	0	0	0		
JD	2,115															
BON	2,709						320	1	11	2	5	23	2	364		
BON (1)	19							2	36	2	10	69	11	130		
BON (2)	266										17			17		
BON (3)	37											217		217		
													28	28		
Number detected		7,311	12,330	6,842	4,925	2,179	2,709	19	266	37	123	710	114			
Number censored		408	208	349	181	64	0	0	0	0						

Table 2.12: Maximum likelihood estimates for summer Chinook salmon released in the Snake River upstream of LGR in 1999. The first or only subscript is the index of the detection site: 1=LGR (juvenile), 2=LGO, 3=LMO, 4=MCN, 5=JD, 6=BON (juvenile), 7=BON (adult), 8=LGR (adult). Where present, the second subscript indicates the adult age class: 1 = 1999 and 2000 adults; 2 = 2001 adults; 3 = 2002 adults.

Category	Parameter	Estimate	S.E.
Juvenile Survival Rate	S_1	0.6506	0.0076
	S_2	0.9123	0.0135
	S_3	0.9403	0.0125
	S_4	0.9093	0.0197
	S_5	1.1069	0.0535
	S_6	0.6162	0.0536
Juvenile Detection Rate	p_1	0.2190	0.0033
	p_2	0.4832	0.0043
	p_3	0.3646	0.0052
	p_4	0.2969	0.0065
	p_5	0.1200	0.0059
	p_6	0.2430	0.0185
Conditional Juvenile Censoring Rate	c_1	0.0558	0.0027
	c_2	0.0169	0.0012
	c_3	0.0510	0.0027
	c_4	0.0368	0.0027
	c_5	0.0294	0.0036
Conditional Transportation Rate	t_1	0.7253	0.0054
	t_2	0.4413	0.0045
	t_3	0.0271	0.0020
	t_4	0.0011	0.0005
Age-Specific Joint Ocean Survival and Maturation	S_{71}	0.0067	0.0011
	S_{72}	0.0410	0.0038
	S_{73}	0.0075	0.0012
Adult Detection Rate	p_{71}	0.1382	0.0312
	p_{72}	0.3056	0.0173
	p_{73}	0.2456	0.0404
Final Reach	λ_1	0.8947	0.0704
	λ_2	0.8158	0.0238
	λ_3	0.7567	0.0706
Age- and Site-Specific TBR	R_{11}	1.9079	0.4131
	R_{12}	2.1083	0.1816
	R_{13}	1.6000	0.3709
	R_{21}	1.3663	0.3115
	R_{22}	1.3971	0.1306

Table 2.12 continued

Category	Parameter	Estimate	S.E. I
Age- and Site-Specific TBR	R_{23}	1.4187	0.3229
	R_{32}	0.7678	0.4125
	R_{33}	3.0031	1.9928

For this release of tagged summer Chinook salmon smolts, the system-wide TBR was estimated to be $\hat{R}_{sys} = 1.232$ ($\widehat{SE} = 0.036$) with an asymptotic 95% confidence interval of (1.164, 1.303). Thus, the transportation system, as operated during the juvenile migration of summer Chinook salmon in 1999, was estimated to increase the smolt-to-adult return rate by 23% for tagged fish. Had the release group been treated as untagged smolts, the transportation system was estimated to have increased the smolt-to-adult return rate by 39% ($\hat{R}_{sys}^U = 1.386$, $\widehat{SE} = 0.088$; Table 2.13). The difference in system-wide TBR values between tagged and untagged smolts was caused by the assumption that all untagged smolts entering the bypass systems were transported (i.e., $t_i^U = 1$ for $i = 1, 2, 3$.)

Table 2.14 gives estimates of other performance measures for summer Chinook salmon released in 1999 upriver of Lower Granite Dam. The estimated ocean return rate for non-transported fish was $\hat{O}_{NT} = 0.0552$ ($\widehat{SE} = 0.005$), while the estimated ocean return rates for transported fish ranged from $\hat{O}_{T_3} = 0.0376$ ($\widehat{SE} = 0.014$) to $\hat{O}_{T_1} = 0.0592$ ($\widehat{SE} = 0.004$). The probability of returning from the release site to BON as an adult was $\widehat{SAR}_{(v+1)} = 0.0236$ ($\widehat{SE} = 0.001$) for tagged fish and $\widehat{SAR}_{(v+1)}^U = 0.0265$ ($\widehat{SE} = 0.002$) for untagged fish. The probability of returning from the release site to LGR as an adult, assuming 100% adult detection at LGR, was $\widehat{SAR}_{(v+u)} = 0.0193$ ($\widehat{SE} = 0.001$) for tagged fish and $\widehat{SAR}_{(v+u)}^U = 0.0216$ ($\widehat{SE} = 0.001$) for untagged fish. Return probabilities were higher for untagged fish due to the assumption that all untagged smolts entering bypass systems were transported, together with the estimated benefit of transportation. The return age distribution was $(\hat{A}_1, \hat{A}_2, \hat{A}_3) = (0.1192, 0.7509, 0.1299)$ with standard errors $\widehat{SE} = (0.013, 0.017, 0.014)$ for tagged fish, and $(\hat{A}_1^U, \hat{A}_2^U, \hat{A}_3^U) = (0.1172, 0.7282, 0.1546)$ with standard errors $\widehat{SE} = (0.014, 0.029, 0.029)$ for untagged fish. The conditional return distribution was $(\hat{\mu}_1, \hat{\mu}_2, \hat{\mu}_3) = (0.0064, 0.0404, 0.0073)$ with standard errors $\widehat{SE} = (0.001, 0.002, 0.001)$. This result implies that the probability of returning as an age-1 adult, conditional on having

Table 2.14: Estimated performance measures for summer Chinook salmon released in the Snake River upstream of LGR in 1999.

Performance Measure		Estimate	Standard Error
Ocean Return Rate			
Non-transported	O_{NT}	0.0552	0.005
Site-1 transport	O_{T_1}	0.0592	0.004
Site-2 transport	O_{T_2}	0.0450	0.003
Site-3 transport	O_{T_3}	0.0376	0.014
Site- $v + 1$ Smolt-to-Adult Return Rate			
Tagged	$SAR_{(v+1)}$	0.0236	0.001
Untagged	$SAR_{(v+1)}^U$	0.0265	0.002
Site- $v + u$ Smolt-to-Adult Return Rate			
Tagged	$SAR_{(v+u)}$	0.0193	0.001
Untagged	$SAR_{(v+u)}^U$	0.0216	0.001
Age Distribution, Tagged Fish			
	A_1	0.1192	0.013
	A_2	0.7509	0.017
	A_3	0.1299	0.014
Age Distribution, Untagged Fish			
	A_1^U	0.1172	0.014
	A_2^U	0.7282	0.029
	A_3^U	0.1546	0.029
Conditional Return Probability, Tagged Fish			
	μ_1	0.0064	0.001
	μ_2	0.0404	0.002
	μ_3	0.0073	0.001
Conditional Return Probability, Untagged Fish			
	μ_1^U	0.0058	0.001
	μ_2^U	0.0361	0.002
	μ_3^U	0.0080	0.002
Upriver Adult survival			
Tagged	S_A	0.8175	0.022
Untagged	S_A^U	0.8159	0.022

2.8 Summary

Current practices of estimating juvenile survival, adult return rates, adult survival, and transportation effects treats each part of the life history and migration separately. Adult information is not used in estimating juvenile survival, and aspects of salmon life history (e.g. distribution of age at maturity) are ignored in calculating transportation effects and

adult return rates. This is partly due to the relative paucity of PIT-tag detection data from migrating adults in the past. With new and improved adult PIT-tag detection sites, we can now model the life history of migrating salmon from their release point above LGR to their return to LGR, and derive estimates of multiple quantities of interest at once. The life-cycle release-recapture model presented in this chapter does just that, providing both maximum likelihood estimates and standard errors of model parameters.

Several different measures of transportation effects are defined in this chapter, as well as other performance measures such as smolt-to-adult ratios (SARs) and ocean return rates. Expressing performance measures as functions of the model parameters focuses attention on the definitions of the measures to be estimated. It also provides easily computed maximum likelihood estimates of the measures, as well as asymptotic variance estimates based upon the theory of maximum likelihood.

Maximum likelihood estimators from multinomial distributions, and in particular from release-recapture data, have well-understood properties. Previous PIT-tag studies have shown only limited violations of model assumptions for juvenile migrations, and minimal effect on estimators in the case of assumption violations (e.g., see Skalski et al., 1998; Smith et al., 1998; Muir et al., 2001a). Rather than depending on *ad hoc* estimators based on only part of the available data and requiring bootstrap methods to estimate standard errors, we can use model-based estimators and standard errors from available PIT-tag data.

Chapter 3

ADULT RADIO-TAG MODEL**3.1 Introduction**

Since 1996, the University of Idaho and NOAA Fisheries (National Oceanic and Atmospheric Administration, National Marine Fisheries Service) have collected extensive radiotelemetry data from migrating adult salmonids in the Columbia and Snake rivers. These data provide both large-scale and small-scale information about salmon movement and survival between and at dams. The 2000 and 2004 biological opinions on the Columbia River Power System (NOAA Fisheries, 2000a, 2004 [on remand]) name measuring and minimizing unaccountable loss as a research objective, yet until now, no formal modeling work has been done to estimate unaccountable loss and large-scale (“system”) survival rates from these data. The main objective of this chapter is to develop a release-recapture model that can be used to analyze adult radiotelemetry data to estimate both unaccountable loss and system survival rates.

Radiotelemetry data are expensive to collect, and there is a possibility that current radiotelemetry studies will be replaced with less expensive PIT-tag studies. However, it is unknown if radiotelemetry data provide substantially more information about large-scale survival and unaccountable loss rates than PIT-tag data. One way to address this question is to compare estimates of system survival and unaccountable loss rates resulting from two types of models: one developed for radiotelemetry data, and one developed for PIT-tag data. A secondary objective of this chapter is to compare the large-scale information available from PIT-tag data to that available from radio-tag data. A sequence of models will be developed, ranging from simple PIT-tag models (Models 0 and 1) to complex radiotelemetry models (e.g., Models 5b and 6), each of which is designed to estimate dam-to-dam survival, system survival, and unaccountable loss. Each model will be fit to a single radiotelemetry data set that has been simplified to the level used by the model. For example, data for the PIT-tag

models will include only dam detections, while the radio-tag models will incorporate more types of data (e.g., tributary detections). Thus, comparisons between the models will reflect both differences in the models and differences in the types of data used.

The models developed in this chapter vary in the types of data used and assumptions made, with the more complex models using more types of data and potentially able to answer more questions. Based on comparisons between the models, a single model will be recommended for use in future analyses of the currently available large-scale radiotelemetry data, and a recommendation will be made on the future use of either radio tags or PIT tags to estimate unaccountable loss rates and system survival.

Radiotelemetry data provide a wealth of information about the migration of adult salmon. With the tailrace and base of each federally owned dam heavily wired with antenna arrays, detailed accounts of salmon movements approaching and during dam passage are available. The very detailed information is useful for analyzing problems with dam passage, but it is unnecessary for this chapter's goal of estimating system survival and unaccountable loss rates, or for answering large-scale questions such as (1) what is the probability of surviving from one dam to the next, and (2) what is the effect of fallback or tributary visits on subsequent survival? With the small-scale movements at the dams removed from the data, only the relatively large-scale movements between dams and tributaries are left.

Figures 3.1 and 3.2 show several possible migration paths observable from radiotelemetry data. The paths in Figure 3.1 are simple and mostly linear. Figure 3.2 shows paths that are considerably more complex, with multiple tributary visits in multiple tributaries and several fallback events. It is obvious from Figures 3.1 and 3.2 that at any point, a fish makes a decision to go either upstream or downstream, or to enter a tributary, if available. The migration decisions may be assumed to occur only at the base and top of dams and at the tributary mouths, i.e., at the detection points. Migration decisions of surviving individuals can be reduced to binary choices: ascend the dam or not, fall back or not, go directly to the next dam or go to a tributary, remain in the tributary permanently or return to the river, go upstream or downstream. With binary migration decisions, an attempt may be made at parameterizing a release-recapture model. However, the possibility of fallback or downstream travel in general, as well as upstream travel, at each detection point raises

the theoretical possibility of endless cycling. A release-recapture model including unlimited dam ascension and fallback would allow for the endless sequence of ascension, fallback, reascension, fallback, reascension, fallback, etc. This is both mathematically intractable and unrealistic. As Figure 3.2(b) demonstrates, however, some individuals travel in temporary cycles of fallback and reascension. Allowing for even temporary cycling with a limited number of fallback or "turnaround" events explicitly modeled is also mathematically intractable, involving as many auxiliary likelihoods as observed variations in migratory behavior. This is because at each decision or detection point, the complete preceding detection history dictates which decisions are viable. Thus, explicitly modeling multidirectional migratory behavior is not practical if the focus is on large-scale survival and movement.

The alternative to modeling multidirectional movement is to reduce the migration to linear or nearly linear paths, removing downstream travel and keeping upstream travel, both dam-to-dam and dam-to-tributary travel. By focusing on the final detection for each individual, it is possible to estimate unaccountable loss. If the effect of tributary visits on upstream travel is of interest, tributary-to-dam travel may be included. If the effect on upstream travel of fallback (or downstream travel in general) is of interest, information on fallback may be incorporated into the model without attempting to model the downstream travel itself.

In a sense, modeling only upstream travel requires reducing the data to its essence: where did the fish start, where was its last ("terminal") detection, where was it detected between its release and its terminal detection. All fish in the current studies were tagged and released as adults just downstream of Bonneville Dam. If known-source fish are used, then it is possible to identify straying as a terminal detection in a non-natal tributary. In particular, a fish is labeled a stray if it was last detected in a tributary but known to have originated further upstream. Without known-source fish, it is not possible to identify straying, but it is nevertheless possible to estimate transition (survival and movement) probabilities, as well as unaccountable loss.

In this chapter, a sequence of release-recapture models is developed to estimate large-scale survival and unaccountable loss during the adult upriver migration from radiotelemetry data from tagged adult salmon. Survival is estimated between neighboring dams and from

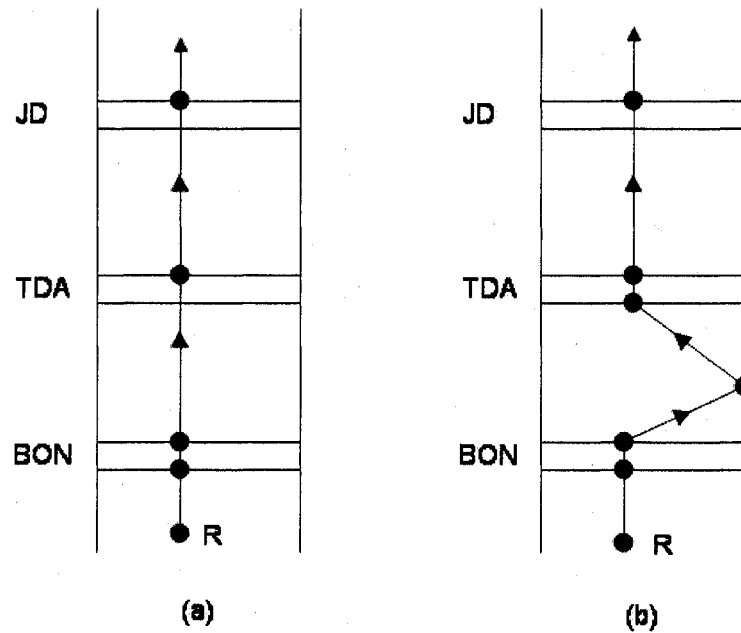


Figure 3.1: Two possible migration paths from radiotelemetry data requiring no simplification. The release point is marked *R*; double horizontal bars indicate the base and top of a dam. Dots indicate detection. The first path (a) shows directed upstream passage with no fallback and no tributary visits. The second path (b) shows upstream passage with one tributary visit between BON and TDA, and no fallback.

dams to tributaries, as well as from the initial release to the final dam. The release-recapture models developed here vary in the types of detections included (dam or tributary) and in the assumptions made about the effects of tributary use and fallback on subsequent survival. One model uses tag-recapture data from the adult trap at Lower Granite Dam. Two performance measures, perceived survival to the top of the final dam and the unaccountable loss rate, are defined and estimated for a sample data set for each model. A secondary goal of this chapter is to compare the information available from the radiotelemetry data to that available from PIT-tag data. With this goal in mind, the simpler models are applied to

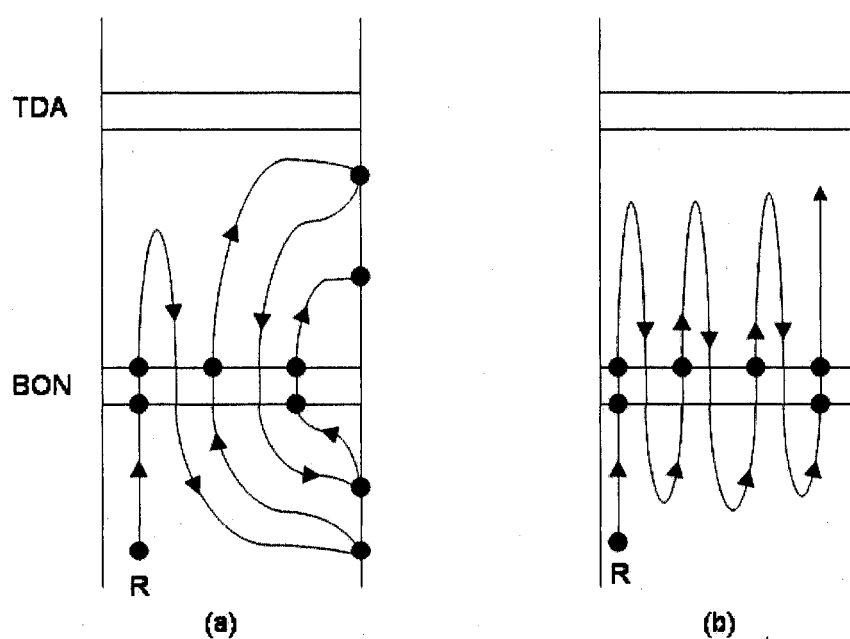


Figure 3.2: Two possible migration paths from radiotelemetry data requiring simplification. The first path (a) exhibits two fallback events and multiple visits to tributary sites downstream of BON and between BON and TDA, ending between BON and TDA. The second path (b) shows temporary cycling between fallback and reascension over BON.

radio-tag data that has been simplified to mimic PIT-tag data.

In Section 3.2, the sample data set used in this chapter is described, along with the types of radiotelemetry data available and the basic data-processing steps. Section 3.3 describes the basic statistical methods and assumptions used in this chapter. Sections 3.4 through 3.10 present the sequence of models, and Section 3.11 compares the models and provides general comments and recommendations.

3.2 Data

3.2.1 Example Data Set: 1996 Chinook Salmon

The data for which the models in this chapter are designed were collected and processed jointly by the University of Idaho, Idaho Cooperative Fish and Wildlife Research Unit, and NOAA Fisheries, with funding provided by the U.S. Army Corps of Engineers. More information on the data is available at the Adult Anadromous Fish Radiotelemetry Project at <http://rtagweb.nwfsc.noaa.gov/home/index.cfm>; the data can be downloaded from the same site.

The first year for which significant system-wide radiotelemetry data from adult salmon were available is 1996. The data from spring and summer Chinook salmon (*Oncorhynchus tshawytscha*) released in that year are presented for all models in this chapter. A total of 846 adult spring and summer Chinook salmon were collected at Bonneville Dam and outfitted with radio tags from early April through late June of 1996. The tagged Chinook were released at Skamania Landing (RKM 225.7) and Dodson Landing (RKM 225.6) on the Columbia River, just downstream of Bonneville (RKM 234). The following dams had radio receiver arrays: BON, TDA, JD, MCN, and PR on the Columbia River; and IH, LMO, and LGR on the Snake River. Tagged fish from this release group were detected at BON (base and top), TDA (top only), JD (top only), MCN (base and top), PR (base and top), IH (base and top), and LGR (base and top). Detections at LMO were available at neither the base nor the top of the dam, but were available at the tailrace to the dam. Tailrace detections were treated as base-of-dam detections for LMO. The models developed here are designed for use with data containing either Snake River detections or Mid-Columbia

detections (e.g., PR), but not both. Focus was on the Snake River detections; detections at PR were treated as tributary detections. Dams were numbered sequentially as follows: 1=BON, 2=TDA, 3=JD, 4=MCN, 5=IH, 6=LMO, and 7=LGR. Model 0 uses only top-of-dam detections, so LMO is not included in Model 0 data; LGR used the numeric label 7 for Model 0, nevertheless.

Detections were available from multiple tributaries of the Columbia and Snake rivers. All tributaries between two neighboring dams were treated as a single tributary, with the Mid-Columbia River viewed as a large tributary between dams 4 (MCN) and 5 (IH). Had focus been directed at fish heading to spawning sites off the Columbia upriver of MCN, then the Snake River detections would be incorporated as tributary detections instead. Detections occurred at the tributary sites listed in Table 3.1. Although several detection sites labeled as “tributaries” are not actually tributaries, they fit the purposes of tributary detections within the models, e.g., detection at these sites implies passage of the previous dam.

Table 3.1: Names, model detection site labels, and locations (RKM) of tributary receiver arrays from the 1996 Chinook salmon data set. River kilometer (RKM) values represent the number of kilometers between the detection site and the mouth of the Columbia River. All tributaries are of the Columbia River unless otherwise noted. Sites followed by an asterisk (*) had no detections.

Site Name	Detection Site	RKM
Cowlitz River	T_0	112.0
Kalama River*	T_0	118.4
Lewis River*	T_0	141.4
Willamette River	T_0	168.8
Washougal River*	T_0	194.4
Sandy River	T_0	194.9
Tanner Creek	T_0	232.0
Wind River	T_1	248.6, 249.2
Little White River	T_1	260.1, 260.7, 261.3
White Salmon River	T_1	270.3, 270.8, 271.0
Hood River	T_1	272.6
Klickitat River	T_1	290.3
Deschutes River	T_2	327.1, 328.9

Table 3.1 continued

Site Name	Detection Site	RKM
Sherar's Falls ¹	T_2	396.3
John Day River	T_3	350.8
Umatilla River*	T_3	469.8
Walla Walla River	T_4	512.6
Yakima River	T_4	545.9
Charbonneau Park ²	T_5	538.9, 539.4
Clearwater River ³	T_7	753.5
Snake River ⁴	T_7	758.9

Table 3.2 presents the number of unique tagged fish detected at each detection site, regardless of fallback or final detection site. Because the various models developed in this chapter each use different types of data, and some detections associated with fallback are not used in these models, the actual detections used for each model differ somewhat from the summary shown here. Model-specific data summaries are presented with each model in this chapter.

Table 3.2: Detection sites and the number of unique tagged fish detected at those sites in the 1996 spring/summer Chinook salmon radio-tag data set, regardless of fallback or final detection site.

Site Name	Detection Site	No. of fish detected
Initial release	N	846
Tributaries downstream of BON	T_0	11
Base of BON	D_{1B}	779
Top of BON	D_{1T}	700
Tributaries between BON and TDA	T_1	303
Base of TDA	D_{2B}	0
Top of TDA	D_{2T}	426

¹Sherar's Falls is approximately 70 km up the Deschutes River from the Columbia River.

²These detections are not at a tributary, but are at Charbonneau Park and across the river from Charbonneau Park, just upstream from Ice Harbor Dam on the Snake River. They are treated as tributary detections (1) because they indicate passage of and travel upriver from Ice Harbor, and (2) because the park may act as a resting area for salmon in much the same way as a tributary might.

³The Clearwater River is a tributary of the Snake River, upriver of Lower Granite Dam.

⁴These detections were in the Snake River upstream of Lower Granite Dam. They are treated as tributary detections at site T_7 .

Table 3.1 continued

Site Name	Detection Site	No. of fish detected
Tributaries between TDA and JD	T_2	78
Base of JD	D_{3B}	0
Top of JD	D_{3T}	355
Tributaries between JD and MCN	T_3	47
Base of MCN	D_{4B}	287
Top of MCN	D_{4T}	284
Tributaries between MCN and IH	T_4	150
Base of IH	D_{5B}	118
Top of IH	D_{5T}	101
Tributaries between IH and LMO	T_5	43
Base of LMO ⁵	D_{6B}	76
Top of LMO	D_{6T}	0
Tributaries between LMO and LGR	T_6	0
Base of LGR	D_{7B}	104
Top of LGR	D_{7T}	87
Tributaries upstream of LGR	T_7	73

3.2.2 Data Collection and Processing

Adult migrating salmon (no jacks) are collected and designated for radio-tagging at the adult trapping facility at Bonneville Dam (BON) as they pass the dam. A radio transmitter (i.e., "tag") is inserted into each fish's stomach, with the radio antenna coming out of the fish's mouth. The fish is released downstream of BON after holding to ensure that the transmitter is not regurgitated. Each transmitter has a unique identification number. Fixed-site radio receiver arrays are placed at several dams on the Columbia and Snake rivers, with extensive arrays situated at the tailrace and base of the dam, and with smaller arrays at the top of the adult fish ladders. Single fixed-site arrays are placed in the mouths of major tributaries to the Columbia and Snake rivers. Each transmitter emits with a radio signal on a unique frequency and code combination. As the tagged fish passes a receiver array, the array's antenna reads the signal and the date, time, frequency, tag code, and signal strength are recorded.

⁵These detections were in the tailrace of LMO, not actually at the base of the dam.

In addition to the fixed-site receivers, mobile tracking of radio tags by plane, boat, and truck is done. These data are inappropriate for release-recapture modeling, and are not used here. Also, tag-recovery data are available from hatcheries, fisheries, and spawning grounds. Because of unknown recovery and reporting rates, these data are not used in the models developed here. Only data from the fixed-site receivers are used.

Records are downloaded from each fixed-site receiver, with all detected frequencies noted. Some readings are noise, and must be removed from the data. Data technicians clean the data by filtering out the noise and determining from the strength of the signals which represent valid readings. Fish do not pass dams, tributaries, and radio receivers instantaneously, so the data typically contain multiple readings of a given tag as the fish passes a particular receiver. Data technicians must condense these multiple readings to find a representative record of the fish's migration path. Generally, records for a given tag (or fish) at a receiver are characterized by the first and last records there. An attempt is made to distinguish between repeated visits to a receiver location and repeated readings during a single visit. Typically, consecutive readings separated by several hours (e.g., 6 hours) are identified as representing separate visits. Each data record deemed valid is given a code indicating the location of the receiver and thus of the detection. The codes indicate the dam or tributary where the receiver was located, which part of the dam the detection came from, and whether the fish had been detected there before.

The cleaned data contain information on the tag identification number, location and type of the detection (first or last), and date and time of the detection. An example of the cleaned data from a single Chinook salmon tagged and released in 1996 is given in Appendix A. The cleaned data must be converted to detection histories for each fish. Only some of the available records are used in the detection histories, namely the "first approach" (A1) and "last top" (LT) records at each dam, and the first (F) and last (L) detections from fixed-site receivers at each tributary. The A1 codes represent detections at the bases of dams, while LT codes represent detections at the tops of dams⁶. If a fish falls back over a dam it has

⁶In 1996, neither A1 nor LT detections were available for Lower Monumental (LMO); F records from the tailrace of LMO were used in place of A1 records for LMO for analysis of the 1996 data set.

already passed and attempts to reascend the dam, its records may include a second “first approach” and/or “last top” record. Each record is assigned a detection site name based on its detection code, using the following protocol:

(1) The dams are numbered sequentially going upriver, from Bonneville (BON, dam 1) to the dam farthest upriver (dam K). Either the mid-Columbia dams (e.g., Priest Rapids) or the Snake River dams (e.g., Lower Granite) may be included, but not both. The river or river portion that is excluded may be treated as a tributary.

(2) At dam k , base-of-dam detections (A1 codes, or F codes for LMO) are labeled D_{kB} , top-of-dam detections (LT codes) are labeled D_{kT} , and all detections in tributaries⁷ between dams k and $k + 1$ are labeled T_k .

(3) Tributary detections downstream of the release point (at BON) are labeled T_0 , and tributary detections upstream of dam K are labeled T_K .

(4) Repeated records at a given tributary site T_k , with no intervening records at other sites, are condensed to a single record.

Thus, each detection site has a two-part label, with the first part indicating whether it is a dam (“D”) or a tributary (“T”), and the second part indicating the number of the dam (1 through K) or tributary (0- K) and, if a dam, whether the detection site is at the base (“B”) or the top (“T”) of the fish ladder. For example, the detection site at the base of dam 1 is labeled D_{1B} , the site at the top of dam 3 is labeled D_{3T} , and the site in the tributary between dams 4 and 5 is labeled T_4 . In order, the possible detection sites are T_0 , D_{1B} , D_{1T} , T_1 , D_{2B} , D_{2T} , T_2 , ..., $D_{K-1,T}$, T_{K-1} , D_{KB} , D_{KT} , T_K . Finally, the detection sites assigned to each record of a particular fish are listed in chronological order, giving a detection history for the fish. The detection history for the sample data in Appendix A is

$$R \ D_{1B} \ D_{1T} \ T_1 \ D_{2T} \ D_{2T} \ D_{1B} \ D_{1T} \ D_{3T} \ D_{1B} \ D_{1T} \ T_1 \ D_{2T} \ T_2 \ D_{1B} \ D_{2T} \ D_{3T} \ D_{4B} \ D_{4T} \ D_{5B} \\ D_{5T} \ D_{5B} \ D_{5T} \ T_5 \ D_{6B}. \quad (3.1)$$

⁷All tributaries between neighboring dams are labeled identically here, and the models developed treat them as a single tributary. The model and data may be modified to distinguish among the different tributaries, if desired.

The detection histories resulting from the above steps are simplified from the available data, but must be simplified still further in order to analyze them in this chapter. Details of this secondary simplification process depend on the model with which the data will be used, but some aspects of the simplification process are common to all models.

With the small-scale movements at the dams removed from the data, only the relatively large-scale movements between dams and tributaries are left. Reconsider the sample migration paths shown in Figures 3.1 and 3.2. The path in Figure 3.1(a) shows the fish moving straight upriver in a linear fashion. The path in Figure 3.1(b) is slightly more complex, with a temporary visit to a tributary between BON and TDA. The more complex paths in Figure 3.2 include multiple tributary visits and fallback events. Because only travel directed upstream (including toward tributaries) will be modeled in this chapter, the detection records must be converted to linear (or nearly linear) records, omitting detections during downstream travel or fallback. Thus, the path in Figure 3.2(a) becomes that in Figure 3.3.

Reducing the data to upstream-directed travel is straightforward for individuals who did not exhibit fallback or “turn-around” behavior, because their migration paths are already nearly linear. There are some issues to consider in simplifying the paths of fallback or turn-around fish, however, as exemplified by the migration paths shown in Figures 3.4(a) and 3.5(a). First, consider Figure 3.4(a). Here, the fish ascended the first dam (BON) with detections at both its base and top, then ascended TDA with only a top detection, fell back over TDA, and ended in a tributary between BON and TDA. If the fish were known to have originated above TDA, it would be labeled a stray. This fish swam farther upriver than it needed to, if its goal were the tributary of its final detection. Should the detection history include the information that the fish reached TDA from BON in estimating BON-TDA survival? On one hand, the fish did survive from BON to TDA. On the other hand, it did not remain above TDA, so may not be considered a “success” as far as getting past TDA is concerned⁸. By focusing on upstream travel and terminal detections, the fact that the fish swam to TDA from BON is inherently ignored, because the fish did not remain above

⁸This is contrary to the protocol used in Bjornn et al. (2000), in which dam passage is considered successful for any fish that reached the top of the dam, regardless of future fallback or final destination.

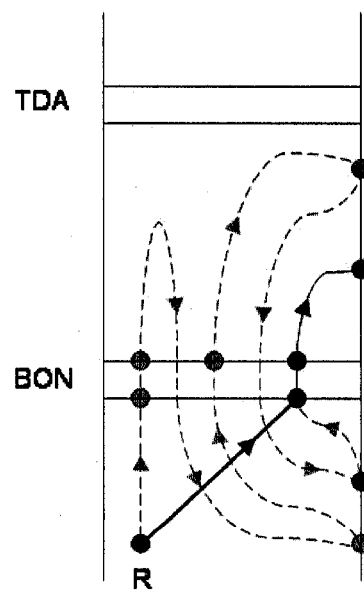


Figure 3.3: Simplification of migration path in Figure 3.2(a), i.e., removal of non-terminal tributary detections and reduction to the post-fallback path. The dotted paths indicate the portion of the detection history removed due to the fallback or removal of the tributary visit; the heavy portion of the path replaces the dotted portion.

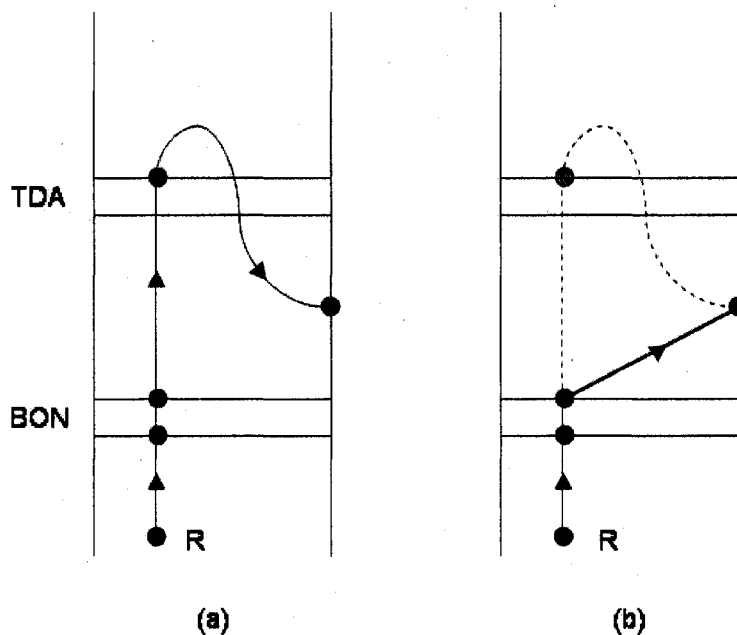


Figure 3.4: A migration path showing fallback over dam TDA followed by exit to a tributary between BON and TDA (a). Ignoring the portion of the path retraced by the fallback yields the reduced migration path in (b). The dotted path indicates the portion of the detection history removed due to the fallback; the heavy portion of the path replaces the dotted portion.

TDA. The simplified path is shown in Figure 3.4(b).

Next, consider Figure 3.5(a). This fish passed BON with detections at the base and top, ascended TDA with detection at the top, fell back over both TDA and BON, reascended both with detections only at the base and top of BON, then ascended JD, with its terminal detection at the top of JD. Note that the fish swam upriver from below BON to above TDA twice. Which of these paths should be used, the pre-fallback path or the post-fallback path? In this case, they are nearly identical, except that the fish was not detected at TDA the second time it ascended TDA. Whether the pre-fallback path (Figure 3.5(b)) or the

post-fallback path (Figure 3.5(c)) is used affects estimation of detection at TDA and parameterization of a model that allows for differential survival of fallback fish. The pre-fallback path used in Figure 3.5(b) contributes information on survival of non-fallback fish between BON and TDA, while the post-fallback path in Figure 3.5(c) contributes information on survival of fallback fish between BON and TDA. As with the path in Figure 3.4(a), it may be argued that although the fish reached TDA via the pre-fallback path, it did not successfully remain above TDA until the post-fallback path; therefore, the pre-fallback path is somewhat misleading. In particular, if the fish had not reascended TDA, then its final detection would be below TDA and its foray above TDA would have been ignored (e.g., Figure 3.4); therefore, its pre-fallback path should be ignored, and the simplified path in Figure 3.5(c) should be used.

Using only one of the two paths past TDA in Figure 3.5(a) provides different information on the detection rate at the top of TDA: the fish was detected on the pre-fallback path, but not on the post-fallback path. Using pre-fallback paths, however, may positively bias detection probabilities, because a fish must be detected at the top of a dam (or higher) before being identified as having fallen back over that dam. Thus, detection affects perceived fallback rates, and pre-fallback paths will tend to include more top-of-dam detections than post-fallback paths. On the other hand, there is no reason to assume that fallback affects conditional detection rates, so using post-fallback paths (e.g., Figure 3.5(c)) should not bias estimates of detection rate. In general, post-fallback paths are used in this chapter.

The secondary data simplification process involves two steps:

- (1) Remove non-terminal tributary detections, or tributary “visits,” from the detection histories (Figure 3.6). This is optional, and may be omitted if the effects of tributary visits on subsequent transition probabilities is of interest (i.e., Models 3b, 5b, 5c, and 6).

- (2) Ignore downstream travel by using post-fallback paths; for examples, see Figures 3.5, 3.7, and 3.8. If the effect of fallback on subsequent transition probabilities is of interest, detection histories may retain information on where the post-fallback paths began (e.g., Models 4, 5a, 5b, 5c, and 6).

Fallback is identified from a capture history by repeated detections at a dam site, or by detection at a downriver site following detection at an upriver site. Because repeated

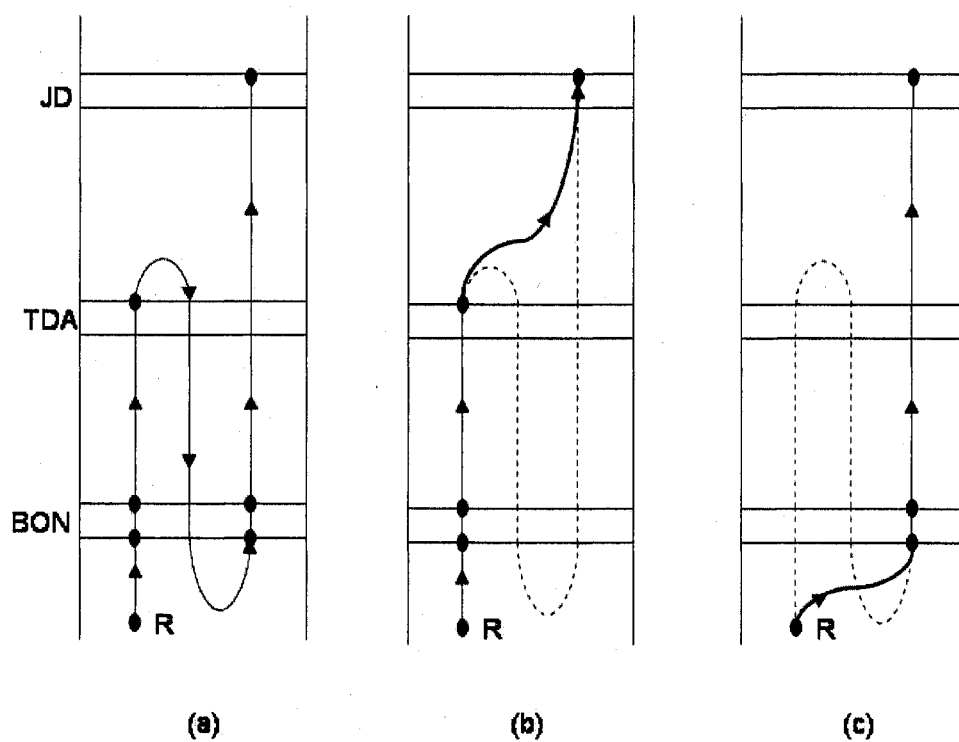


Figure 3.5: A migration path including fallback over dams TDA and BON (a), with the reduced migration path using (b) the pre-fallback path and (c) the post-fallback path. The dotted paths indicate the portion of the detection history removed due to the fallback or removal of the tributary visit; the heavy portion of the path replaces the dotted portion.

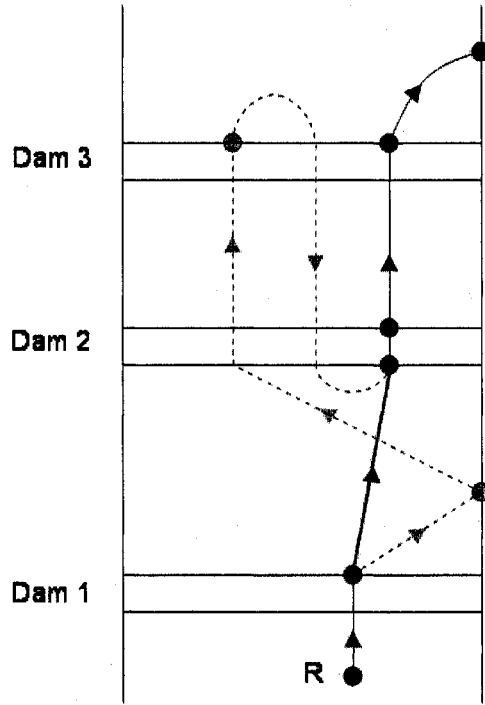


Figure 3.6: A non-simplified migration path with both a tributary visit and fallback, and the simplified migration path with the tributary visit removed and the path reduced to the post-fallback path. The dotted paths indicate the portion of the detection history removed due to the fallback or removal of the tributary visit; the heavy portion of the path replaces the dotted portion.

detections during a single visit are initially removed from the data, repeated detections at a site (e.g., $\dots, D_{1T} D_{1T} \dots$) indicate fallback at that site. If fallback information is used in the model, the code “FB” should be inserted in place of the string of detections removed indicating the first fallback event.

The sample detection history in Equation (3.1) (from the data in Appendix A) reduces to the following simplified detection history if both tributary detections and fallback are

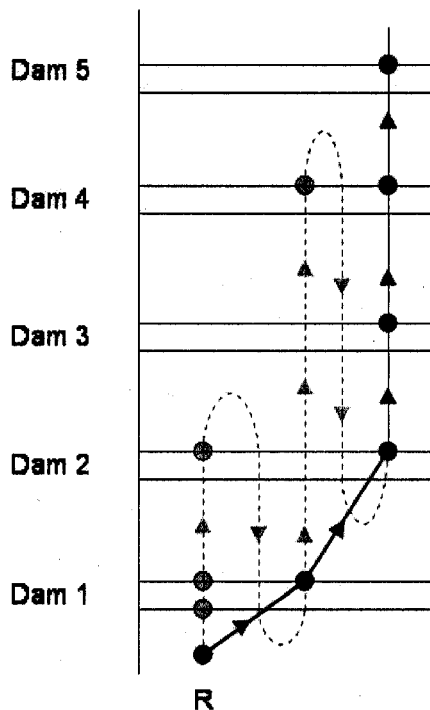


Figure 3.7: A non-simplified migration path with multiple fallback events, and the simplified migration path reduced to the post-fallback path. The dotted paths indicate the portion of the detection history removed due to the fallback; the heavy portion of the path replaces the dotted portion.

included:

$$R \text{ } FB \text{ } D_{1B} \text{ } D_{2T} \text{ } D_{3T} \text{ } D_{4B} \text{ } D_{4T} \text{ } D_{5B} \text{ } D_{5T} \text{ } T_5 \text{ } D_{6B}. \quad (3.2)$$

The order in which steps (1) and (2) are taken may affect the outcome. Removing tributary visits before determining the post-fallback paths may remove the information necessary to identify fallback. Consider Figure 3.9 as an example. Figure 3.9(a) shows the migration path of a fish that ascended both dams 1 and 2 with detections at both dams, then fell back over dam 2, visited the tributary T_1 , reascended dam 2 without detection,

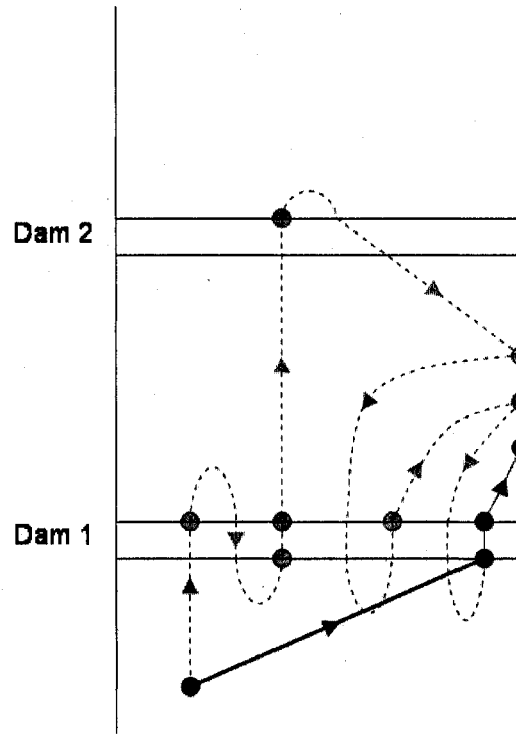


Figure 3.8: A non-simplified migration path with both multiple tributary visits and multiple fallback events, and the simplified migration path with the tributary visits removed and the path reduced to the post-fallback path. The dotted paths indicate the portion of the detection history removed due to the fallback or removal of tributary visits; the heavy portion of the path replaces the dotted portion.

and ended at tributary T_2 . Removing the non-terminal tributary detection (i.e., T_1) before reducing the detection history to the post-fallback path results in the simplified migration path shown in Figure 3.9(b). Figure 3.9(b) shows the pre-fallback path to the top of dam 2, because without the non-terminal tributary detection at T_1 , it is not apparent that any fallback occurred. Figure 3.9(c), on the other hand, shows the simplified migration path that results if the detection history is reduced to the post-fallback path before removing the non-terminal tributary detection. The difference between Figures 3.9(b) and 3.9(c) is in detection at dam 2, and in parameterizing the simplified detection history's probability

for a model that incorporates fallback information.

Which of the above two steps to do first depends on the goal of the data analysis. In general, reducing each detection history to its post-fallback path before removing non-terminal tributary detections is preferable if the goal is to understand a particular data set (as it typically is), because it produces a more accurate picture of the fish's migration path. One of the goals of this chapter, however, is to compare the information gleaned from radio-telemetry data to that learned from less detailed data, such as PIT-tag data. If the PIT-tag data available from dam detections were augmented with tag-recovery data from spawning sites or hatcheries, then superficially the data would resemble radio-tag data in which non-terminal tributary detections were removed before detection histories were reduced to post-fallback paths. For this reason, the data used in this chapter were simplified by first removing the non-terminal tributary detections, and then reducing to post-fallback paths. For practical purposes, however, the discrepancies between the two simplification methods exemplified by Figure 3.9 occurred rarely in the data set considered in this chapter. This issue affects only the data used with Models 0, 1, 2, and 4, because the other models use all tributary detections.

3.3 Statistical Methods

3.3.1 Overview

The models developed in this chapter are release-recapture models using radiotelemetry data as detections. The data for a tagged individual is a detection history (equivalently, capture history), recording the sites where the individual was detected, in the order of detection; see Section 3.2 for more information on data format and procedures. The models developed here are modifications of the basic Cormack-Jolly-Seber (CJS) model (Cormack, 1964, Jolly, 1965, Seber, 1965), in that single detections at each site are used, estimation of survival is the main focus, and the expected number of fish with a given detection history is parameterized with biological parameters such as survival and detection rates. It should be noted, however, that while the CJS model estimates survival in time, the goal here is to estimate survival primarily in space, and only secondarily in time. The basic estimable

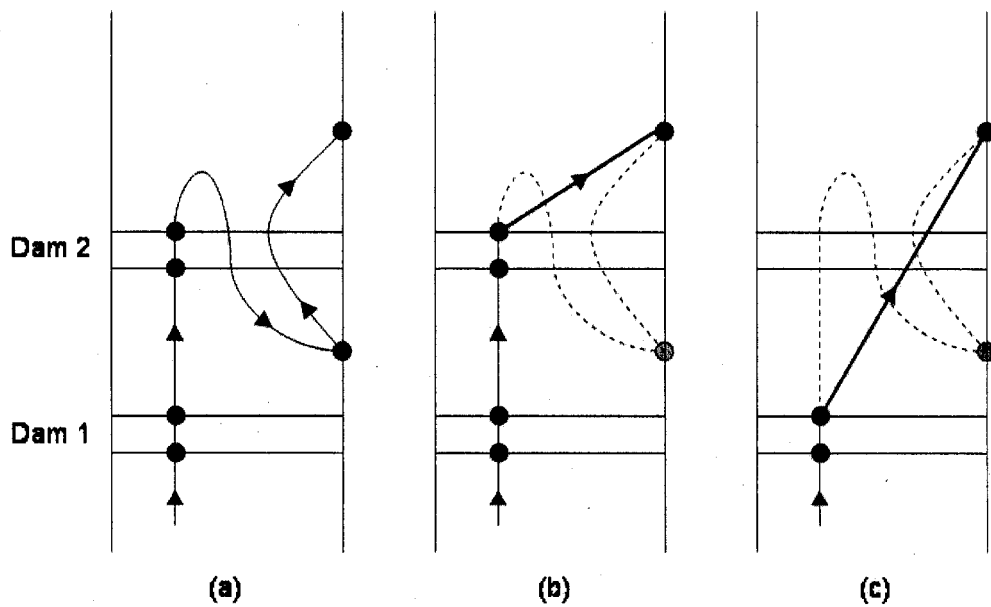


Figure 3.9: A migration path (a) with fallback followed by a tributary visit, reascension, and exit to a tributary. Removing the tributary visit (b) before reducing the path to the post-fallback path also removes evidence of fallback. Reducing to the post-fallback path (c) first also removes the tributary visit and detection at dam 2. The dotted paths indicate the portion of the detection history removed due to the fallback or removal of the tributary visit.

parameter in the models developed here is more accurately the joint probability of surviving and moving from site i to site j , or the probability of “transition” from site i to site j (ϕ_{ij}), rather than simply survival. This is because in most models, there is a choice of direction upon leaving certain sites: moving directly toward the next dam, or moving toward the next tributary. This choice of direction replaces the strictly linear aspect of travel through time in the CJS model with a more complex aspect of travel through space.

The models developed in this chapter use multinomial likelihoods, with three basic types of parameters: (1) transition probabilities (i.e., joint survival and directed movement; ϕ_{ij}), (2) detection rates (p_i); and (3) fallback parameters (f_i). Fallback is not included in every model. The fallback parameter f_i requires explanation. The movement modeled in this chapter is directed strictly upstream, either to the next dam or to a tributary between the current site and the next dam. No downstream movement is explicitly modeled, and fallback is not explicitly modeled. However, fallback information is incorporated in some models via a fallback parameter, f_i . The parameter f_i is not the probability the falling back at site i , but rather the probability of becoming a fallback fish between site i and the next detection site (upstream), conditional on reaching site i originally. “Becoming a fallback fish” means that the fish swims upstream from site i to at least the next detection site; falls back at some point upstream of site i (i.e., swims downstream past previously passed sites, at least as far as the dam upstream of site i); turns around again to swim upstream; and is detected at a site in the reach following site i . Figure 3.10 shows several examples of fallback paths that would be parameterized with f_i , with site i indicated. The parameter f_i does not give the fallback rate at site i , and should not be interpreted as such. Instead, it allows fish to move from the pre-fallback state to the post-fallback state, which then allows for estimation of an effect of fallback on future transition probabilities.

A sequence of models is presented in this chapter, ranging from simple to complex, and varying over the following characteristics: the number of detections per dam, the type of tributary detections used, the presence of memory effect of tributary visits, and the use of memory effect of fallback. Additionally, the last model uses data from the sampling room (adult trap) at Lower Granite Dam. For each model, the notation and parameters are defined, sufficient statistics are described, and the likelihood is presented. Two performance

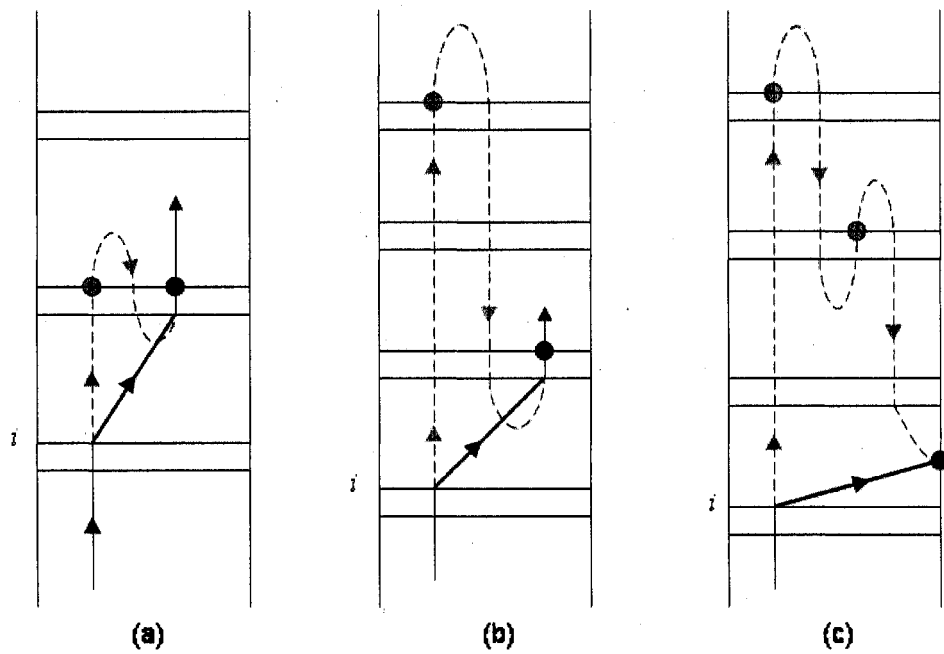


Figure 3.10: Three migration paths parameterized with the fallback parameter f_i : (a) repeated detections at the dam immediately upriver of site i ; (b) detection at the dam immediately upriver of site i , following a detection farther upriver; and (c) a detection at the tributary site immediately upriver of site i , following several detections farther upriver. The dotted paths indicate the portion of the detection history removed due to the fallback, and the heavy portions of the path replace the dotted portions.

measures are also defined, described below. Each model is fit to the 1996 Chinook salmon data set. Several of the models have many parameters, not all of which are required for any particular data set. Thus, for each model, the likelihood is tailored to the 1996 Chinook data set. Maximum likelihood estimates of the model parameters and of the two performance measures are presented.

3.3.2 Performance Measures

The first performance measure defined for these models is perceived survival from the release point to the top of the final dam (dam K), or perceived system survival, denoted S_{sys} . As usual, this parameter is actually a transition probability rather than strictly survival. Additionally, if the release group included fish that were directed to tributaries downstream of dam K , then these fish should have legitimately left the river before reaching dam K . The parameter S_{sys} treats these fish and any others that fail to reach dam K as mortality; thus, the survival described by S_{sys} is survival within the population of tagged fish migrating in the river, rather than actual biological survival.

Because of the possibility of either legitimate turn-offs or straying to downstream tributaries, a more useful performance measure is the probability of unaccountable loss from the release point, μ_R . Fish that reach dam K or that permanently leave the river at a tributary downstream of dam K are considered accounted for, while fish that “disappear” in the river are considered unaccounted for. The “unaccountable loss” category includes fish that experienced mortality before reaching the tributary leading to their spawning grounds. Such mortality may be due to natural causes such as disease or predation, to harvest, or to complications of dam passage and/or fallback. Unaccountable loss also includes the probability of mainstem spawning, and the probability of fallback that is not followed by a detection. Such fallback is not detected and is not modeled in the models in this chapter, and as such is included in unaccountable loss. Radio tags returned by fisherman may be used to calculate unaccountable loss only if the harvest rate and tag-return rate are known. Without these pieces of information, the probability of harvest is included in unaccountable loss.

Both perceived system survival and unaccountable loss are defined recursively for each

model. The recursive parameters facilitate generalization of the definitions of these two performance measures. They also allow these performance measures to be defined and estimated for any starting point in the model, not just for the release point. For example, it is possible to define the probability of unaccountable loss for fish that reached a particular dam. However, only perceived survival and unaccountable loss from the initial release point are explicitly considered in this model.

In general, system survival (S_{sys}) is defined in terms of the recursively defined parameters, η_R , $\eta_{D_{kT}}$, and η_{T_k} for detection sites $k = 1, \dots, K - 1$. The parameter η_R is the joint probability of moving from the release site to the top of the first dam (site D_{1T}), and then surviving through the rest of the system from site D_{1T} . The parameter $\eta_{D_{kT}}$ (or η_{T_k}) is the joint probability of moving from the top of dam k (or tributary T_k , respectively) to the top of dam $k + 1$, and then surviving through the rest of the system from site $D_{k+1,T}$, for $k = 1, \dots, K - 1$. The more complex models include $\eta_{D_{kT}}$ and η_{T_k} parameters defined for different cases relative to tributary and fallback status. For all models, system survival, or survival from the release to the top of dam D_{KT} , is defined as:

$$S_{sys} = \eta_R, \quad (3.3)$$

where the definition of η_R varies with the model. The simpler models also have closed-form formulas for S_{sys} .

Unaccountable loss (i.e., the probability of unaccountable loss) is defined in terms of the recursively defined parameters μ_i , where

$$1 - \mu_i = Pr[\text{Reach site } D_{KT} \text{ (the last dam site) or permanently exit the river at a tributary} \mid \text{Reach site } i]. \quad (3.4)$$

Unaccountable loss from site i is μ_i ; unaccountable loss from the initial release is μ_R . Formulas for μ_R depend on the model. Closed-form definitions of μ_R are presented for the simpler models. The more complex models include $\mu_{D_{kT}}$ and μ_{T_k} parameters defined for different cases relative to tributary and fallback status.

Approximate variance formulas for \hat{S}_{sys} and $\hat{\mu}_R$ are found via the Delta Method (Seber, 1982, pp. 7-9). Formulas for S_{sys} and μ_R are presented for each model; approximate variance formulas and the partial derivatives necessary for the Delta Method are presented in Appendix B. For all formulas, maximum likelihood estimators are found by replacing each model parameter with its maximum likelihood estimate.

3.3.3 Model Assumptions

The assumptions underlying the models presented in this chapter can be grouped into three categories: those common to all models (C), those common to the models with tributary detections (T), and those common to models recognizing fallback (F). The assumptions in these groups are listed and discussed below. Additional assumptions specific to individual models are presented with the models.

The assumptions common to all the models developed here are the typical assumptions of single-release, multiple-recapture models, and are listed below.

(AC.1) All tagged fish present at a given detection site have a common probability of future transition and detection, regardless of detection at the earlier site.

(AC.2) All tagged fish present and directed upriver at a given detection site at a dam have a common probability of detection at that site, regardless of previous detection.

(AC.3) The fate of each tagged individual is independent of the fate of all other tagged individuals.

(AC.4) Detection of radio signals from radiotelemetry tags occurs over a negligible distance at each detection site.

(AC.5) Individuals selected for radio-tagging are representative of the population of interest.

(AC.6) Tagging and release has no effect on subsequent survival, movement, fallback, or detection rates.

(AC.7) There is no tag loss after release.

(AC.8) The raw radio signal data are collected and processed correctly according to procedures developed by UI and NOAA Fisheries.

(AC.9) The data processed according to the procedures of UI and NOAA Fisheries are then processed and simplified correctly for the desired model.

Assumption (AC.1) implies that detection at a particular site has no effect on subsequent survival, movement, and detection probabilities. In other words, the act of being detected neither helps nor hurts tagged individuals. This assumption is required by the multinomial model, and is reasonable in that remote sensing rather than direct handling of the fish is used in detection, and that dam passage generally implies passing the area covered by the receivers. Nevertheless, tagged fish that pass a dam via the navigation locks are unlikely to be detected at the dam, and may experience differential survival rates during dam passage. Bjornn et al. (2000) report that fewer than 1% of tagged Chinook salmon passed BON via the navigation lock in 1996. If this value is typical of all dams, then navigation lock passage should not be a concern.

Assumption (AC.1) also implies that the release group is homogeneous with respect to transition (survival and movement) rates. This assumption may be violated if the release group contains individuals directed toward spawning sites located in different regions of the Columbia River Basin. Fish that are headed for the Cowlitz River in South Central Washington are likely to have a different probability of entering that tributary than fish headed for the Yakima River or the Snake River. Violations of Assumption (AC.1) will result in point estimates that are averages of the true values for unique groups in the release group, and in negatively biased variance estimates. One approach to handling this problem is that used in Models 3b, 4, 5a, 5b, 5c and 6, in which individuals detected in a tributary or known to have fallen back may experience a memory effect of the tributary visit or fallback on subsequent transition rates. If tributary visits or fallback are more likely near the mouth of the natal tributary⁹, then the memory effects partially account for heterogeneity induced by spawning location. However, the effects of tributary visits and fallback occur after rather than before the fish has visited the tributary or fallen back, and so the memory effects cannot fully account for the different transition rates likely in mixed-stock release groups. Without

⁹Bjornn et al. (2000) found that the final distribution of fish that fell back over one or more dams was similar to that of fish that did not fall back.

knowing which individuals are headed toward which tributary, it is impossible to fully account for stock-induced heterogeneity, as it is impossible to accurately assign individuals to different migration groups before observing their migration tendencies. This problem can be avoided by using only known-source fish, preferably from a single source (hatchery or spawning location). With multiple yet known sources, the model may be applied separately to the different groups.

Assumption (AC.2) indicates that all fish are assumed to have a common detection probability at each detection site located at dams, regardless of spawning location or past detections. This implies that receivers are equally effective at all ladders at a given dam, and that all fish that pass a dam have the same probability of passing via the fish ladders rather than via the navigation locks. Note that detection rates do not depend on previous fallback or tributary visits, but that detection does require fish to be directed upriver. This is because fish are generally not detected at either the top or base of a dam as they fall back over it.

Assumptions (AC.1) and (AC.2) also imply either that all individuals that pass a site pass it during a short period of time, when they may be expected to experience similar river and dam conditions, or that transition and detection rates are unaffected by temporal changes in these conditions. Violations of these assumptions can be limited by using known-source fish from similar stocks, all released at the same time. Assumption (AC.3) is reasonable due to the size of the release group. Assumptions (AC.1), (AC.2), and (AC.3) together imply a multinomial error structure for the model.

Assumption (AC.4) means that the estimated transition rates apply to travel between detection sites, rather than travel at detection sites. This assumption is likely violated because radio receivers pick up signals over a range of distances, rather than just at the receiver. This type of violation is limited by the processing of the raw data, however, in which technicians determine the validity of each detection based on the signal strength. Thus, detections included in the processed data are likely to be those from fish that actually passed the receiver, rather than those that came near and then turned away without passing. Because transition probabilities refer primarily to space rather than to time, the fact that some fish linger at detection sites should not be problematic.

Assumptions (AC.5) implies that model results may be applied to the population of interest. This assumption is less likely to be violated if single-stock or known-source fish are used in the release. Assumptions (AC.6) through (AC.9) imply that the data are reliable.

Models that include tributary detections use several common assumptions, listed below.

(AT.1) All fish present at a given dam (detection) site have a common probability of entering any of the tributaries between that dam site and the next dam, regardless of the tributary in question and of detection at the current and previous sites.

(AT.2) All fish present at any tributary between a given two dams have a common probability of returning to the river and surviving to the next dam upriver, regardless of the tributary in question and of past detections.

(AT.3) The detection rate in each tributary is 100%, regardless of past detections.

(AT.4) All fish that return to the mainstem of the river from any tributary continue migrating upriver, regardless of past detections.

Assumptions (AT.1) and (AT.2) allow all tributaries between two dams to be treated as a single tributary, considerably simplifying both the data and the model. Violations of these assumptions caused by stock-induced heterogeneity may be limited by using known-source fish. With a mixed-stock, non-known-source release group, the memory effects used in Models 3b, 4, 5a, 5b, 5c, and 6 may reduce lack of fit.

Assumption (AT.3) is necessary because there is generally only a single antenna array in each tributary mouth, which prohibits estimation of tributary detection rates from the tagging data. Without estimates of tributary detection rates, it is impossible to usefully incorporate tributary memory effects or to make probability statements about transitions between dams. With multiple antenna arrays, this assumption may be relaxed. Most tributary receivers were in operation at least 90% of the possible operation hours. Only the receiver in the Walla Walla River had significant outages; the Walla Walla River receiver was in operation 54.6% of the time (Bjornn et al., 2000). Assumption (AT.4) allows the model to focus only on upstream-directed travel. Because the data simplification process removes all detected downstream-directed travel, this assumption is reasonable for the simplified data.

It should be noted that Assumptions (AT.1) and (AT.3) are necessary for all tributary

models, while Assumptions (AT.2) and (AT.4) are necessary only for those models that recognize tributary detections followed by dam detections (i.e., Models 3a, 3b, 5a, 5b, 5c, and 6).

The models that include fallback information each use the following assumptions:

(AF.1) All fish present at a given detection site that have not previously fallen back have the same probability of future fallback, regardless of detection at that site.

(AF.2) Each fish experiences at most one fallback event during its migration in the river.

(AF.3) All fallback events are detected in which the fallback fish reascends at least one dam.

(AF.4) All fish that reascend dams after falling back are detected at the first dam they reascend. If this assumption is violated, then the wrong site is identified as the origin of the fallback transition.

Assumption (AF.1) is similar in nature to Assumptions (AC.1) and (AT.1), and violations of it may be handled in the same way as violations of these assumptions. Assumption (AF.2) allows use of only the first fallback event, which simplifies the data and model considerably. This assumption is likely to be violated, because some fish fall back multiple times as they explore the tributaries. However, fallback rates are generally low, and it seems reasonable that the first fallback has the largest effect on subsequent transition probabilities. If effects of additional fallback events are less than the effect of the initial event, then effects of violations of Assumption (AF.2) will be minimized.

Assumptions (AF.3) and (AF.4) imply that the fallback data are reliable and exhaustive, and give meaning to the fallback parameters (f_i). If Assumption (AF.3) is violated, then the fallback parameters f_i will be negatively biased, and the transition parameters involving fallback or its delayed effects may be biased. Assumption (AF.4) allows for proper identification of the sites from which each fallback transition originated, i.e., for proper parameterization with the f_i parameter. Violations of Assumption (AF.4) will lead to biased estimates of f_i and transition parameters involving fallback. High detection rates at dams will limit violations of both Assumptions (AF.3) and (AF.4).

3.4 Model 0: Single Dam Detections

The simplest release-recapture model for the adult upstream migration acknowledges no tributary entry or detections, uses only single detections at the dams, and ignores the possibility of fallback. This model uses either PIT-tag detections, which are taken from the interiors of the fish ladders at dams, or radio-tag detections that have been reduced to the level of PIT-tag detections, i.e., single detections at the adult fish ladders. The model presented here (Model 0) is effectively what the more complex models presented in the remainder of the chapter would be if they were reduced to PIT-tag models. For any radio-tag data set, Model 0 can be used to determine if information is lost by using PIT-tag data rather than radio-tag data (as the radio-tag data are used in later models). Model 0 uses simplified radio-tag data, and is designed for detections at K dams. Model 0 models only upstream travel, and ignores fallback.

3.4.1 Data Description

The basic method of data simplification necessary for all models in this chapter is described in Section 3.2. Extra simplification is necessary for Model 0, because it uses neither tributary detections nor multiple detections at a single dam. All tributary detections must be omitted. The simplified data as they appear after performing the steps in Section 3.2 contain both base-of-dam detections (D_{kB}) and top-of-dam detections (D_{kT}). Detections at the tops of the fish ladders indicate successful dam passage, and seem most analogous to PIT-tag detections, which are in the interiors of the fish ladders. Thus, after removing all tributary detections, all base-of-dam detections should be removed, as well. The data for each individual are expressed as a detection history, the simplified sequence of observed detection sites for that individual, beginning with the release (R). With only top-of-dam detections and no tributary detections, valid detection histories for Model 0 are those such as $R D_{1T} D_{2T} D_{4T}$. This detection history indicates that the fish was released and then seen at the tops of dams 1, 2, and 4, in that order. Although an individual with this detection history may have explored tributaries either upstream or downstream of dam 4, there is no indication of this here. Likewise, a fish with this detection history may have fallen

back over these dams multiple times, but only the individual's final ascents of dams 1, 2, and 4 are indicated. If dams 1 through 4 are the four dams on the lower Columbia River, then this detection history is consistent with migration both to the upper Columbia River upstream of McNary, and to the Snake River, as well as with death upstream of McNary. It is also possible that a fish with this detection history fell back over one or more of these dams, ending downstream of dam 4 (McNary), but without being detected during or after fallback.

Because this model is meant to be a PIT-tag model, the tributary detections should be removed before the data are reduced to the post-fallback paths. This is because PIT-tag data do not include tributary detections, but may indicate fallback.

3.4.2 Notation

Let K represent the number of dams modeled. The main process modeled in the release-recapture models in this chapter is the transition from one detection site to the next. Transitions combine both survival and movement, which cannot be separately estimated. In general in this chapter, the index i indicates a detection site from which a transition may be made. The probability of surviving and moving from site i to the next site, $i + 1$, is the transition parameter $\phi_{i,i+1}$:

$$\phi_{i,i+1} = Pr[\text{Survive and move from site } i \text{ to site } i + 1 \mid \text{Reach site } i],$$

where $i = R, D_{1T}, D_{2T}, \dots, D_{K-1,T}$. The transition parameter $\phi_{i,i+1}$ includes both survival and movement from the top of one dam to the top of the next. Thus, the natural river reach arising out of Model 0 includes a dam and the pool of the next dam downstream. Because Model 0 does not use tributary detections and ignores fallback behavior or other downstream travel, the parameter $\phi_{i,i+1}$ represents the probability of getting from site i to site $i + 1$, regardless of intervening behavior. The transition from site i to site $i + 1$ may include a fallback event, or entry into and return from a tributary. In general, we can interpret $\phi_{i,i+1}$ as the probability of remaining in the migrating population in the mainstem of the river from site i to site $i + 1$. The complement of $\phi_{i,i+1}$ includes both exit to a

tributary and fallback with no subsequent detection as well as both natural and fishing mortality.

Conditional detection and non-detection parameters at site i are p_i and $q_i = 1 - p_i$, respectively, each conditional on reaching site i . Let $\lambda = \phi_{D_{K-1,T}, D_{KT}} p_{KT}$ be the “final reach” parameter, the joint conditional probability of the transition from site $D_{K-1,T}$ to site D_{KT} and detection at D_{KT} , conditional on reaching $D_{K-1,T}$. The transition parameter $\phi_{D_{K-1,T}, D_{KT}}$ and the detection parameter p_{KT} cannot be separately estimated.

There are several possible fates for fish in a release group. Each individual in the release group may arrive at the final detection site (D_{KT}), exit to a tributary below site D_{KT} , fall back and evade subsequent detection, spawn in the mainstem, or die during migration via either harvest or natural mortality. The latter 4 possibilities are indistinguishable, and appear collectively in detection histories with final detections downstream of site D_{KT} . Any detection site may be the site of last detection for a fish. The probability of not being detected after site i , conditional on reaching that site, is χ_i :

$$\begin{aligned} \chi_i &= Pr[\text{Not detected after site } i \mid \text{Reach site } i] \\ &= \begin{cases} 1 - \phi_{i,i+1} + \phi_{i,i+1} q_{i+1} \chi_{i+1} & \text{for } i = R, D_{1T}, \dots, D_{K-2T}; \\ 1 - \lambda & \text{for } i = D_{K-1T}. \end{cases} \end{aligned} \quad (3.5)$$

The probability of any detection history can be expressed in terms of the $\phi_{i,i+1}$ parameters together with the χ_i parameters. For example, the probability of the detection history $R D_{1T} D_{2T} D_{4T}$ is

$$Pr[R D_{1T} D_{2T} D_{4T}] = \phi_{R, D_{1T}} p_{D_{1T}} \phi_{D_{1T}, D_{2T}} p_{D_{2T}} \phi_{D_{2T}, D_{3T}} q_{D_{3T}} \phi_{D_{3T}, D_{4T}} p_{D_{4T}} \chi_{D_{4T}}.$$

The parameters estimated by Model 0 are listed in Table 3.3.

Table 3.3: Parameters used in Model 0, the Simple Dam Detections model.

Parameter	Definition
$\phi_{i,i+1}$	Probability of surviving and moving from site i to site $i + 1$, given reaching site i , for $i = R, D_{1T}, \dots, D_{K-2T}$;

Table 3.3 continued

Parameter	Definition
p_i	Probability of being detected at site i , given reaching site i , for $i = D_{1T}, \dots, D_{K-1,T}$;
q_i	Probability of avoiding detection at site i , given reaching site i , for $i = D_{1T}, \dots, D_{K-1,T}$; $= 1 - p_i$;
λ	Joint probability of surviving and moving from site $D_{K-1,T}$ to D_{KT} and being detected at site D_{KT} , given reaching site $D_{K-1,T}$;
χ_i	Probability of not being detected after site i , given reaching site i , for $i = R, D_{1T}, \dots, D_{K-1,T}$.

3.4.3 Likelihood

The likelihood for Model 0 can be expressed in terms of simple summary statistics (Table 3.4). The necessary summary statistics are the number of fish detected at each site (a_i) and the number of these detected fish that are detected again upstream (b_i). Also useful, and defined in terms of the a_i and b_i statistics, are the numbers of fish detected after each site, whether or not they were detected at the site (g_i). The g_i statistics can be expressed in terms of the a_i and b_i statistics as follows:

$$\begin{aligned}
 g_R &= b_R; \\
 g_{D_{1T}} &= g_R + b_{D_{1T}} - a_{D_{1T}}; \\
 g_{D_{kT}} &= g_{D_{k-1,T}} + b_{D_{kT}} - a_{D_{kT}} \quad \text{for } k = 2, \dots, K-1.
 \end{aligned}$$

The summary statistics are listed in Table 3.4, and the minimal sufficient statistics are listed in Table 3.5. The full model for K dams has $2K - 1$ parameters and $2K - 1$ minimal sufficient statistics, so the maximum likelihood estimates may be found either by numerically maximizing the likelihood or by equating the minimal sufficient statistics to their expected values.

Table 3.4: Summary statistics for Model 0, the Single Dam Detection model. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i , $i = D_{1T}, \dots, D_{KT}$;
b_i	Number of fish detected at site i that were later detected upstream, $i = R, D_{1T}, \dots, D_{K-1,T}$;
g_i	Number of fish detected after site i , $i = R, D_{1T}, \dots, D_{K-1,T}$.

Table 3.5: Minimal sufficient statistics for Model 0, the Single Dam Detection model. The number of dams is K .

Statistic	Definition
$a_{D_{kT}}$	Number of fish detected at site D_{kT} , $k = 1, \dots, K - 1$;
b_R	Number of fish detected after the initial release;
$b_{D_{kT}}$	Number of fish detected at site D_{kT} and again upstream, $k = 1, \dots, K - 1$.

The likelihood for Model 0 can be expressed as

$$\begin{aligned}
 L \propto & \chi_R^{N-g_R} \phi_{R,D_{1T}}^{g_R} p_{D_{1T}}^{a_{D_{1T}}} q_{D_{1T}}^{g_R-a_{D_{1T}}} \chi_{D_{1T}}^{a_{D_{1T}}-b_{D_{1T}}} \\
 & \times \prod_{k=2}^{K-1} \left\{ \phi_{D_{k-1,T},D_{kT}}^{g_{D_{k-1,T}}} p_{D_{kT}}^{a_{D_{kT}}} q_{D_{kT}}^{g_{D_{k-1,T}}-a_{D_{kT}}} \chi_{D_{kT}}^{a_{D_{kT}}-b_{D_{kT}}} \right\} \lambda^{a_{D_{kT}}}, \quad (3.6)
 \end{aligned}$$

where N is the release size. Equation (3.6) may be tailored to a particular data set by specifying K , removing any extraneous parameters, and renaming parameters according to observed detections, if necessary. This is done for the 1996 Chinook salmon data set in Section 3.4.5.

3.4.4 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival, is S_{sys} , defined as follows:

$$S_{sys} = \eta_R,$$

where

$$\begin{aligned}\eta_R &= \phi_{R,D_{1T}}\eta_{D_{1T}}; \\ \eta_{D_{kT}} &= \phi_{D_{kT},D_{k+1,T}}\eta_{D_{k+1,T}}, \quad k = 1, \dots, K-1,\end{aligned}\tag{3.7}$$

and where $\phi_{D_{K-1,T},D_{KT}} = \lambda$ under the assumption of 100% detection at site D_{KT} . Under that assumption, survival from the release point to site D_{KT} is

$$S_{sys} = \phi_{R,D_{1T}} \left\{ \prod_{k=1}^{K-1} \phi_{D_{kT},D_{k+1,T}} \right\}.\tag{3.8}$$

The variance estimator of \hat{S}_{sys} is defined in Appendix B.

The only fates of tagged fish recognized in Model 0 are reaching site D_{KT} or disappearing (“loss”) before reaching D_{KT} . Thus, unaccountable loss (μ_R) is simply the complement of perceived survival to D_{KT} (i.e., $\mu_R = 1 - \eta_R$). Formally,

$$\mu_R = 1 - \phi_{R,D_{1T}}(1 - \mu_{D_{1T}}),$$

where

$$\begin{aligned}1 - \mu_{D_{kT}} &= \phi_{D_{kT},D_{k+1,T}}(1 - \mu_{D_{k+1,T}}), & k = 1, \dots, K-1; \\ 1 - \mu_{D_{KT}} &= 1, & k = K.\end{aligned}$$

Thus,

$$\mu_R = 1 - \eta_R.\tag{3.9}$$

The variance estimator of $\hat{\mu}_R$ is defined in Appendix B.

3.4.5 1996 Chinook Data Set

The observed summary statistics for Model 0 from the 1996 data set are given in Table 3.6.

Table 3.6: Observed summary statistics for Model 0 (Single Dam Detections Model) from 1996 Chinook data set. The release size is N . Descriptions of summary statistics are listed in Table 3.4.

Statistic	Value	Statistic	Value	Statistic	Value
N	846	b_R	754	g_R	754
a_{D1T}	700	b_{D1T}	419	g_{D1T}	473
a_{D2T}	421	b_{D2T}	312	g_{D2T}	364
a_{D3T}	352	b_{D3T}	279	g_{D3T}	291
a_{D4T}	282	b_{D4T}	99	g_{D4T}	108
a_{D5T}	101	b_{D5T}	79	g_{D5T}	86
a_{D6T}	0	b_{D6T}	0	g_{D6T}	86
a_{D7T}	87	b_{D7T}	0		

Table 3.6 shows that no fish were detected at dam 6, LMO. Thus, even if it were possible to separately estimate the transition and detection parameters at the final reach ($\phi_{D_{6T}, D_{7T}}$ and $p_{D_{7T}}$), it would be impossible to separately estimate the final two transitions parameters, $\phi_{D_{5T}, D_{6T}}$ and $\phi_{D_{6T}, D_{7T}}$. Instead, it is necessary to combine these two transition parameters to form a new parameter, $\phi_{D_{5T}, D_{7T}} = \phi_{D_{5T}, D_{6T}} \phi_{D_{6T}, D_{7T}}$. This is the final transition parameter, so it forms one factor of the estimable “final reach” reach parameter $\lambda \equiv \phi_{D_{5T}, D_{7T}} p_{D_{7T}}$. In summary, the estimable parameters for the 1996 Chinook data set are the transition parameters $\phi_{R, D_{1T}}, \phi_{D_{1T}, D_{2T}}, \phi_{D_{2T}, D_{3T}}, \phi_{D_{3T}, D_{4T}}, \phi_{D_{4T}, D_{5T}}$, the detection parameters $p_{D_{1T}}, p_{D_{2T}}, p_{D_{3T}}, p_{D_{4T}}, p_{D_{5T}}$, and the “final reach” parameter $\lambda \equiv \phi_{D_{5T}, D_{7T}} p_{D_{7T}}$. The likelihood for Model 0, tailored to the 1996 Chinook data set, is

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \phi_{R, D_{1T}}^{g_R} p_{D_{1T}}^{a_{D_{1T}}} q_{D_{1T}}^{g_R - a_{D_{1T}}} \chi_{D_{1T}}^{a_{D_{1T}} - b_{D_{1T}}} \phi_{D_{1T}, D_{2T}}^{g_{D_{1T}}} p_{D_{2T}}^{a_{D_{2T}}} q_{D_{2T}}^{g_{D_{1T}} - a_{D_{2T}}} \chi_{D_{2T}}^{a_{D_{2T}} - b_{D_{2T}}} \\
& \times \phi_{D_{2T}, D_{3T}}^{g_{D_{2T}}} p_{D_{3T}}^{a_{D_{3T}}} q_{D_{3T}}^{g_{D_{2T}} - a_{D_{3T}}} \chi_{D_{3T}}^{a_{D_{3T}} - b_{D_{3T}}} \phi_{D_{3T}, D_{4T}}^{g_{D_{3T}}} p_{D_{4T}}^{a_{D_{4T}}} q_{D_{4T}}^{g_{D_{3T}} - a_{D_{4T}}} \chi_{D_{4T}}^{a_{D_{4T}} - b_{D_{4T}}} \\
& \times \phi_{D_{4T}, D_{5T}}^{g_{D_{4T}}} p_{D_{5T}}^{a_{D_{5T}}} q_{D_{5T}}^{g_{D_{4T}} - a_{D_{5T}}} \chi_{D_{5T}}^{a_{D_{5T}} - b_{D_{5T}}} \lambda^{a_{D_{7T}}}.
\end{aligned} \tag{3.10}$$

3.4.6 Results

Program USER¹⁰ was used to fit Model 0 to the data via maximum likelihood. Maximum likelihood estimates of the parameters from Model 0 are listed in Table 3.7. The log-likelihood was -1903.4948, with an AIC of 3828.990. The perceived system survival rate (from the release to the top of the last dam [LGR]) is estimated at $\hat{S}_{sys} = 0.1028$ ($\widehat{SE} = 0.0104$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.8972$ ($\widehat{SE} = 0.0104$). Because the release group is composed of fish from different stocks and because Model 0 does not use tributary detections, it is reasonable that perceived system survival is low.

Table 3.7: Maximum likelihood estimates of parameters from Model 0, the Single Dam Detections model.

Category	Parameter	Estimate	S.E.
Transition	$\phi_{R,D_{1T}}$	0.9341	0.0130
	$\phi_{D_{1T},D_{2T}}$	0.6216	0.0196
	$\phi_{D_{2T},D_{3T}}$	0.7479	0.0216
	$\phi_{D_{3T},D_{4T}}$	0.8452	0.0284
	$\phi_{D_{4T},D_{5T}}$	0.3582	0.0292
Detection	$p_{D_{1T}}$	0.8858	0.0146
	$p_{D_{2T}}$	0.8571	0.0183
	$p_{D_{3T}}$	0.9555	0.0121
	$p_{D_{4T}}$	0.9083	0.0276
	$p_{D_{5T}}$	0.9080	0.0310
Final Reach	λ	0.7822	0.0411

3.5 Model 1: No Tributary Detections

Radiotelemetry data differ from PIT-tag data in that distinct detections are possible from multiple sites at the same dam. In particular, both base-of-dam (D_{kB} for dam k) and top-of-dam (D_{kT}) detections are available. Modeling data with two dam detections instead of one allows for estimation of the conditional probability of ascending the dam, given having reached the base of the dam. Furthermore, using two detections at the final dam (K) allows

¹⁰<http://www.cbr.washington.edu/paramEst/USER/>

separate estimates of both survival to the base of that dam and detection at that dam. Model 1 uses both base-of-dam and top-of-dam detections at the dams, but like Model 0, does not use tributary detections or acknowledge travel to tributaries or downstream travel.

3.5.1 Data Description

The extra simplification necessary for Model 1 after the basic steps outlined in Section 3.2 is to omit all tributary detections. As with Model 0, detection histories for Model 1 are sequences of observed detection sites, in order and starting with the release (R). Unlike Model 0 detection histories, Model 1 detection histories may include base-of-dam detections. For example, $R D_{1B} D_{1T} D_{2T}$ is a valid detection history for Model 1, indicating a fish that was detected at both the base and the top of the fish ladder at dam 1 and at the top of the ladder at dam 2. An individual with this detection history was not detected after the detection at the top of dam 2. Because the data simplification method uses detections from post-fallback paths, it is possible that an individual with this detection history ascended dams upriver of dam 2, but fell back over them all, with the detections shown occurring on the ascent after the fallback. Fallback after the D_{2T} detection that is not followed by a dam detection is possible, but not represented. It is also possible that a fish with this detection history explored tributaries, but such behavior is not represented here.

Because this model is meant to be similar to a PIT-tag model, the tributary detections should be removed before the data are reduced to the post-fallback paths. This is because PIT-tag data do not include tributary detections, but may indicate fallback.

3.5.2 Notation

The same types of notation and parameters are used in all models. The number of dams in the general model is K and i indicates a site from which a transition is made. The transition parameter $\phi_{i,i+1}$ is the joint probability of surviving and moving from site i to site $i + 1$:

$$\phi_{i,i+1} = Pr[\text{Survive and move from site } i \text{ to site } i + 1 \mid \text{Reach site } i],$$

where $i = R, D_{1B}, D_{1T}, D_{2B}, \dots, D_{KB}$. Model 1 uses two types of transition parameters: $\phi_{D_{k-1,T}, D_{kB}}$ and $\phi_{D_{kB}, D_{kT}}$. The former, $\phi_{D_{k-1,T}, D_{kB}}$, represents survival and movement from the top of one dam to the base of the next, while the latter, $\phi_{D_{kB}, D_{kT}}$, represents the probability of ascending dam k , given having reached the base of the dam. As in Model 0, the movement characterized by the parameter $\phi_{D_{k-1,T}, D_{kB}}$ may include fallback events or tributary entry and exit. The complement of $\phi_{D_{k-1,T}, D_{kB}}$ includes non-detected fallback and exit to a tributary as well as natural and fishing mortality.

The data simplification process requires that base-of-dam and top-of-dam detection sites remain paired in determining post-fallback paths. Thus, it appears that any simplified detection history with both D_{kB} and D_{kT} implies that the fish did not fall back between these two detections. However, tributary detections are removed from the detection histories before reducing the detection histories to their post-fallback paths for Model 1. Thus, it is possible that a simplified detection history with detections at both D_{kB} and D_{kT} is ignoring tributary entry between these two detections. For example, it is possible that a fish with detection history beginning $R D_{1B} D_{1T} \dots$ reached site D_{1B} and was detected there, then turned around to investigate tributaries below dam 1, returned to site D_{1B} without being detected there, and ascended dam 1, and was finally detected at site D_{1T} . This means that the transition parameter $\phi_{D_{kB}, D_{kT}}$ represents the overall probability of getting to the top of dam k , conditional only on reaching the base of dam k ; it may include travel to tributaries between reaching site D_{kB} and ascending to site D_{kT} .

Conditional detection and non-detection parameters at site i are p_i and $q_i = 1 - p_i$, respectively, each conditional on reaching site i . Because of the base-of-dam detection at the final dam (K), λ has a different definition in Model 1 than in Model 0: $\lambda = \phi_{D_{KB}, D_{KT}} p_{KT}$ is the joint conditional probability of the transition from site D_{KB} to site D_{KT} and detection at D_{KT} , conditional on reaching D_{KB} . If it is assumed that the detection rate at the top of dam K is 100%, then λ is the probability of ascending dam K , conditional upon reaching its base. On the other hand, if it is assumed that all fish that reach the base of dam K go on to ascend it, then λ is simply the detection rate at the top of that dam. In any case, using both detection sites at dam K allows for estimation of the transition probability from the top of the previous dam ($K - 1$) to the base of the final dam. The transition to dam K

is estimable here, but is not estimable in Model 0 or from PIT-tag data in general.

The possible fates of tagged fish in Model 1 are the same as those in Model 0, except that Model 1 includes extra detection sites. None of these detection sites is optional for fish who continue migrating, so the form of the “last detection” parameters, χ_i , is the same here as for Model 0. In general, the probability of not being detected after site i , conditional on reaching that site, is χ_i :

$$\begin{aligned}\chi_i &= Pr[\text{Not detected after site } i \mid \text{Reach site } i] \\ &= \begin{cases} 1 - \phi_{i,i+1} + \phi_{i,i+1}q_{i+1}\chi_{i+1} & \text{for } i = R, D_{1B}, \dots, D_{K-1,T}; \\ 1 - \lambda & \text{for } i = D_{KB}. \end{cases} \quad (3.11)\end{aligned}$$

Detection history probabilities can be expressed using the $\phi_{i,i+1}$ parameters together with the χ_i parameters. For example, the probability of the detection history $R D_{1B} D_{1T} D_{2T}$ is

$$Pr[R D_{1B} D_{1T} D_{2T}] = \phi_{R,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}} p_{D_{1T}} \phi_{D_{1T},D_{2B}} q_{D_{2B}} \phi_{D_{2B},D_{2T}} p_{D_{2T}} \chi_{D_{2T}}.$$

The parameters estimated by Model 1 are listed in Table 3.8.

Table 3.8: Parameters used in Model 1, the No Tributary Detections model.

Parameter	Definition
$\phi_{i,i+1}$	Probability of surviving and moving from site i to site $i + 1$, given reaching site i , for $i = R, D_{1B}, D_{1T}, \dots, D_{K-1,T}$;
p_i	Probability of being detected at site i , given having reached site i , for $i = D_{1B}, D_{1T}, \dots, D_{KB}$;
q_i	Probability of avoiding detection at site i , given having reached site i , for $i = D_{1B}, D_{1T}, \dots, D_{KB}$; $= 1 - p_i$;
λ	Joint probability of surviving and moving from site D_{KB} to D_{KT} and being detected at site D_{KT} , given reaching site D_{KB}
χ_i	Probability of not being detected after site i , given having reached site i , for $i = R, D_{1B}, D_{1T}, \dots, D_{KB}$.

3.5.3 Likelihood

The likelihood for Model 1 can be expressed using the summary statistics listed in Table 3.9. The necessary summary statistics are of the same form as those needed in Model 0: a_i is the number of fish detected at site i , b_i is the number of fish detected at site i that are later detected upstream, and g_i is the number of fish detected after site i . The g_i statistics can be expressed in terms of the other statistics as follows:

$$\begin{aligned}
 g_R &= b_R; \\
 g_{D_{1B}} &= g_R + b_{D_{1B}} - a_{D_{1B}}; \\
 g_{D_{kB}} &= g_{D_{k-1,T}} + b_{D_{kB}} - a_{D_{kB}} && \text{for } k = 2, \dots, K; \\
 g_{D_{kT}} &= g_{D_{kB}} + b_{D_{kT}} - a_{D_{kT}} && \text{for } k = 1, \dots, K-1.
 \end{aligned}$$

There are $4K - 1$ minimal sufficient statistics (Table 3.10) in the full model, with an equal number of parameters.

Table 3.9: Summary statistics for Model 1, the No Tributary model. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i , $i = D_{1B}, \dots, D_{KT}$;
b_i	Number of fish detected at site i that were later detected upstream, $i = R, D_{1B}, \dots, D_{KB}$;
g_i	Number of fish detected after site i , $i = R, D_{1B}, \dots, D_{KB}$.

Table 3.10: Minimal sufficient statistics for Model 1, the No Tributary model. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i , $i = D_{1B}, \dots, D_{KB}$;
b_R	Number of fish detected after the initial release;
b_i	Number of fish detected at site i and later upstream, $i = D_{1B}, \dots, D_{KB}$.

The likelihood for Model 1 is:

$$\begin{aligned}
 L \propto & \chi_R^{N-g_R} \phi_{R,D_{1B}}^{g_R} p_{D_{1B}}^{a_{D_{1B}}} q_{D_{1B}}^{g_R-a_{D_{1B}}} \chi_{D_{1B}}^{a_{D_{1B}}-b_{D_{1B}}} \\
 & \times \prod_{k=1}^{K-1} \left\{ \phi_{D_{kB},D_{kT}}^{g_{D_{kB}}} \phi_{D_{kT},D_{k+1,B}}^{g_{D_{kT}}} p_{D_{kT}}^{a_{D_{kT}}} q_{D_{kT}}^{g_{D_{kB}}-a_{D_{kT}}} p_{D_{k+1,B}}^{a_{D_{k+1,B}}} q_{D_{k+1,B}}^{g_{D_{kT}}-a_{D_{k+1,B}}} \right. \\
 & \left. \times \chi_{D_{k+1,B}}^{a_{D_{k+1,B}}-b_{D_{k+1,B}}} \chi_{D_{kT}}^{a_{D_{kT}}-b_{D_{kT}}} \right\} \lambda_{a_{D_{KT}}}, \quad (3.12)
 \end{aligned}$$

where N is the release size. Equation (3.12) may be tailored to a particular data set by specifying K , removing any extraneous parameters, and renaming parameters according to observed detections, if necessary. This is done for the 1996 Chinook salmon data set in Section 3.5.5.

3.5.4 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival, is S_{sys} , defined as follows:

$$S_{sys} = \eta_R,$$

where

$$\begin{aligned}
 \eta_R &= \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \eta_{D_{1T}}; \\
 \eta_{D_{kT}} &= \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}}, \quad k = 1, \dots, K-1; \\
 \eta_{D_{KT}} &= 1,
 \end{aligned} \quad (3.13)$$

and where $\phi_{D_{KB},D_{KT}} = \lambda$ under the assumption of 100% detection at site D_{KT} . Under that assumption, perceived system survival is:

$$S_{sys} = \phi_{R,D_{1B}} \prod_{k=1}^{K-1} \left\{ \phi_{D_{kB},D_{kT}} \phi_{D_{kT},D_{k+1,B}} \right\} \phi_{D_{KB},D_{KT}} \quad (3.14)$$

The variance estimator of \hat{S}_{sys} is defined in Appendix B.

As with Model 0, the only fates recognized in Model 1 are reaching site D_{KT} or disappearing before reaching that point. Thus, unaccountable loss (μ_R) is the complement of survival to D_{KT} : $\mu_R = 1 - \eta_R$. Formally,

$$\mu_R = 1 - \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} (1 - \mu_{D_{1T}}),$$

where

$$\begin{aligned} 1 - \mu_{D_{kT}} &= \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}} (1 - \mu_{D_{k+1,T}}), & k = 1, \dots, K-1; \\ 1 - \mu_{D_{KT}} &= 1, & k = K. \end{aligned}$$

Thus,

$$\mu_R = 1 - \eta_R. \quad (3.15)$$

The variance estimator of $\hat{\mu}_R$ is defined in Appendix B.

3.5.5 1996 Chinook Data Set

The observed summary statistics for Model 1 from the 1996 data set are given in Table 3.11.

Table 3.11: Observed summary statistics for Model 1 (No Tributary Model) from 1996 Chinook data set. The release size is N . Descriptions of summary statistics are listed in Table 3.9.

Statistic	Value	Statistic	Value	Statistic	Value	Statistic	Value
N	846	b_R	820				
a_{D1B}	776	b_{D1B}	706	a_{D1T}	694	b_{D1T}	417
a_{D2B}	0	b_{D2B}	0	a_{D2T}	421	b_{D2T}	313
a_{D3B}	0	b_{D3B}	0	a_{D3T}	351	b_{D3T}	291
a_{D4B}	281	b_{D4B}	265	a_{D4T}	279	b_{D4T}	113
a_{D5B}	115	b_{D5B}	107	a_{D5T}	101	b_{D5T}	96
a_{D6B}	73	b_{D6B}	67	a_{D6T}	0	b_{D6T}	0
a_{D7B}	102	b_{D7B}	85	a_{D7T}	87	b_{D7T}	0

There were no detections at the base of dams 2 (TDA) or 3 (JD), nor at the top of dam 6 (LMO). As with Model 0, it is necessary to combine certain transition parameters to form estimable transition parameters according to the observed detections: $\phi_{D_{1T}, D_{2T}} = \phi_{D_{1T}, D_{2B}} \phi_{D_{2B}, D_{2T}}$, $\phi_{D_{2T}, D_{3T}} = \phi_{D_{2T}, D_{3B}} \phi_{D_{3B}, D_{3T}}$, and $\phi_{D_{6B}, D_{7B}} = \phi_{D_{6B}, D_{6T}} \phi_{D_{6T}, D_{7B}}$. The remaining transition parameters indicated in Table 3.8 with $K = 7$ are estimable.

The likelihood for Model 1, tailored to the 1996 Chinook data set, is as follows:

$$\begin{aligned}
 L \propto & \chi_R^{N-g_R} \phi_{R, D_{1B}}^{g_R} p_{D_{1B}}^{a_{D_{1B}}} q_{D_{1B}}^{g_R - a_{D_{1B}}} \chi_{D_{1B}}^{a_{D_{1B}}} \phi_{D_{1B}, D_{1T}}^{g_{D_{1B}}} p_{D_{1T}}^{a_{D_{1T}}} q_{D_{1T}}^{g_{D_{1B}} - a_{D_{1T}}} \chi_{D_{1T}}^{a_{D_{1T}}} \phi_{D_{1T}}^{-b_{D_{1T}}} \\
 & \times \phi_{D_{1T}, D_{2T}}^{g_{D_{1T}}} p_{D_{2T}}^{a_{D_{2T}}} q_{D_{2T}}^{g_{D_{1T}} - a_{D_{2T}}} \chi_{D_{2T}}^{a_{D_{2T}}} \phi_{D_{2T}, D_{3T}}^{g_{D_{2T}}} p_{D_{3T}}^{a_{D_{3T}}} q_{D_{3T}}^{g_{D_{2T}} - a_{D_{3T}}} \chi_{D_{3T}}^{a_{D_{3T}}} \phi_{D_{3T}}^{-b_{D_{3T}}} \\
 & \times \phi_{D_{3T}, D_{4B}}^{g_{D_{3T}}} p_{D_{4B}}^{a_{D_{4B}}} q_{D_{4B}}^{g_{D_{3T}} - a_{D_{4B}}} \chi_{D_{4B}}^{a_{D_{4B}}} \phi_{D_{4B}, D_{4T}}^{g_{D_{4B}}} p_{D_{4T}}^{a_{D_{4T}}} q_{D_{4T}}^{g_{D_{4B}} - a_{D_{4T}}} \chi_{D_{4T}}^{a_{D_{4T}}} \phi_{D_{4T}}^{-b_{D_{4T}}} \quad (3.16) \\
 & \times \phi_{D_{4T}, D_{5B}}^{g_{D_{4T}}} p_{D_{5B}}^{a_{D_{5B}}} q_{D_{5B}}^{g_{D_{4T}} - a_{D_{5B}}} \chi_{D_{5B}}^{a_{D_{5B}}} \phi_{D_{5B}, D_{5T}}^{g_{D_{5B}}} p_{D_{5T}}^{a_{D_{5T}}} q_{D_{5T}}^{g_{D_{5B}} - a_{D_{5T}}} \chi_{D_{5T}}^{a_{D_{5T}}} \phi_{D_{5T}}^{-b_{D_{5T}}} \\
 & \times \phi_{D_{5T}, D_{6B}}^{g_{D_{5T}}} p_{D_{6B}}^{a_{D_{6B}}} q_{D_{6B}}^{g_{D_{5T}} - a_{D_{6B}}} \chi_{D_{6B}}^{a_{D_{6B}}} \phi_{D_{6B}, D_{7B}}^{g_{D_{6B}}} p_{D_{7B}}^{a_{D_{7B}}} q_{D_{7B}}^{g_{D_{6B}} - a_{D_{7B}}} \chi_{D_{7B}}^{a_{D_{7B}}} \phi_{D_{7B}}^{-b_{D_{7B}}} \lambda^{a_{D_{7T}}}.
 \end{aligned}$$

3.5.6 Results

Program USER¹¹ was used to fit Model 1 to the data via maximum likelihood. Maximum likelihood estimates of the parameters from Model 1 are listed in Table 3.12. The log-likelihood was -2457.4142, with an AIC of 4956.828. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.1028$ ($\widehat{SE} = 0.0104$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.8972$ ($\widehat{SE} = 0.0104$). These estimates are identical to the estimates of S_{sys} and μ_R attained from Model 0, a result that was expected because the only difference between Models 0 and 1 is the additional type of dam detections used in Model 1; neither Model 0 nor Model 1 uses fallback information or tributary detections, which might be expected to affect estimates of perceived system survival and unaccountable loss. Model 0 is identical to the adult portion of the PIT-tag model developed in Chapter 2; it is apparent that using extra detections at dams is unnecessary for estimating large-scale survival and unaccountable loss. The benefit of Model 1 over Model 0 is that Model 1

¹¹<http://www.cbr.washington.edu/paramEst/USER/>

provides an estimate of the transition rate to the base of the final dam, as well as estimates of dam ascension rates, $\phi_{D_{kB}, D_{kT}}$, which may be of interest.

Table 3.12: Maximum likelihood estimates of parameters from Model 1, the No Tributary Detections model.

Category	Parameter	Estimate	S.E.
Transition	$\phi_{R, D_{1B}}$	0.9744	0.0060
	$\phi_{D_{1B}, D_{1T}}$	0.9549	0.0127
	$\phi_{D_{1T}, D_{2T}}$	0.6237	0.0197
	$\phi_{D_{2T}, D_{3T}}$	0.7493	0.0215
	$\phi_{D_{3T}, D_{4B}}$	0.8330	0.0202
	$\phi_{D_{4B}, D_{4T}}$	0.9910	0.0216
	$\phi_{D_{4T}, D_{5B}}$	0.4070	0.0295
	$\phi_{D_{5B}, D_{5T}}$	0.9363	0.0241
	$\phi_{D_{5T}, D_{6B}}$	0.9791	0.0257
	$\phi_{D_{6B}, D_{7B}}$	0.9213	0.0324
Detection	$p_{D_{1B}}$	0.9413	0.0086
	$p_{D_{1T}}$	0.8816	0.0149
	$p_{D_{2T}}$	0.8575	0.0183
	$p_{D_{3T}}$	0.9541	0.0120
	$p_{D_{4B}}$	0.9170	0.0162
	$p_{D_{4T}}$	0.9187	0.0246
	$p_{D_{5B}}$	0.9304	0.0237
	$p_{D_{5T}}$	0.8727	0.0318
Final Reach	$p_{D_{6B}}$	0.6442	0.0469
	$p_{D_{7B}}$	0.9770	0.0161
Final Reach	λ	0.8333	0.0369

3.6 Model 2: Terminal Tributary Model

This model incorporates tributary detections, but only as terminal detections. It does not recognize tributary “visits,” in which a fish enters a tributary and then returns to the river (i.e., mainstem) within a few hours or a few days. Model 2 attempts to estimate survival between dams while accounting for exits from the river to tributaries for the purposes of spawning. Such exits to tributaries may be instances of either homing or straying, depending on the source of the fish (generally unknown). With only single arrays in each tributary, we cannot separate the probability of entering a tributary from the detection

rate there. Therefore, it is assumed that detection rates in all tributaries are 100%. This model recognizes only linear migration behavior, i.e., only upstream travel; no fallback or downstream travel is taken into account by Model 2.

If the terminal tributary detections occurred at or near the spawning grounds, rather than at the tributary mouths, then Model 2 would be appropriate for PIT-tag data in which there are two detections at each dam (base-of-dam and top-of-dam) and in which tags are retrieved or otherwise detected at the spawning grounds at an assumed rate of 100%. The radiotelemetry data include tributary detections only at the tributary mouths, so this interpretation of Model 2 is not perfectly applicable here. Nonetheless, Model 2 is worthwhile as a possible PIT-tag model and as an intermediate radio-tag model between the No Tributary model (Model 1) and the full tributary models (Models 3a, 3b, 5a, 5b, 5c, and 6).

3.6.1 Data Description

Section 3.2 describes the basic method of simplifying the data for all models. The extra simplification necessary for this model is to omit all tributary detections that are not terminal detections. The data for each individual are expressed as a detection history, a sequence of observed detection sites, starting with the release (R). Observed sites, as determined via the data simplification process, are listed in order in the detection histories. Because Model 2 recognizes only terminal detections at tributaries, tributaries are possible only as the final site in a detection history. For example, $R D_{1B} D_{1T} D_{2T} T_2$ is a valid detection history, but $R T_0 D_{1B} D_{1T} D_{2T} T_2$ is not.

3.6.2 Notation

Let K represent the number of dams. Tributaries either downstream of the first dam or upstream of the last dam are potential detection sites. The possible detection sites are $T_0, D_{1B}, D_{1T}, T_1, D_{2B}, D_{2T}, T_2, \dots, D_{K-1,T}, T_{K-1}, D_{KB}, D_{KT}, T_K$.

As with Models 0 and 1, the index i indicates a detection site *from* which a transition is made. In Model 2 and all later models, the index j indicates a transition site *to* which

a transition is made. The probability of moving from site i to site j is represented by the transition parameter ϕ_{ij} :

$$\phi_{ij} = Pr[\text{Survive and move from site } i \text{ to site } j \mid \text{Reached site } i], \quad (3.17)$$

where $i = R, D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$, and where

$$j = \begin{cases} D_{1B} \text{ or } T_0 & \text{for } i = R; \\ D_{kT} & \text{for } i = D_{kB}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = D_{kT}, k = 1, \dots, K-1; \\ T_k & \text{for } i = D_{kT}, k = 1, \dots, K. \end{cases} \quad (3.18)$$

The definition of ϕ_{ij} together with the valid combinations of i and j indicate that Model 2 allows only upstream movement and terminal tributary detections. No transition beginning at a tributary is allowed. The parameter of the form $\phi_{D_{kB}, D_{kT}}$ represents the probability of successfully ascending dam k ($k = 1, \dots, K$), conditional on having reached the base of the dam (site D_{kB}). As with Model 1, $\phi_{D_{kB}, D_{kT}}$ includes the possibility of reaching and being detected at site D_{kB} , visiting a tributary T_{k-1} , returning to site D_{kB} without being detected there, and then finally ascending dam k and being detected at the top. However, because fallback paths are removed in such a way that detections at sites D_{kB} and D_{kT} from the same passage of dam k are kept together, it can be assumed that $\phi_{D_{kB}, D_{kT}}$ does not include the probability of fallback and subsequent reascension of dam k . The parameter ϕ_{D_{kT}, T_k} represents the probability of moving from the top of dam k (site D_{kT}) to a tributary between dams k and $k+1$, for $k = 1, \dots, K-1$. A detection history from a fish that ascended dams higher than dam k , fell back over those dams, and finally left the river at tributary T_k would be parameterized with ϕ_{D_{kT}, T_k} in Model 2 because fallback is not recognized in this model. The parameter $\phi_{D_{kT}, D_{k+1,B}}$ represents the probability of moving from the top of dam k to the base of dam $k+1$ for $k = 1, \dots, K-1$, possibly with either fallback or tributary visits between the two dams. Thus, the transitions modeled in Model 2 are not restricted to direct transitions, but may include either fallback or tributary entry and exit.

Let p_i represent the probability of being detected at site i , conditional on reaching that site, and let $q_i = 1 - p_i$ be the probability of not being detected at site i , conditional on reaching that site. It is assumed that the detection rate in the tributaries is 100%, meaning $p_{T_k} = 1$ for $k = 0, \dots, K$. With a tributary detection site upstream of the final dam site, D_{KT} , it is possible to separately estimate the transition parameter $\phi_{D_{KB}, D_{KT}}$ and the detection parameter $p_{D_{KT}}$.

There are several final tag fates possible in Model 2. A fish may be detected for the last time at the release point, at the base or top of any dam, or at any tributary. Unlike Models 0 and 1, it is assumed here that all fish exiting the river to a tributary are detected. This means that fish detected for the last time at a dam site or at the release are assumed not to have entered a tributary; on the other hand, they may have fallen back with no subsequent detections, have been taken in a fishery, or have died in the river. Thus, Model 2 is a first step toward accounting for the “unaccountable loss” from simpler models. Because only terminal tributary detections are used in Model 2, it is assumed that fish detected at a tributary have no later detections. The parameter χ_i is the probability of not being detected after site i , conditional on reaching that site:

$$\chi_i = \Pr[\text{not detected after site } i \mid \text{reach site } i].$$

More specifically,

$$\begin{aligned} \chi_R &= 1 - \phi_{R, T_0} - \phi_{R, D_{1B}}(1 - q_{D_{1B}}\chi_{D_{1B}}); \\ \chi_{D_{kB}} &= 1 - \phi_{D_{kB}, D_{kT}}(1 - q_{D_{kT}}\chi_{D_{kT}}), & k = 1, \dots, K; \\ \chi_{D_{kT}} &= 1 - \phi_{D_{kT}, T_k} - \phi_{D_{kT}, D_{k+1, B}}(1 - q_{D_{k+1, B}}\chi_{D_{k+1, B}}), & k = 1, \dots, K-1; \\ \chi_{D_{KT}} &= 1 - \phi_{D_{KT}, T_K}; \\ \chi_{T_k} &= 1, & k = 0, \dots, K. \end{aligned} \tag{3.19}$$

The parameters used in Model 2 are given in Table 3.13.

Table 3.13: Parameters used in Model 2, the Terminal Tributary model.

Parameter	Definition
ϕ_{ij}	Probability of surviving and moving from site i to site j , given having reached site i , for $i = R, D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$ and j defined as in Equation (3.18);
p_i	Probability of being detected at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$;
q_i	Probability of avoiding detection at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$; $= 1 - p_i$;
χ_i	Probability of not being detected after site i , given having reached site i , for $i \in A_{2i}$.

The ϕ_{ij} and χ_i parameters can be used to express the probabilities of the possible detection histories. For example, the probability of observing the detection history $R D_{1B} D_{1T} T_1$ is

$$Pr[R D_{1B} D_{1T} T_1] = \phi_{R,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}} p_{D_{1T}} \phi_{D_{1T},T_1}.$$

The probability of observing the detection history $R D_{2T} D_{3T} D_{4B}$ is

$$Pr[R D_{1T} D_{2T}] = \phi_{R,D_{1B}} q_{D_{1B}} \phi_{D_{1B},D_{1T}} p_{D_{1T}} \phi_{D_{1T},D_{2B}} q_{D_{2B}} \phi_{D_{2B},D_{2T}} p_{D_{2T}} \chi_{D_{2T}}.$$

The remaining detection histories can be expressed similarly.

3.6.3 Likelihood

With $3K + 1$ possible detection sites, K of which are restricted to final (terminal) detections, the number of possible detection histories increases quickly with K . Thus, the likelihood is most easily expressed using summary statistics, similar to those used in Models 0 and 1. The necessary summary statistics (Table 3.14) are a_i , the number of fish detected at site i , b_i , the number of fish detected at site i and detected later upstream, and g_i , the number of fish detected upstream of site i . The g_i statistics can be expressed in terms of the other

statistics as follows:

$$\begin{aligned}
 g_R &= b_R; \\
 g_{T_0} &= g_R - a_{T_0}; \\
 g_{T_k} &= g_{D_{kT}} - a_{T_k} && \text{for } k = 2, \dots, K-1; \\
 g_{D_{kB}} &= g_{T_{k-1}} + b_{D_{kB}} - a_{D_{kB}} && \text{for } k = 1, \dots, K; \\
 g_{D_{kT}} &= g_{D_{kB}} + b_{D_{kT}} - a_{D_{kT}} && \text{for } k = 1, \dots, K.
 \end{aligned}$$

Model 2 has $5K + 1$ minimal sufficient statistics (Table 3.15) and an equal number of parameters.

Table 3.14: Summary statistics for Model 2, the Terminal Tributary model. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i , $i = T_0, D_{1B}, \dots, D_{KT}, T_K$;
b_R	Number of fish detected after the initial release;
b_i	Number of fish detected at site i that were later detected upstream, $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KB}, D_{KT}$;
g_i	Number of fish detected after site i , $i = R, T_0, D_{1B}, \dots, T_{K-1}, D_{KB}, D_{KT}$.

Table 3.15: Minimal sufficient statistics for Model 2, the Terminal Tributary model. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i , $i = T_0, D_{1B}, D_{1T}, T_1, \dots, D_{KB}, D_{KT}$;
b_R	Number of fish detected after the initial release;
b_i	Number of fish detected at site i and later upstream, $i = D_{1B}, D_{1T}, \dots, D_{K-1,T}, D_{KB}, D_{KT}$.

The likelihood for Model 2 is

$$\begin{aligned}
 L \propto & \chi_R^{N-g_R} \phi_{R,T_0}^{a_{T_0}} \phi_{R,D_{1B}}^{g_{T_0}} \prod_{k=1}^{K-1} \left\{ \phi_{D_{kB},D_{kT}}^{g_{D_{kB}}} \phi_{D_{kT},T_k}^{a_{T_k}} \phi_{D_{kT},D_{k+1,B}}^{g_{T_k}} p_{D_{kB}}^{a_{D_{kB}}} q_{D_{kB}}^{g_{T_{k-1}}-a_{D_{kB}}} \right. \\
 & \times p_{D_{kT}}^{a_{D_{kT}}} q_{D_{kT}}^{g_{D_{kB}}-a_{D_{kT}}} \chi_{D_{kB}}^{a_{D_{kB}}-b_{D_{kB}}} \chi_{D_{kT}}^{a_{D_{kT}}-b_{D_{kT}}} \left. \right\} \phi_{D_{KB},D_{KT}}^{g_{D_{KB}}} \phi_{D_{KT},T_K}^{a_{T_K}} p_{D_{KB}}^{a_{D_{KB}}} q_{D_{KB}}^{g_{T_{K-1}}-a_{D_{KB}}} \\
 & \times p_{D_{KT}}^{a_{D_{KT}}} q_{D_{KT}}^{g_{D_{KB}}-a_{D_{KT}}} \chi_{D_{KB}}^{a_{D_{KB}}-b_{D_{KB}}} \chi_{D_{KT}}^{a_{D_{KT}}-b_{D_{KT}}}, \quad (3.20)
 \end{aligned}$$

where N is the release size. Equation (3.20) may be tailored to a particular data set by specifying K , removing any extraneous parameters, and redefining parameters according to observed detections, if necessary. This is done for the 1996 Chinook salmon data set in the next section.

3.6.4 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival, is S_{sys} , defined as follows:

$$S_{sys} = \eta_R,$$

where

$$\begin{aligned}
 \eta_R &= \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \eta_{D_{1T}}; \\
 \eta_{D_{kT}} &= \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}}, \quad k = 1, \dots, K-1; \\
 \eta_{D_{KT}} &= 1.
 \end{aligned} \quad (3.21)$$

The difference between Models 1 and 2 is that Model 2 incorporates terminal tributary detections while Model 1 ignores all tributary detections. Thus, for both Models 1 and 2, all fish that reach the top of the final dam (dam K) must have avoided all tributaries downstream of dam K , and so Models 1 and 2 use the same formula for η_R and S_{sys} (Equation (3.21)). Because detections at tributary T_K are used in Model 2, however, it is no longer necessary to assume 100% detection at site D_{KT} for Model 2. The variance

estimator of \hat{S}_{sys} is defined in Appendix B.

The possible fates of tagged fish recognized in Model 2 are reaching the top of dam K (site D_{KT}), permanently exiting the mainstem of the river to a tributary, or disappearing before doing either of these actions. Model 2 assumes that no fish return from any tributary. Thus, any fish that survived to site D_{KT} must have avoided all tributaries, while fish that did not survive to site D_{KT} may have entered a tributary and remained there. This means that for Model 2 (and for all subsequent models), unaccountable loss is not the complement of survival to D_{KT} : $\mu_R \neq 1 - \eta_R$. For Model 2, μ_R is defined as follows:

$$\mu_R = 1 - \phi_{R,T_0} - \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} (1 - \mu_{D_{1T}}), \quad (3.22)$$

where

$$\begin{aligned} 1 - \mu_{D_{kT}} &= \phi_{D_{kT},T_k} + \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}} (1 - \mu_{D_{k+1,T}}), & k = 1, \dots, K-1; \\ 1 - \mu_{D_{kT}} &= 1, & k = K. \end{aligned}$$

The variance estimator of $\hat{\mu}_R$ is defined in Appendix B. It should be noted that if the assumption of 100% detection at the tributary antenna arrays is faulty, then the transitions $\phi_{D_{k+1,T},T_k}$ are negatively biased, and so μ_R is positively biased.

3.6.5 1996 Chinook Data Set

The observed summary statistics for Model 2 from the 1996 Chinook data set are given in Table 3.16.

Table 3.16: Observed summary statistics for Model 2 (Terminal Tributary Model). The release size is N . Descriptions of summary statistics are listed in Table 3.14.

Statistic	Value	Statistic	Value
N	846	b_R	825
a_{T0}	7		
$a_{D_{1B}}$	772	$b_{D_{1B}}$	741
$a_{D_{1T}}$	692	$b_{D_{1T}}$	621
a_{T1}	254		

Table 3.16 continued

Statistic	Value	Statistic	Value
a_{D2B}	0	b_{D2B}	0
a_{D2T}	401	b_{D2T}	368
a_{T2}	72		
a_{D3B}	0	b_{D3B}	0
a_{D3T}	343	b_{D3T}	321
a_{T3}	37		
a_{D4B}	274	b_{D4B}	266
a_{D4T}	273	b_{D4T}	253
a_{T4}	150		
a_{D5B}	112	b_{D5B}	107
a_{D5T}	101	b_{D5T}	96
a_{T5}	1		
a_{D6B}	72	b_{D6B}	67
a_{D6T}	0	b_{D6T}	0
a_{T6}	0		
a_{D7B}	102	b_{D7B}	87
a_{D7T}	87	b_{D7T}	71
a_{T7}	73		

There were no detections at sites D_{2B} , D_{3B} , D_{6T} , or T_6 . As with Model 1, it is necessary to redefine the transition parameters associated with these detection sites. In general, the estimable detection parameters are those described in Table 3.13 for $K = 7$, with the following substitutions for parameters $\phi_{D_{1T}, D_{2B}}$, $\phi_{D_{2B}, D_{2T}}$, $\phi_{D_{2T}, D_{3B}}$, $\phi_{D_{3B}, D_{3T}}$, $\phi_{D_{6B}, D_{6T}}$, ϕ_{D_{6T}, T_6} , and $\phi_{D_{6T}, D_{7B}}$:

$$\phi_{D_{1T}, D_{2T}} = \phi_{D_{1T}, D_{2B}} \phi_{D_{2B}, D_{2T}};$$

$$\phi_{D_{2T}, D_{3T}} = \phi_{D_{2T}, D_{3B}} \phi_{D_{3B}, D_{3T}};$$

$$\phi_{D_{6B}, T_6} = \phi_{D_{6B}, D_{6T}} \phi_{D_{6T}, T_6} = 0;$$

$$\phi_{D_{6B}, D_{7T}} = \phi_{D_{6B}, D_{6T}} \phi_{D_{6T}, D_{7B}}.$$

The likelihood for Model 2, tailored to the 1996 Chinook data set, is

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \phi_{R,T_0}^{a_{T_0}} \phi_{R,D_{1B}}^{g_{T_0}} p_{D_{1B}}^{a_{D_{1B}}} q_{D_{1B}}^{g_{T_0}-a_{D_{1B}}} \chi_{D_{1B}}^{a_{D_{1B}}-b_{D_{1B}}} \phi_{D_{1B},D_{1T}}^{g_{D_{1B}}} p_{D_{1T}}^{a_{D_{1T}}} q_{D_{1T}}^{g_{D_{1B}}-a_{D_{1T}}} \chi_{D_{1T}}^{a_{D_{1T}}-b_{D_{1T}}} \\
& \times \phi_{D_{1T},T_1}^{a_{T_1}} \phi_{D_{1T},D_{2T}}^{g_{T_1}} p_{D_{2T}}^{a_{D_{2T}}} q_{D_{2T}}^{g_{T_1}-a_{D_{2T}}} \chi_{D_{2T}}^{a_{D_{2T}}-b_{D_{2T}}} \phi_{D_{2T},T_2}^{a_{T_2}} \phi_{D_{2T},D_{3T}}^{g_{T_2}} p_{D_{3T}}^{a_{D_{3T}}} q_{D_{3T}}^{g_{T_2}-a_{D_{3T}}} \chi_{D_{3T}}^{a_{D_{3T}}-b_{D_{3T}}} \\
& \times \phi_{D_{3T},T_3}^{a_{T_3}} \phi_{D_{3T},D_{4B}}^{g_{T_3}} p_{D_{4B}}^{a_{D_{4B}}} q_{D_{4B}}^{g_{T_3}-a_{D_{4B}}} \chi_{D_{4B}}^{a_{D_{4B}}-b_{D_{4B}}} \phi_{D_{4B},D_{4T}}^{g_{D_{4B}}} p_{D_{4T}}^{a_{D_{4T}}} q_{D_{4T}}^{g_{D_{4B}}-a_{D_{4T}}} \chi_{D_{4T}}^{a_{D_{4T}}-b_{D_{4T}}} \\
& \times \phi_{D_{4T},T_4}^{a_{T_4}} \phi_{D_{4T},D_{5B}}^{g_{T_4}} p_{D_{5B}}^{a_{D_{5B}}} q_{D_{5B}}^{g_{T_4}-a_{D_{5B}}} \chi_{D_{5B}}^{a_{D_{5B}}-b_{D_{5B}}} \phi_{D_{5B},D_{5T}}^{g_{D_{5B}}} p_{D_{5T}}^{a_{D_{5T}}} q_{D_{5T}}^{g_{D_{5B}}-a_{D_{5T}}} \chi_{D_{5T}}^{a_{D_{5T}}-b_{D_{5T}}} \\
& \times \phi_{D_{5T},T_5}^{a_{T_5}} \phi_{D_{5T},D_{6B}}^{g_{T_5}} p_{D_{6B}}^{a_{D_{6B}}} q_{D_{6B}}^{g_{T_5}-a_{D_{6B}}} \chi_{D_{6B}}^{a_{D_{6B}}-b_{D_{6B}}} \phi_{D_{6B},D_{7B}}^{g_{D_{6B}}} p_{D_{7B}}^{a_{D_{7B}}} q_{D_{7B}}^{g_{D_{6B}}-a_{D_{7B}}} \chi_{D_{7B}}^{a_{D_{7B}}-b_{D_{7B}}} \\
& \times \phi_{D_{7B},D_{7T}}^{g_{D_{7B}}} p_{D_{7T}}^{a_{D_{7T}}} q_{D_{7T}}^{g_{D_{7B}}-a_{D_{7T}}} \chi_{D_{7T}}^{a_{D_{7T}}-b_{D_{7T}}} \phi_{D_{7T},T_7}^{a_{T_7}}. \tag{3.23}
\end{aligned}$$

3.6.6 Results

Program USER¹² was used to fit Model 2 to the data via maximum likelihood. Maximum likelihood estimates of the parameters from Model 2 are listed in Table 3.17. The log-likelihood was -2926.7083, with an AIC of 5911.417. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.0863$ ($\widehat{SE} = 0.0097$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2784$ ($\widehat{SE} = 0.0154$). Because of the detection site in the tributary above dam 7, it is not necessary to assume 100% detection at the top of dam 7. The estimated detection rate at site D_{7T} is approximately 100%, however ($\hat{p}_{D_{7T}} = 0.9726$, $\widehat{SE} = 0.0191$), so the assumption of perfect detection used in Models 0 and 1 is reasonable.

The perceived system survival rate estimated from Model 2 is slightly smaller than the estimates from Models 0 and 1: $\hat{S}_{sys} = 0.0863$ ($\widehat{SE} = 0.0097$) for Model 2 versus $\hat{S}_{sys} = 0.1098$ ($\widehat{SE} = 0.0104$) for Models 0 and 1. The difference between Model 2 and Model 1 is that Model 2 uses terminal tributary detections, whereas Model 1 ignores all tributary information. The tributary information used by Model 2 may produce larger dam-to-dam transition rates if the terminal tributary detections imply dam passage that is otherwise undetected. Examination of the estimates of $\phi_{D_{kB},D_{kT}}$ and $\phi_{D_{kT},D_{k+1,B}}$ for Models 2 and 1 shows some increased transition estimates for Model 2. However, because

¹²<http://www.cbr.washington.edu/paramEst/USER/>

tributary detections were removed from the unsimplified data before fallback paths were removed for Model 1 (and 0), it is also possible that the tributary data used in Model 2 implied some fallback events that were not observed during the data simplification process for Models 0 and 1. In such a case, the transition rate between the dams on either side of such a tributary detection would be lower for Model 2, because only the post-fallback migration paths are used. Comparison of Tables 3.12 and 3.17 shows that some dam-to-dam transition rate estimates are smaller for Model 2 than for Model 1; these decreases are sufficient to offset the increases in other transitions, and so the perceived system survival estimate is smaller for Model 2 than for Model 1 (and 0). The difference between Models 2 and 0 or 1 is not large, however. In general, it is impossible to predict which factor will be more significant, upstream tributary detections implying dam passage, or downstream tributary detections implying fallback, and so it is impossible to predict how using terminal tributary detections will affect estimates of perceived system survival. Nevertheless, it seems reasonable to expect little difference between the system survival estimates of Models 1 and 2.

The estimate of the unaccountable loss rate was much lower for Model 2 than for Models 0 and 1: $\hat{\mu}_R = 0.2784$ ($\widehat{SE} = 0.0154$) for Model 2 versus $\hat{\mu}_R = 0.8972$ ($\widehat{SE} = 0.0104$) for Models 0 and 1. This is reasonable if the data include many records with final detections in tributaries. Model 2 views these fish as "accounted for," whereas Models 0 and 1 view them as losses between dams. Table 3.16 shows that 501 fish, or 59% of the release group, were last detected in tributaries downstream of LGR, so the very large decrease in $\hat{\mu}_R$ from Models 0 and 1 to Model 2 was to be expected. With a mixed-stock release group such as that considered here, it is apparent that Model 2, with its use of tributary detections, adds considerable information on unaccountable loss relative to Models 0 and 1. Currently, radio tags provide tributary information, but PIT tags do not. If tributary detection of PIT tags becomes available in the future, then Model 2 may be used with PIT-tag data. Until then, radio tags appear more useful than PIT tags in estimating unaccountable loss rates, but only slightly more useful in estimating (perceived) system survival.

Table 3.17: Maximum likelihood estimates of parameters from Model 2, the Terminal Tributary model.

Category	Parameter	Estimate	S.E.
Transition	ϕ_{R,T_0}	0.0083	0.0031
	$\phi_{R,D_{1B}}$	0.9692	0.0062
	$\phi_{D_{1B},D_{1T}}$	0.9731	0.0075
	ϕ_{D_{1T},T_1}	0.3184	0.0166
	$\phi_{D_{1T},D_{2T}}$	0.5859	0.0180
	ϕ_{D_{2T},T_2}	0.1540	0.0167
	$\phi_{D_{2T},D_{3T}}$	0.7657	0.0202
	ϕ_{D_{3T},T_3}	0.1034	0.0161
	$\phi_{D_{3T},D_{4B}}$	0.8345	0.0199
	$\phi_{D_{4B},D_{4T}}$	0.9753	0.0103
	ϕ_{D_{4T},T_4}	0.5149	0.0294
	$\phi_{D_{4T},D_{5B}}$	0.4132	0.0290
	$\phi_{D_{5B},D_{5T}}$	0.9614	0.0199
	ϕ_{D_{5T},T_5}	0.0086	0.0086
	$\phi_{D_{5T},D_{6B}}$	0.9657	0.0263
	$\phi_{D_{6B},D_{7B}}$	0.9336	0.0301
	$\phi_{D_{7B},D_{7T}}$	0.8573	0.0354
Detection	$p_{D_{1B}}$	0.9416	0.0084
	$p_{D_{1T}}$	0.8673	0.0127
	$p_{D_{2T}}$	0.8578	0.0169
	$p_{D_{3T}}$	0.9582	0.0109
	$p_{D_{4B}}$	0.9172	0.0162
	$p_{D_{4T}}$	0.9370	0.0148
	$p_{D_{5B}}$	0.9304	0.0237
	$p_{D_{5T}}$	0.8727	0.0318
	$p_{D_{6B}}$	0.6442	0.0469
	$p_{D_{7B}}$	0.9775	0.0157
Final Reach	$p_{D_{7T}}$	0.9726	0.0191
	λ	0.8161	0.0415

3.7 Model 3: Tributary Model

Model 3 allows for tributary detections that are not terminal detections, as well as the terminal tributary detections allowed in Model 2. A non-terminal tributary detection occurs when a tagged fish enters a tributary, is detected by the antenna array, and within minutes or hours returns from the tributary to the mainstem to continue its migration. This type of behavior (i.e., a tributary visit) may provide the fish with a temperature refugium in hot

temperatures or a resting place on its migration. Figure 3.1(b) shows an example of visiting behavior. It should be noted that the placement of the antenna array in the tributary mouth affects the definition of a visit for a particular tributary. Fish that near the antennas but are not detected are not classified as having entered the tributary. Model 3 assumes 100% detection in the tributaries, and does not incorporate fallback or other downstream travel. Fish that exhibit visiting behavior are assumed to resume migrating upstream upon returning from the tributary to the river.

It is conceivable that individuals that enter a tributary temporarily in one reach experience differential survival and tributary entry rates in following reaches. For example, a fish that rested in a tributary may have a higher probability of surviving the following reach than a fish that did not use the lower tributary. On the other hand, fish in tributaries may be at higher risk of injury from fisheries than mainstem fish, and so may have lower survival rates after returning to the mainstem. Alternatively, one reason a fish might enter a tributary and then return to the river is to explore the tributary to determine whether it leads to the fish's spawning grounds. Thus, a fish that enters a tributary in one reach and then returns to the river may be in the exploration mode, and be more likely to enter a tributary in the following reach than a fish that did not explore the tributaries in the lower reach. These possibilities suggest non-independent behavior from reach to reach, or a "memory" effect of tributary behavior from previous reaches.

Two models are presented in this section, both allowing for tributary visiting behavior (i.e., non-terminal tributary detections). Model 3a assumes that tributary behavior in one reach does not affect parameters in later reaches, i.e., that reaches are independent with respect to tributary behavior. Model 3a is thus a "memory-free" model. Model 3b allows tributary visits in a given reach to affect survival and tributary entry and exit rates in the following reach, i.e., Model 3b allows for non-independent reaches, and is thus a "memory" model. Model 3a is nested in Model 3b, and the two models may be compared via a likelihood ratio test. Both Models 3a and 3b use the same data, so the data are described for both before detailed descriptions of the two models.

3.7.1 Data Description

The routine used to simplify the data for all models is described in Section 3.2. No extra simplification is necessary for Models 3a and 3b. Detection histories for Models 3a and 3b are sequences of observed detection sites, starting with the release (R). Unlike detection histories for Model 2, those for Models 3a and 3b may include tributary sites before the final detection.

3.7.2 Model 3a: Memory-Free Tributary Model

Model 3a assumes no effect of entering and then exiting a tributary in reach k on survival, detection, or tributary parameters in upstream reaches or in ascending dam $k + 1$, for $k = 1, \dots, K$.

3.7.2.1 Notation

The same basic notation used in previous models is used here. The number of dams is K . The index i indicates (re-)release sites, i.e., sites *from* which transitions may be made. The index j indicates recapture sites, i.e., sites *to* which transitions may be made. The transition parameter ϕ_{ij} represents the probability of moving from site i to site j . It is assumed that the detection rate in the tributaries is 100%. Thus, for $i = D_{kT}$ and $j = D_{k+1,B}$ ($k = 1, \dots, K - 1$), the parameter ϕ_{ij} is the probability of surviving and moving from the top of dam k to the base of dam $k + 1$ without entering any tributary between the two dams. This contrasts with the interpretation of $\phi_{D_{kT}, D_{k+1,B}}$ in Models 1 and 2, where $\phi_{D_{kT}, D_{k+1,B}}$ is the probability of surviving and reaching the base of dam $k + 1$, given having reached the top of dam k , regardless of any intervening tributary behavior. The release index i may be any site downstream of the final site (i.e., $i = R, T_0, D_{1B}, D_{1T}, T_1, D_{2B}, \dots, D_{KT}$). The recapture index j is restricted, based on the release index:

$$j = \begin{cases} D_{1B} \text{ or } T_0 & \text{for } i = R; \\ D_{kT} & \text{for } i = D_{kB}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = D_{kT}, k = 1, \dots, K-1; \\ T_k & \text{for } i = D_{kT}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = T_k, k = 0, \dots, K-1. \end{cases} \quad (3.24)$$

As with previous models, let p_i and $q_i = 1 - p_i$ represent the probabilities of being detected and of not being detected, respectively, at site i , conditional on reaching site i , with $p_{T_k} = 1$ for $k = 0, \dots, K$.

The possible fates of tagged fish recognized by Model 3a include permanent exit to a tributary, fallback with no subsequent detection, and both natural and fishing mortality. Because of the assumption of the 100% tributary detection, if a fish is last seen at a dam, it is assumed that the fish remained in the river, either dying there or falling back with no subsequent detection; only fish with final detections at tributaries are assumed to have successfully entered a tributary. Because fish that enter a tributary may later return to the river to continue migrating, however, it is necessary to parameterize the probability of evading detection after entering a tributary using the model parameters. The probability of not being detected after site i , given having reached that site, is χ_i :

$$\begin{aligned} \chi_R &= 1 - \phi_{R,T_0} - \phi_{R,D_{1B}}(1 - q_{D_{1B}}\chi_{D_{1B}}); \\ \chi_{D_{kB}} &= 1 - \phi_{D_{kB},D_{kT}}(1 - q_{D_{kT}}\chi_{D_{kT}}), & k = 1, \dots, K; \\ \chi_{D_{kT}} &= 1 - \phi_{D_{kT},T_k} - \phi_{D_{kT},D_{k+1,B}}(1 - q_{D_{k+1,B}}\chi_{D_{k+1,B}}), & k = 1, \dots, K-1; \\ \chi_{D_{KT}} &= 1 - \phi_{D_{KT},T_K}; \\ \chi_{T_k} &= 1 - \phi_{T_k,D_{k+1,B}}(1 - q_{D_{k+1,B}}\chi_{D_{k+1,B}}), & k = 0, \dots, K-1. \end{aligned} \quad (3.25)$$

The parameters used in Model 3a are given in Table 3.18.

Table 3.18: Parameters used in Model 3a, the Memory-Free Tributary model.

Parameter	Definition
ϕ_{ij}	Probability of surviving and moving from site i to site j , given having reached site i , for $i = R, T_0, D_{1B}, \dots, D_{KT}$ and j defined as in Equation (3.24);
p_i	Probability of being detected at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$;
q_i	Probability of avoiding detection at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$; $= 1 - p_i$;
χ_i	Probability of not being detected after site i , given having reached site i , for $i = R, T_0, D_{1B}, \dots, D_{KT}$.

Using the ϕ_{ij} and χ_i parameters, the detection history $R T_0 D_{1B} D_{1T} T_1$ has probability

$$Pr[R T_0 D_{1B} D_{1T} T_1] = \phi_{R,T_0} \phi_{T_0,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}} p_{D_{1T}} \phi_{D_{1T},D_{2B}} q_{D_{2B}} \phi_{D_{2B},D_{2T}} q_{D_{2T}} \phi_{D_{2T},T_2} \chi_{T_2}.$$

3.7.2.2 Likelihood

With $3K + 1$ detection sites, each of which may be visited by any fish heading for spawning grounds upstream of site T_K , there are 2^{3K+1} possible detection histories. The likelihood is most easily expressed using summary statistics as in Models 0, 1, and 2. The necessary summary statistics (Table 3.19) are a_i , the number of fish detected at site i ; b_i , the number of fish detected at site i and detected later upstream; and g_i , the number of fish detected upstream of site i . The g_i statistics can be expressed in terms of the other statistics as follows:

$$\begin{aligned} g_R &= b_R; \\ g_{T_0} &= g_R + b_{T_0} - a_{T_0}; \\ g_{T_k} &= g_{D_{kT}} + b_{T_k} - a_{T_k} && \text{for } k = 1, \dots, K-1; \\ g_{D_{kB}} &= g_{T_{k-1}} + b_{D_{kB}} - a_{D_{kB}} && \text{for } k = 1, \dots, K; \\ g_{D_{kT}} &= g_{D_{kB}} + b_{D_{kT}} - a_{D_{kT}} && \text{for } k = 1, \dots, K. \end{aligned}$$

The difference between the summary statistics for Model 2 and those for Model 3a is that b_i may be non-zero for tributary sites in Model 3a. The subset of the statistics comprising the minimal sufficient statistic is given in Table 3.20. Either a_{T_K} or $b_{D_{KT}}$ must be included in the minimal sufficient statistic, but due to the relations $a_{T_K} = g_{D_{KT}}$ and $g_{D_{KT}} = g_{D_{KB}} + b_{D_{KT}} - a_{D_{KT}}$, it is not necessary to include both a_{T_K} and $b_{D_{KT}}$.

Table 3.19: Summary statistics for Model 3a, the Memory-Free Tributary model. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i , $i = R, T_0, D_{1B}, \dots, D_{KT}, T_K$;
b_R	Number of fish detected after the initial release;
b_i	Number of fish detected both at site i and later upstream, for $i = T_0, D_{1B}, \dots, D_{KB}, D_{KT}$;
g_i	Number of fish detected upstream from site i , $i = R, T_0, D_{1B}, \dots, D_{KT}$.

Table 3.20: Minimal sufficient statistics for Model 3a, the Memory-Free Tributary model. Either a_{T_K} or $b_{D_{KT}}$ is necessary, but not both. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i , $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$;
b_R	Number of fish detected after the initial release;
b_i	Number of fish detected at site i and later upstream, for $i = T_0, D_{1B}, \dots, D_{KT}$.

The likelihood for Model 3a can be expressed in terms of the summary statistics as follows:

$$\begin{aligned}
 L \propto & \chi_R^{N-b_R} \phi_{R,T_0}^{a_{T_0}} \phi_{R,D_{1B}}^{b_R-a_{T_0}} \\
 & \prod_{k=1}^K \left\{ \phi_{T_{k-1},D_{kB}}^{b_{T_{k-1}}} \phi_{D_{kB},D_{kT}}^{g_{D_{kB}}} \phi_{D_{kT},T_k}^{a_{T_k}} \phi_{D_{kT},D_{k+1,B}}^{g_{D_{kT}}-a_{T_k}} p_{D_{kB}}^{a_{D_{kB}}} q_{D_{kB}}^{g_{T_{k-1}}-a_{D_{kB}}} p_{D_{kT}}^{a_{D_{kT}}} \right. \\
 & \quad \left. \times q_{D_{kT}}^{g_{D_{kB}}-a_{D_{kT}}} \chi_{D_{kB}}^{a_{D_{kB}}-b_{D_{kB}}} \chi_{D_{kT}}^{a_{D_{kT}}-b_{D_{kT}}} \chi_{T_{k-1}}^{a_{T_{k-1}}-b_{T_{k-1}}} \right\}, \quad (3.26)
 \end{aligned}$$

where K is the number of dams and N is the size of the initial release. Equation (3.26) may be tailored to a particular data set by specifying K , removing any extraneous parameters, and renaming parameters according to observed detections, if necessary. This is done for the 1996 Chinook salmon data set in the next section.

The number of minimal sufficient statistics, $6K + 1$, is equal to the number of parameters for Model 3a. Equal numbers of minimal sufficient statistics and parameters implies that the maximum likelihood estimates of the parameters are the method of moment estimates using the minimal sufficient statistics. Formulas for the maximum likelihood estimators for Model 3a are given in Table 3.21.

Table 3.21: Maximum likelihood estimators (MLEs) of parameters for Model 3a, the Memory-Free Tributary model. The number of dams is K .

Parameter	MLE	Appropriate Sites
ϕ_{R,T_0}	a_{T_0}/N	
$\phi_{R,D_{1B}}$	$\frac{(b_R - a_{T_0})g_{D_{1B}}a_{D_{1B}}}{Ng_{T_0}b_{D_{1B}}}$	
$\phi_{D_{kB},D_{kT}}$	$\frac{b_{D_{kB}}a_{D_{kT}}g_{D_{kT}}}{a_{D_{kB}}g_{D_{kB}}b_{D_{kT}}}$	$k = 1, \dots, K$
$\phi_{D_{kT},D_{k+1,B}}$	$\frac{b_{D_{kT}}(g_{D_{kT}} - a_{T_k})a_{D_{k+1,B}}g_{D_{k+1,B}}}{a_{D_{kT}}g_{D_{kT}}g_{T_k}b_{D_{k+1,B}}}$	$k = 1, \dots, K - 1$
ϕ_{D_{kT},T_k}	$\frac{b_{D_{kT}}a_{T_k}}{a_{D_{kT}}g_{D_{kT}}}$	$k = 1, \dots, K$
$\phi_{T_k,D_{k+1,B}}$	$\frac{b_{T_k}a_{D_{k+1,B}}g_{D_{k+1,B}}}{a_{T_k}g_{T_k}b_{D_{k+1,B}}}$	$k = 0, \dots, K - 1$
p_i	b_i/g_i	$i = \text{any dam site}$

3.7.2.3 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival, is S_{sys} , defined as follows:

$$S_{sys} = \eta_R,$$

where

$$\begin{aligned}\eta_R &= (\phi_{R,T_0}\phi_{T_0,D_{1B}} + \phi_{R,D_{1B}})\phi_{D_{1B},D_{1T}}\eta_{D_{1T}}; \\ \eta_{D_{kT}} &= (\phi_{D_{kT},T_k}\phi_{T_k,D_{k+1,B}} + \phi_{D_{kT},D_{k+1,B}})\phi_{D_{k+1,B},D_{k+1,T}}\eta_{D_{k+1,T}}, \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}} &= 1.\end{aligned}\tag{3.27}$$

This gives

$$\begin{aligned}S_{sys} &= (\phi_{R,T_0}\phi_{T_0,D_{1B}} + \phi_{R,D_{1B}}) \\ &\times \prod_{k=1}^{K-1} \left\{ \phi_{D_{kB},D_{kT}}(\phi_{D_{kT},T_k}\phi_{T_k,D_{k+1,B}} + \phi_{D_{kT},D_{k+1,B}}) \right\} \phi_{D_{KB},D_{KT}}.\end{aligned}\tag{3.28}$$

The variance estimator of \hat{S}_{sys} is defined in Appendix B.

Model 3 allows for fish to return from tributaries to the mainstem of the river. The estimator of unaccountable loss must account for tributary return probabilities, because any fish that enters a tributary and then returns to the river with no further detections should be included in the unaccountable loss category, rather than the category of fish that permanently left the river at the tributary. It is not possible to separately estimate return to the river from the tributary and survival from the tributary to the next dam. However, under the assumption that once a fish has returned from a tributary to the river, survival from the tributary to the next dam is approximately 100%, the parameter $\phi_{T_k,D_{k+1,B}}$ is approximately the probability of returning to the river from tributary T_k , conditional on reaching that site. As with Model 2, if the assumption of 100% detection at the tributary antenna arrays is faulty, then the transitions $\phi_{D_{k+1,T},T_k}$ and $\phi_{D_{k+1,T},T_k}^T$ are negatively biased, and so μ_R is positively biased.

For Model 3a, the probability of unaccountable loss from the release point is μ_R , defined as follows:

$$\mu_R = 1 - \phi_{R,T_0}(1 - \mu_{T_0}) - \phi_{R,D_{1B}}\phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}),\tag{3.29}$$

where

$$\begin{aligned}
 1 - \mu_{T_k} &= 1 - \phi_{T_k, D_{k+1}, B} + \phi_{T_k, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}), & k = 0, \dots, K-1; \\
 1 - \mu_{D_{kT}} &= \phi_{D_{kT}, T_k} (1 - \mu_{T_k}) + \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}), & k = 1, \dots, K-1; \\
 1 - \mu_{D_{KT}} &= 1, & k = K.
 \end{aligned}$$

The variance estimator of $\hat{\mu}_R$ is defined in Appendix B.

3.7.2.4 1996 Chinook Data Set

The summary statistics for Model 3a observed in the 1996 Chinook salmon data set data are given in Table 3.19.

Table 3.22: Observed summary statistics for Model 3a (Memory-Free Tributary Model). The release size is N . Descriptions of summary statistics are listed in Table 3.19.

Statistic	Value	Statistic	Value
N	846	b_R	825
a_{T0}	11	b_{T0}	4
a_{D1B}	772	b_{D1B}	741
a_{D1T}	692	b_{D1T}	621
a_{T1}	294	b_{T1}	40
a_{D2B}	0	b_{D2B}	0
a_{D2T}	401	b_{D2T}	368
a_{T2}	75	b_{T2}	3
a_{D3B}	0	b_{D3B}	0
a_{D3T}	343	b_{D3T}	321
a_{T3}	45	b_{T3}	8
a_{D4B}	272	b_{D4B}	264
a_{D4T}	273	b_{D4T}	253
a_{T4}	150	b_{T4}	0
a_{D5B}	112	b_{D5B}	107
a_{D5T}	101	b_{D5T}	96
a_{T5}	42	b_{T5}	41
a_{D6B}	71	b_{D6B}	66
a_{D6T}	0	b_{D6T}	0
a_{T6}	0	b_{T6}	0

Table 3.22 continued

Statistic	Value	Statistic	Value
a_{D7B}	102	b_{D7B}	87
a_{D7T}	87	b_{D7T}	71
a_{T7}	73		

Table 3.22 shows that no fish were detected at sites D_{2B} , D_{3B} , D_{6T} , or T_6 . The transition parameters $\phi_{D_{1T}, D_{2B}}$, $\phi_{T_1, D_{2B}}$, $\phi_{D_{2B}, D_{2T}}$, $\phi_{D_{2T}, D_{3B}}$, $\phi_{T_2, D_{3B}}$, $\phi_{D_{3B}, D_{3T}}$, $\phi_{D_{6B}, D_{6T}}$, ϕ_{D_{6T}, T_6} , $\phi_{D_{6T}, D_{7B}}$, and $\phi_{T_6, D_{7B}}$ cannot be estimated; instead, the following combined parameters can be estimated:

$$\phi_{D_{1T}, D_{2T}} = \phi_{D_{1T}, D_{2B}} \phi_{D_{2B}, D_{2T}};$$

$$\phi_{T_1, D_{2T}} = \phi_{T_1, D_{2B}} \phi_{D_{2B}, D_{2T}};$$

$$\phi_{D_{2T}, D_{3T}} = \phi_{D_{2T}, D_{3B}} \phi_{D_{3B}, D_{3T}};$$

$$\phi_{T_2, D_{3T}} = \phi_{T_2, D_{3B}} \phi_{D_{3B}, D_{3T}};$$

$$\phi_{D_{6B}, D_{7B}} = \phi_{D_{6B}, D_{6T}} \phi_{D_{6T}, D_{7B}}.$$

Table 3.22 also shows no subsequent detections of fish detected at site T_4 , which includes all detections in the Columbia River upriver of McNary Dam, or in tributaries between McNary and Ice Harbor dams. It is necessary to fix $\phi_{T_4, D_{5B}}$ to 0, giving $\chi_{T_4} = 1$. The remaining transition parameters indicated in Table 3.18 are estimable with $K = 7$.

The likelihood for Model 3a, tailored to the 1996 data set, is:

$$\begin{aligned}
L \propto & \chi_R^{N-b_R} \phi_{R, T_0}^{a_{T_0}} \phi_{R, D_{1B}}^{b_R - a_{T_0}} \chi_{T_0}^{a_{T_0} - b_{T_0}} \phi_{T_0, D_{1B}}^{b_{T_0}} p_{D_{1B}}^{a_{D_{1B}}} q_{D_{1B}}^{g_{T_0} - a_{D_{1B}}} \chi_{D_{1B}}^{a_{D_{1B}} - b_{D_{1B}}} \phi_{D_{1B}, D_{1T}}^{g_{D_{1B}}} p_{D_{1T}}^{a_{D_{1T}}} \\
& \times q_{D_{1T}}^{g_{D_{1B}} - a_{D_{1T}}} \chi_{D_{1T}}^{a_{D_{1T}} - b_{D_{1T}}} \phi_{D_{1T}, T_1}^{a_{T_1}} \phi_{D_{1T}, D_{2T}}^{g_{D_{1T}} - a_{T_1}} \chi_{T_1}^{a_{T_1} - b_{T_1}} \phi_{T_1, D_{2T}}^{b_{T_1}} p_{D_{2T}}^{a_{D_{2T}}} q_{D_{2T}}^{g_{T_1} - a_{D_{2T}}} \chi_{D_{2T}}^{a_{D_{2T}} - b_{D_{2T}}} \\
& \times \phi_{D_{2T}, T_2}^{a_{T_2}} \phi_{D_{2T}, D_{3T}}^{g_{D_{2T}} - a_{T_2}} \chi_{T_2}^{a_{T_2} - b_{T_2}} \phi_{T_2, D_{3T}}^{b_{T_2}} p_{D_{3T}}^{a_{D_{3T}}} q_{D_{3T}}^{g_{T_2} - a_{D_{3T}}} \chi_{D_{3T}}^{a_{D_{3T}} - b_{D_{3T}}} \phi_{D_{3T}, T_3}^{a_{T_3}} \phi_{D_{3T}, D_{4B}}^{g_{D_{3T}} - a_{T_3}} \\
& \times \chi_{T_3}^{a_{T_3} - b_{T_3}} \phi_{T_3, D_{4B}}^{b_{T_3}} p_{D_{4B}}^{a_{D_{4B}}} q_{D_{4B}}^{g_{T_3} - a_{D_{4B}}} \chi_{D_{4B}}^{a_{D_{4B}} - b_{D_{4B}}} \phi_{D_{4B}, D_{4T}}^{g_{D_{4B}}} p_{D_{4T}}^{a_{D_{4T}}} q_{D_{4T}}^{g_{D_{4B}} - a_{D_{4T}}} \chi_{D_{4T}}^{a_{D_{4T}} - b_{D_{4T}}} \\
& \times \phi_{D_{4T}, T_4}^{a_{T_4}} \phi_{D_{4T}, D_{5B}}^{g_{D_{4T}} - a_{T_4}} p_{D_{5B}}^{a_{D_{5B}}} q_{D_{5B}}^{g_{T_4} - a_{D_{5B}}} \chi_{D_{5B}}^{a_{D_{5B}} - b_{D_{5B}}} \phi_{D_{5B}, D_{5T}}^{g_{D_{5B}}} p_{D_{5T}}^{a_{D_{5T}}} q_{D_{5T}}^{g_{D_{5B}} - a_{D_{5T}}} \chi_{D_{5T}}^{a_{D_{5T}} - b_{D_{5T}}}
\end{aligned}$$

$$\begin{aligned}
& \times \phi_{D_{5T}, T_5}^{a_{T_5}} \phi_{D_{5T}, D_{6B}}^{g_{D_{5T}} - a_{T_5}} \chi_{T_5}^{a_{T_5} - b_{T_5}} \phi_{T_5, D_{6B}}^{b_{T_5}} p_{D_{6B}}^{a_{D_{6B}}} q_{D_{6B}}^{g_{T_5} - a_{D_{6B}}} \chi_{D_{6B}}^{a_{D_{6B}} - b_{D_{6B}}} \phi_{D_{6B}, D_{7B}}^{g_{D_{6B}}} p_{D_{7B}}^{a_{D_{7B}}} \\
& \times q_{D_{7B}}^{g_{D_{6B}} - a_{D_{7B}}} \chi_{D_{7B}}^{a_{D_{7B}} - b_{D_{7B}}} \phi_{D_{7B}, D_{7T}}^{g_{D_{7B}}} p_{D_{7T}}^{a_{D_{7T}}} q_{D_{7T}}^{g_{D_{7B}} - a_{D_{7T}}} \chi_{D_{7T}}^{a_{D_{7T}} - b_{D_{7T}}} \phi_{D_{7T}, T_7}^{a_{T_7}}. \quad (3.30)
\end{aligned}$$

3.7.2.5 Results

Program USER¹³ was used to fit Model 3a to the data via maximum likelihood. Maximum likelihood estimates of the parameters from Model 3a are listed in Table 3.23. The log-likelihood was -3219.6910, with an AIC of 6507.382. The estimate of $\phi_{T_5, D_{6B}}$ is high ($\hat{\phi}_{T_5, D_{6B}} = 1.0020$, $\widehat{SE} = 0.0272$); this is reasonable, because the site T_5 is actually Charbonneau Park, a river-side park located on the Snake River just upriver of Ice Harbor Dam, rather than a real tributary. It makes sense that most or all fish detected at T_5 continued upriver.

The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.1057$ ($\widehat{SE} = 0.0106$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2803$ ($\widehat{SE} = 0.0156$). Both these estimates are higher for Model 3a than for Model 2. This is due to the non-terminal tributary detections used by Model 3a. More fish are perceived entering tributaries by Model 3a than by Model 2 (i.e., $\hat{\phi}_{D_{kT}, T_k}$ is higher for Model 3a than for Model 2), and these fish may return to the river to continue migrating in Model 3a (i.e., $\phi_{T_k, D_{k+1}, B} > 0$ for Model 3a). This means that while all fish entering a tributary in Model 2 are accounted for (i.e., $\mu_{T_k} = 0$ for Model 2), a proportion of fish entering tributaries in Model 3a are not accounted (i.e., $\mu_{T_k} > 0$ for Model 3a), resulting in a higher estimate of μ_R for Model 3a than for Model 2. The perceived system survival is higher for Model 3a than for Model 2 because although $\hat{\phi}_{D_{kT}, D_{k+1}, B}$ is smaller for Model 3a than for Model 2, the “reach survival” estimate for Model 3a ($\hat{\phi}_{D_{kT}, T_k} \hat{\phi}_{T_k, D_{k+1}, B} + \hat{\phi}_{D_{kT}, D_{k+1}, B}$) is often slightly larger than the comparable estimate for Model 2 ($\hat{\phi}_{D_{kT}, D_{k+1}, B}$). In general, the unaccountable loss and perceived system survival estimates from Model 3a should be more accurate than the estimates from Model 2. If there had been few non-terminal tributary detections in the Model 3a data, however, then the difference between Models 3a and 2 would be minimal.

¹³<http://www.cbr.washington.edu/paramEst/USER/>

Table 3.23: Maximum likelihood estimates of parameters from Model 3a, the Memory-Free Tributary model.

Category	Parameter	Estimate	S.E.
Transition	ϕ_{R,T_0}	0.0130	0.0039
	$\phi_{R,D_{1B}}$	0.9644	0.0066
	$\phi_{T_0,D_{1B}}$	0.3645	0.1453
	$\phi_{D_{1B},D_{1T}}$	0.9731	0.0075
	ϕ_{D_{1T},T_1}	0.3685	0.0172
	$\phi_{D_{1T},D_{2T}}$	0.5352	0.0181
	$\phi_{T_1,D_{2T}}$	0.1377	0.0202
	ϕ_{D_{2T},T_2}	0.1604	0.0170
	$\phi_{D_{2T},D_{3T}}$	0.7593	0.0203
	$\phi_{T_2,D_{3T}}$	0.0401	0.0227
	ϕ_{D_{3T},T_3}	0.1257	0.0175
	$\phi_{D_{3T},D_{4B}}$	0.8123	0.0209
	$\phi_{T_3,D_{4B}}$	0.1782	0.0571
	$\phi_{D_{4B},D_{4T}}$	0.9751	0.0104
	ϕ_{D_{4T},T_4}	0.5149	0.0294
	$\phi_{D_{4T},D_{5B}}$	0.4132	0.0290
	$\phi_{D_{5B},D_{5T}}$	0.9614	0.0199
	ϕ_{D_{5T},T_5}	0.3629	0.0448
	$\phi_{D_{5T},D_{6B}}$	0.6031	0.0478
	$\phi_{T_5,D_{6B}}$	1.0020	0.0272
	$\phi_{D_{6B},D_{7B}}$	0.9327	0.0306
	$\phi_{D_{7B},D_{7T}}$	0.8573	0.0354
	ϕ_{D_{7T},T_7}	0.8161	0.0415
Detection	$p_{D_{1B}}$	0.9416	0.0084
	$p_{D_{1T}}$	0.8673	0.0127
	$p_{D_{2T}}$	0.8578	0.0169
	$p_{D_{3T}}$	0.9582	0.0109
	$p_{D_{4B}}$	0.9103	0.0168
	$p_{D_{4T}}$	0.9370	0.0148
	$p_{D_{5B}}$	0.9304	0.0237
	$p_{D_{5T}}$	0.8727	0.0318
	$p_{D_{6B}}$	0.6346	0.0472
	$p_{D_{7B}}$	0.9775	0.0157
	$p_{D_{7T}}$	0.9726	0.0191

3.7.3 Model 3b: Memory Tributary Model

Model 3b allows entering and then exiting a tributary in a given reach to affect survival and tributary parameters in the following reach, i.e., there is a possible “memory effect” of tributary visits. Detection rates in tributaries are assumed to be 100%, as in Model 3a, and detection rates at dams are assumed to be unaffected by tributary behavior. The memory effects of tributary visits are assumed to last only through the following reach. For this purpose, define the reach immediately following tributary k (i.e., the tributary between dams k and $k + 1$) to extend from the base of dam $k + 1$ to the base of dam $k + 2$ for $k = 0, \dots, K - 2$, or from the base of dam K through tributary K for $k = K - 1$. The stretch of river between tributary k and the base of dam $k + 1$ is not included in the reach following T_k here because only individuals who visited tributary k are parameterized with the transition parameter between tributary k and dam $k + 1$ (i.e., $\phi_{T_k, D_{k+1, B}}$), so there is no need to adjust this parameter for these fish.

3.7.3.1 Notation

The transition parameters ϕ_{ij} for Model 3b are the same as those for Model 3a for individuals who did not enter the tributary in the reach immediately preceding site i . An alternative transition parameter, ϕ_{ij}^T , is defined for individuals who entered and then exited (i.e., “visited” or “dipped-in”) the tributary in the reach immediately preceding site i :

$$\phi_{ij}^T = Pr[\text{Survive and move from site } i \text{ to site } j \mid \text{Entered and exited tributary} \quad (3.31) \\ \text{in the reach immediately preceding site } i],$$

where $i = D_{1B}, D_{1T}, T_1, \dots, D_{KB}, D_{KT}$, and where

$$j = \begin{cases} D_{kT} & \text{for } i = D_{kB}, k = 1, \dots, K; \\ D_{k+1,B} \text{ or } T_k & \text{for } i = D_{kT}, k = 1, \dots, K-1; \\ T_k & \text{for } i = D_{KT}; \\ D_{k+1,B} & \text{for } i = T_k, k = 1, \dots, K-1. \end{cases} \quad (3.32)$$

The possible tag fates are the same here as for Model 3a, but here fish who entered a tributary in the preceding reach must be distinguished from those who did not. Define χ_i to be the probability of not being detected after site i , having reached site i . The parameter χ_i^T is the analogous probability for fish that entered the tributary in the reach directly below site i . If the fish entered the tributary in reach $k-1$, then either $\chi_{D_{kB}}^T$, $\chi_{D_{kT}}^T$, or $\chi_{T_k}^T$ is used, as appropriate.

$$\begin{aligned} \chi_R &= 1 - \phi_{R,T_0} - \phi_{R,D_{1B}}(1 - q_{D_{1B}}\chi_{D_{1B}}); \\ \chi_{D_{kB}} &= 1 - \phi_{D_{kB},D_{kT}}(1 - q_{D_{kT}}\chi_{D_{kT}}), & k = 1, \dots, K; \\ \chi_{D_{kT}} &= 1 - \phi_{D_{kT},T_k} - \phi_{D_{kT},D_{k+1,B}}(1 - q_{D_{k+1,B}}\chi_{D_{k+1,B}}), & k = 1, \dots, K-1; \\ \chi_{D_{KT}} &= 1 - \phi_{D_{KT},T_K}; \\ \chi_{T_k} &= 1 - \phi_{T_k,D_{k+1,B}}(1 - q_{D_{k+1,B}}\chi_{D_{k+1,B}}^T), & k = 0, \dots, K-1; \\ \chi_{D_{kB}}^T &= 1 - \phi_{D_{kB},D_{kT}}^T(1 - q_{D_{kT}}\chi_{D_{kT}}^T), & k = 1, \dots, K; \\ \chi_{D_{kT}}^T &= 1 - \phi_{D_{kT},T_k}^T - \phi_{D_{kT},D_{k+1,B}}^T(1 - q_{D_{k+1,B}}\chi_{D_{k+1,B}}), & k = 1, \dots, K-1; \\ \chi_{D_{KT}}^T &= 1 - \phi_{D_{KT},T_K}^T; \\ \chi_{T_k}^T &= 1 - \phi_{T_k,D_{k+1,B}}^T(1 - q_{D_{k+1,B}}\chi_{D_{k+1,B}}^T), & k = 1, \dots, K-1. \end{aligned} \quad (3.33)$$

The parameters used in Model 3b are given in Table 3.24.

Table 3.24: Parameters used in Model 3b, the Memory Tributary model. The number of dams is K .

Parameter	Definition
ϕ_{ij}	Probability of surviving and moving from site i to site j , given having reached site i without entering the tributary in the reach immediately preceding site i (if any), for $i = R, T_0, D_{1B}, \dots, D_{KT}$ and j defined as in Equation (3.32);
ϕ_{ij}^T	Probability of surviving and moving from site i to site j , given having reached site i and having entered the tributary in the reach immediately preceding site i , for $i = D_{1B}, \dots, D_{KT}$ and j defined as in Equation (3.32);
p_i	Probability of being detected at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$;
q_i	Probability of avoiding detection at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$; $= 1 - p_i$;
χ_i	Probability of not being detected after site i , given having reached site i without entering the tributary in the reach immediately preceding site i (if any), for $i = R, T_0, D_{1B}, \dots, D_{KT}$;
χ_i^T	Probability of not being detected after site i , given having reached site i and having entered the tributary in the reach immediately preceding site i , for $i = D_{1B}, \dots, D_{KT}$.

The parameters in Table 3.24 can be used to express the probabilities of the detection histories. For example, the detection history $R T_0 D_{1B} D_{1T} T_2 D_{3T} D_{4B}$ has probability

$$\begin{aligned}
 &Pr[R T_0 D_{1B} D_{1T} T_2 D_{3T} D_{4B}] \\
 &= \phi_{R,T_0} \phi_{T_0,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}}^T p_{D_{1T}} \phi_{D_{1T},D_{2B}}^T q_{D_{2B}} \phi_{D_{2B},D_{2T}} q_{D_{2T}} \phi_{D_{2T},T_2} \phi_{T_2,D_{3B}} q_{D_{3B}} \\
 &\times \phi_{D_{3B},D_{3T}}^T p_{D_{3T}} \phi_{D_{3T},D_{4B}}^T p_{D_{4B}} \chi_{D_{4B}}.
 \end{aligned} \tag{3.34}$$

As a comparison, the probability of the detection history $R D_{1B} D_{1T} T_2 D_{3T} D_{4B}$ is

$$\begin{aligned}
 &Pr[R D_{1B} D_{1T} T_2 D_{3T} D_{4B}] \\
 &= \phi_{R,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}} p_{D_{1T}} \phi_{D_{1T},D_{2B}} q_{D_{2B}} \phi_{D_{2B},D_{2T}} q_{D_{2T}} \phi_{D_{2T},T_2} \phi_{T_2,D_{3B}} q_{D_{3B}} \\
 &\times \phi_{D_{3B},D_{3T}}^T p_{D_{3T}} \phi_{D_{3T},D_{4B}}^T p_{D_{4B}} \chi_{D_{4B}}.
 \end{aligned} \tag{3.35}$$

The only difference between these two detection histories is that the first detection history includes site T_0 , and the second detection history does not. Thus, the probability in Equation (3.34) uses the transition parameters $\phi_{D_{1B}, D_{1T}}^T$ and $\phi_{D_{1T}, D_{2B}}^T$, whereas the probability in Equation (3.35) uses transition parameters $\phi_{D_{1B}, D_{1T}}$ and $\phi_{D_{1T}, D_{2B}}$. Both Equation (3.34) and Equation (3.35) use the final detection parameter $\chi_{D_{4B}}$ instead of $\chi_{D_{4B}}^T$, because the tributary site T_3 is not included in the detection history.

3.7.3.2 Likelihood

The likelihood for Model 3b is most usefully expressed in terms of summary statistics similar to those used in Model 3a. Like Model 3a, necessary summary statistics are the number detected at a given site (i.e., a_i), the number detected at a site and later at an upstream site (i.e., b_i), and the number detected upstream of a given site (i.e., g_i). For Model 3b, these statistics must be characterized by whether or not the fish was detected at the preceding tributary. The g_i and g_i^T statistics can be expressed in terms of the other statistics as follows:

$$\begin{aligned}
 g_R &= b_R; \\
 g_{T_0} &= g_R + b_{T_0} - a_{T_0}; \\
 g_{D_{1B}} &= g_{T_0} - b_{T_0} + b_{D_{1B}} - a_{D_{1B}}; \\
 g_{T_k} &= g_{D_{kT}} + b_{T_k} - a_{T_k} && \text{for } k = 1, \dots, K-1; \\
 g_{T_k}^T &= g_{D_{kT}}^T + b_{T_k}^T - a_{T_k}^T && \text{for } k = 1, \dots, K-1; \\
 g_{D_{kB}} &= g_{T_{k-1}} + g_{T_{k-1}}^T - b_{T_{k-1}} - b_{T_{k-1}}^T + b_{D_{kB}} - a_{D_{kB}} && \text{for } k = 2, \dots, K; \\
 g_{D_{kB}}^T &= b_{T_{k-1}} + b_{T_{k-1}}^T + b_{D_{kB}}^T - a_{D_{kB}}^T && \text{for } k = 1, \dots, K; \\
 g_{D_{kT}} &= g_{D_{kB}} + b_{D_{kT}} - a_{D_{kT}} && \text{for } k = 1, \dots, K; \\
 g_{D_{kT}}^T &= g_{D_{kB}}^T + b_{D_{kT}}^T - a_{D_{kT}}^T && \text{for } k = 1, \dots, K.
 \end{aligned}$$

The summary statistics for Model 3b are listed in Table 3.25, and the minimal sufficient statistics are listed in Table 3.26. There are $10K - 1$ minimal sufficient statistics, and an equal number of parameters. The formulas in Table 3.21 can be used to find initial values

for a numerical routine to maximize the likelihood, with the same initial value used for both ϕ_{ij} and ϕ_{ij}^T .

Table 3.25: Summary statistics for Model 3b, the Memory Tributary model. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i that were not detected at the tributary preceding site i (if any), $i = T_0, D_{1B}, \dots, D_{KT}, T_K$;
a_i^T	Number of fish detected at both site i and the tributary preceding site i , $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}, T_K$;
b_R	Number of fish detected after the initial release;
b_i	Number of fish detected at both site i and later upstream, but not at the tributary preceding site i (if any), $i = T_0, D_{1B}, \dots, D_{KT}$;
b_i^T	Number of fish detected at the tributary preceding site i , at site i , and later upstream, $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$;
g_i	Number of fish detected upstream of site i but not at the tributary preceding site i (if any), $i = R, T_0, D_{1B}, \dots, D_{KT}$;
g_i^T	Number of fish detected upstream of site i and at the tributary preceding site i , $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$.

Table 3.26: Minimal sufficient statistics for Model 3b, the Memory Tributary model. The number of dams is K .

Statistic	Definition
a_{T_0}	Number of fish detected at site T_0 ;
a_{T_k}	Number of fish detected at site T_k that were not detected at the preceding tributary, $k = 1, \dots, K - 1$;
$a_{T_k}^T$	Number of fish detected at site T_k that were also detected at the preceding tributary, $k = 1, \dots, K - 1$;
b_R	Number of fish detected after the initial release;
b_{T_0}	Number of fish detected at site T_0 and later upstream;
b_{T_k}	Number of fish detected at site T_k and later upstream, but not at the tributary preceding site T_k , $k = 1, \dots, K - 1$;
$b_{T_k}^T$	Number of fish detected at the tributary preceding site T_k , at site T_k , and later upstream of T_k , $k = 1, \dots, K - 1$;
$a_{D_{kB}} - b_{D_{kB}}$	Number of fish detected at site D_{kB} that were detected neither at the tributary preceding site D_{kB} nor at any site upstream of D_{kB} , $k = 1, \dots, K$;

3.7.3.3 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival, is S_{sys} , defined as follows:

$$S_{sys} = \eta_R,$$

where

$$\begin{aligned} \eta_R &= \phi_{R,T_0} \phi_{T_0,D_{1B}} \phi_{D_{1B},D_{1T}}^T \eta_{D_{1T}}^T + \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \eta_{D_{1T}}; \\ \eta_{D_{kT}} &= \phi_{D_{kT},T_k} \phi_{T_k,D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}}^T \eta_{D_{k+1,T}}^T \\ &\quad + \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}}, \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}} &= 1; \\ \eta_{D_{kT}}^T &= \phi_{D_{kT},T_k}^T \phi_{T_k,D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}}^T \eta_{D_{k+1,T}}^T \\ &\quad + \phi_{D_{kT},D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}}, \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}}^T &= 1. \end{aligned} \tag{3.37}$$

The variance estimator of \hat{S}_{sys} is defined in Appendix B.

As in Model 3a, unaccountable loss in Model 3b must account for tributary return probabilities and use the assumption that once a fish has returned from a tributary to the river, survival from the tributary to the next dam is approximately 100%. For Model 3b, the probability of unaccountable loss from the release point is μ_R , defined as follows:

$$\mu_R = 1 - \phi_{R,T_0}(1 - \mu_{T_0}) - \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}), \tag{3.38}$$

where

$$\begin{aligned} 1 - \mu_{T_k} &= 1 - \phi_{T_k,D_{k+1,B}} + \phi_{T_k,D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}}^T (1 - \mu_{D_{k+1,T}}^T), \quad k = 0, \dots, K-1; \\ 1 - \mu_{T_k}^T &= 1 - \phi_{T_k,D_{k+1,B}}^T + \phi_{T_k,D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}}^T (1 - \mu_{D_{k+1,T}}^T), \quad k = 1, \dots, K-1; \\ 1 - \mu_{D_{kT}} &= \phi_{D_{kT},T_k}(1 - \mu_{T_k}) + \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}}(1 - \mu_{D_{k+1,T}}), \quad k = 1, \dots, K-1; \end{aligned}$$

$$\begin{aligned}
1 - \mu_{D_{kT}} &= 1, & k &= K; \\
1 - \mu_{D_{kT}}^T &= \phi_{D_{kT}, T_k}^T (1 - \mu_{T_k}^T) + \phi_{D_{kT}, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}), & k &= 1, \dots, K-1; \\
1 - \mu_{D_{kT}}^T &= 1, & k &= K.
\end{aligned}$$

The variance estimator of $\hat{\mu}_R$ is defined in Appendix B.

3.7.3.4 1996 Chinook Data Set

The summary statistics for Model 3b, observed from the 1996 Chinook salmon data set, are presented in Table 3.27.

Table 3.27: Observed summary statistics for Model 3b (Memory Tributary Model). The release size is N . Descriptions of summary statistics are listed in Table 3.25

Statistic	Value	Statistic	Value	Statistic	Value	Statistic	Value
N	846			b_R	825		
a_{T0}	11			b_{T0}	4		
a_{D1B}	768	a_{D1B}^T	4	b_{D1B}	737	b_{D1B}^T	4
a_{D1T}	688	a_{D1T}^T	4	b_{D1T}	618	b_{D1T}^T	3
a_{T1}	292	a_{T1}^T	2	b_{T1}	40	b_{T1}^T	0
a_{D2T}	370	a_{D2T}^T	31	b_{D2T}	338	b_{D2T}^T	30
a_{T2}	66	a_{T2}^T	9	b_{T2}	1	b_{T2}^T	2
a_{D3T}	340	a_{D3T}^T	3	b_{D3T}	318	b_{D3T}^T	3
a_{T3}	44	a_{T3}^T	1	b_{T3}	7	b_{T3}^T	1
a_{D4B}	266	a_{D4B}^T	6	b_{D4B}	258	b_{D4B}^T	6
a_{D4T}	267	a_{D4T}^T	6	b_{D4T}	248	b_{D4T}^T	5
a_{T4}	149	a_{T4}^T	1	b_{T4}	0	b_{T4}^T	0
a_{D5B}	112	a_{D5B}^T	0	b_{D5B}	107	b_{D5B}^T	0
a_{D5T}	101	a_{D5T}^T	0	b_{D5T}	96	b_{D5T}^T	0
a_{T5}	42	a_{T5}^T	0	b_{T5}	41	b_{T5}^T	0
a_{D6B}	40	a_{D6B}^T	31	b_{D6B}	37	b_{D6B}^T	29
a_{D7B}	102	a_{D7B}^T	0	b_{D7B}	87	b_{D7B}^T	0
a_{D7T}	87	a_{D7T}^T	0	b_{D7T}	71	b_{D7T}^T	0
a_{T7}	73	a_{T7}^T	0				

There were no detections at sites D_{2B} , D_{3B} , D_{6T} , or T_6 (Table 3.27). Transition parameters involving these sites cannot be separately estimated, and detection rates at these sites are not meaningful. Instead, it is possible to estimate certain products of the transition

parameters involving these sites, as done in Model 3a. As in Model 3a, the parameters $\phi_{D_{1T}, D_{2T}} \equiv \phi_{D_{1T}, D_{2B}} \phi_{D_{2B}, D_{2T}}$, $\phi_{T_1, D_{2T}}$, $\phi_{D_{2T}, D_{3T}}$, $\phi_{T_2, D_{3T}}$, and $\phi_{D_{6B}, D_{7B}}$ are used in the likelihood. Unlike Model 3a, Model 3b requires the following parameters for transitions following detections at tributaries:

$$\begin{aligned}\phi_{D_{1T}, D_{2T}}^T &= \phi_{D_{1T}, D_{2B}}^T \phi_{D_{2B}, D_{2T}}^T; \\ \phi_{D_{2T}, D_{3T}}^T &= \phi_{D_{2T}, D_{3B}}^T \phi_{D_{3B}, D_{3T}}^T; \\ \phi_{T_2, D_{3T}}^T &= \phi_{T_2, D_{3B}}^T \phi_{D_{3B}, D_{3T}}^T; \\ \phi_{D_{6B}, D_{7B}}^T &= \phi_{D_{6B}, D_{6T}}^T \phi_{D_{6T}, D_{7B}}^T.\end{aligned}$$

The parameter $\phi_{T_1, D_{2T}}^T = \phi_{T_1, D_{2B}}^T \phi_{D_{2B}, D_{2T}}^T$ is not needed for this data set (Table 3.27).

Certain other parameters from the general model are not needed for the 1996 data set due to the observed summary statistics (Table 3.27). With no detections at site T_6 , the parameters $\phi_{D_{7B}, D_{7T}}^T$ and ϕ_{D_{7T}, T_7}^T are neither used in the model nor estimable. Also, because there are no subsequent detections of fish detected at site T_4 , the parameters $\phi_{D_{5B}, D_{5T}}^T$, ϕ_{D_{5T}, T_5}^T , $\phi_{D_{5T}, D_{6B}}^T$, and $\phi_{T_5, D_{6B}}^T$ must be removed. Additionally, it is necessary to fix both $\phi_{T_4, D_{5B}}^T$ and $\phi_{T_4, D_{5B}}^T$ to 0, which also fixes χ_{T_4} and $\chi_{T_4}^T$ to 1. The summary statistic $a_{T_1}^T > 0$ but $b_{T_1}^T = 0$ (Table 3.27), meaning that parameter $\phi_{T_1, D_{2T}}^T$ must be fixed to 0 and removed from the likelihood. Table 3.27 also shows that $a_{D_{1B}}^T - b_{D_{1B}}^T$, $a_{T_3}^T - b_{T_3}^T$, and $a_{D_{4B}}^T - b_{D_{4B}}^T$ are all 0, meaning that the parameters $\phi_{D_{1B}, D_{1T}}^T$, $\phi_{T_3, D_{4B}}^T$, and $\phi_{D_{4B}, D_{4T}}^T$ must all be fixed to 1, giving $\chi_{D_{1B}}^T = q_{D_{1T}} \chi_{D_{1T}}^T$, $\chi_{T_3}^T = q_{D_{4B}} \chi_{D_{4B}}^T$, and $\chi_{D_{4B}}^T = q_{D_{4T}} \chi_{D_{4T}}^T$. Also, $a_{D_{3T}}^T - b_{D_{3T}}^T$ is 0. Because every fish detected at site D_{3T} (who had previously entered tributary T_2) was also detected upstream of site D_{3T} , it makes sense to fix to 1 the sum of the transition probabilities from D_{3T} : $\phi_{D_{3T}, T_3}^T + \phi_{D_{3T}, D_{4B}}^T = 1$, yielding $\phi_{D_{3T}, T_3}^T = 1 - \phi_{D_{3T}, D_{4B}}^T$ and $\chi_{D_{3T}}^T = \phi_{D_{3T}, D_{4B}}^T q_{D_{4B}} \chi_{D_{4B}}^T$. Thus, it is not necessary to include both $\phi_{D_{3T}, D_{4B}}^T$ and ϕ_{D_{3T}, T_3}^T in the likelihood. The parameters $\chi_{D_{1B}}^T$, $\chi_{D_{3T}}^T$, and $\chi_{D_{4B}}^T$ may all be expressed as products of other parameters, and have zero exponents, so they may be removed from the likelihood for Model 3b when fitting it to the 1996 Chinook data set.

The Model 3b likelihood tailored to the 1996 Chinook salmon data is as follows:

$$\begin{aligned}
L \propto & \chi_{R,T_0}^{N-b_R} \phi_{R,T_0}^{a_{T_0}} \phi_{R,D_{1B}}^{b_R-a_{T_0}} \chi_{T_0}^{a_{T_0}-b_{T_0}} \phi_{T_0,D_{1B}}^{b_{T_0}} p_{D_{1B}}^{a_{D_{1B}}+a_{D_{1B}}^T} q_{D_{1B}}^{g_{T_0}-a_{D_{1B}}-a_{D_{1B}}^T} \chi_{D_{1B}}^{a_{D_{1B}}-b_{D_{1B}}} \phi_{D_{1B},D_{1T}}^{g_{D_{1B}}} \\
& \times p_{D_{1T}}^{a_{D_{1T}}+a_{D_{1T}}^T} q_{D_{1T}}^{g_{D_{1B}}+g_{D_{1B}}^T-a_{D_{1T}}-a_{D_{1T}}^T} \chi_{D_{1T}}^{a_{D_{1T}}-b_{D_{1T}}} (\chi_{D_{1T}}^T)^{a_{D_{1T}}^T-b_{D_{1T}}^T} \phi_{D_{1T},T_1}^{a_{T_1}} (\phi_{D_{1T},T_1}^T)^{a_{T_1}^T} \\
& \times \phi_{D_{1T},D_{2T}}^{g_{D_{1T}}-a_{T_1}} (\phi_{D_{1T},D_{2T}}^T)^{g_{D_{1T}}^T-a_{T_1}^T} \chi_{T_1}^{a_{T_1}-b_{T_1}} \phi_{T_1,D_{2T}}^{b_{T_1}} p_{D_{2T}}^{a_{D_{2T}}+a_{D_{2T}}^T} q_{D_{2T}}^{g_{T_1}+g_{T_1}^T-a_{D_{2T}}-a_{D_{2T}}^T} \\
& \times \chi_{D_{2T}}^{a_{D_{2T}}-b_{D_{2T}}} (\chi_{D_{2T}}^T)^{a_{D_{2T}}^T-b_{D_{2T}}^T} \phi_{D_{2T},T_2}^{a_{T_2}} (\phi_{D_{2T},T_2}^T)^{a_{T_2}^T} \phi_{D_{2T},D_{3T}}^{g_{D_{2T}}-a_{T_2}} (\phi_{D_{2T},D_{3T}}^T)^{g_{D_{2T}}^T-a_{T_2}^T} \\
& \times \chi_{T_2}^{a_{T_2}-b_{T_2}} (\chi_{T_2}^T)^{a_{T_2}^T-b_{T_2}^T} \phi_{T_2,D_{3T}}^{b_{T_2}} (\phi_{T_2,D_{3T}}^T)^{b_{T_2}^T} p_{D_{3T}}^{a_{D_{3T}}+a_{D_{3T}}^T} q_{D_{3T}}^{g_{T_2}+g_{T_2}^T-a_{D_{3T}}-a_{D_{3T}}^T} \chi_{D_{3T}}^{a_{D_{3T}}-b_{D_{3T}}} \\
& \times \phi_{D_{3T},T_3}^{a_{T_3}} \phi_{D_{3T},D_{4B}}^{g_{D_{3T}}-a_{T_3}} (\phi_{D_{3T},D_{4B}}^T)^{g_{D_{3T}}^T-a_{T_3}^T} \chi_{T_3}^{a_{T_3}-b_{T_3}} (\chi_{T_3}^T)^{a_{T_3}^T-b_{T_3}^T} \phi_{T_3,D_{4B}}^{b_{T_3}} (1 - \phi_{D_{3T},D_{4B}}^T)^{a_{T_3}^T} \\
& \times p_{D_{4B}}^{a_{D_{4B}}+a_{D_{4B}}^T} q_{D_{4B}}^{g_{T_3}+g_{T_3}^T-a_{D_{4B}}-a_{D_{4B}}^T} \chi_{D_{4B}}^{a_{D_{4B}}-b_{D_{4B}}} \phi_{D_{4B},D_{4T}}^{g_{D_{4B}}} p_{D_{4T}}^{a_{D_{4T}}+a_{D_{4T}}^T} \\
& \times q_{D_{4T}}^{g_{D_{4B}}+g_{D_{4B}}^T-a_{D_{4T}}-a_{D_{4T}}^T} \chi_{D_{4T}}^{a_{D_{4T}}-b_{D_{4T}}} (\chi_{D_{4T}}^T)^{a_{D_{4T}}^T-b_{D_{4T}}^T} \phi_{D_{4T},T_4}^{a_{T_4}} (\phi_{D_{4T},T_4}^T)^{a_{T_4}^T} \phi_{D_{4T},D_{5B}}^{g_{D_{4T}}-a_{T_4}} \\
& \times (\phi_{D_{4T},D_{5B}}^T)^{g_{D_{4T}}^T-a_{T_4}^T} p_{D_{5B}}^{a_{D_{5B}}+a_{D_{5B}}^T} q_{D_{5B}}^{g_{T_4}+g_{T_4}^T-a_{D_{5B}}-a_{D_{5B}}^T} \chi_{D_{5B}}^{a_{D_{5B}}-b_{D_{5B}}} \phi_{D_{5B},D_{5T}}^{g_{D_{5B}}} p_{D_{5T}}^{a_{D_{5T}}+a_{D_{5T}}^T} q_{D_{5T}}^{g_{D_{5B}}-a_{D_{5T}}} \\
& \times \chi_{D_{5T}}^{a_{D_{5T}}-b_{D_{5T}}} \phi_{D_{5T},T_5}^{a_{T_5}} \phi_{D_{5T},D_{6B}}^{g_{D_{5T}}-a_{T_5}} \chi_{T_5}^{a_{T_5}-b_{T_5}} \phi_{T_5,D_{6B}}^{b_{T_5}} p_{D_{6B}}^{a_{D_{6B}}+a_{D_{6B}}^T} q_{D_{6B}}^{g_{T_5}-a_{D_{6B}}-a_{D_{6B}}^T} \chi_{D_{6B}}^{a_{D_{6B}}-b_{D_{6B}}} \\
& \times (\chi_{D_{6B}}^T)^{a_{D_{6B}}^T-b_{D_{6B}}^T} \phi_{D_{6B},D_{7B}}^{g_{D_{6B}}} (\phi_{D_{6B},D_{7B}}^T)^{g_{D_{6B}}^T} p_{D_{7B}}^{a_{D_{7B}}+a_{D_{7B}}^T} q_{D_{7B}}^{g_{D_{6B}}+g_{D_{6B}}^T-a_{D_{7B}}-a_{D_{7B}}^T} \chi_{D_{7B}}^{a_{D_{7B}}-b_{D_{7B}}} \\
& \times \phi_{D_{7B},D_{7T}}^{g_{D_{7B}}} p_{D_{7T}}^{a_{D_{7T}}+a_{D_{7T}}^T} q_{D_{7T}}^{g_{D_{7B}}-a_{D_{7T}}-a_{D_{7T}}^T} \chi_{D_{7T}}^{a_{D_{7T}}-b_{D_{7T}}} \phi_{D_{7T},T_7}^{a_{T_7}} \quad (3.39)
\end{aligned}$$

3.7.3.5 Results

Program USER¹⁴ was used to find fit Model 3b to the data via maximum likelihood. Maximum likelihood estimates of the parameters from Model 3b are listed in Table 3.28. The log-likelihood was -3209.1992, with an AIC of 6504.398. As with Model 3a, the estimate of $\phi_{T_5,D_{6B}}$ is high ($\hat{\phi}_{T_5,D_{6B}} = 1.0036$, $\widehat{SE} = 0.0312$).

The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.1057$ ($\widehat{SE} = 0.0106$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2800$ ($\widehat{SE} = 0.0156$). These are the same values seen from Model 3a. The only difference between Models 3a and 3b is

¹⁴<http://www.cbr.washington.edu/paramEst/USER/>

that Model 3b allows for a temporary memory effects of tributary visits, while Model 3a does not. Examination of Table 3.28 shows that although $\hat{\phi}_{ij}$ and $\hat{\phi}_{ij}^T$ may be considerably different for individual detection sites i and j (i.e.g, $\hat{\phi}_{D_{1T}, D_{2T}} = 0.5371$, $\widehat{SE} = 0.0182$ versus $\hat{\phi}_{D_{1T}, D_{2T}}^T = 0.2527$, $\widehat{SE} = 0.2190$), the standard errors on the $\hat{\phi}_{ij}^T$ estimates are large, and there is no consistent pattern in which of $\hat{\phi}_{ij}$ and $\hat{\phi}_{ij}^T$ is larger. A likelihood ratio test comparing Models 3a and 3b indicates no significant overall memory effect of tributary visits ($\chi_9^2 = 20.9836$, $P = 0.0127$), so it is reasonable that \hat{S}_{sys} and $\hat{\mu}_R$ are the same for Models 3a and 3b. It is conceivable that with a known-source or single-source release group, or in a different study year, tributary visits may have a more significant effect than detected here. For this data set, however, the extra structure in Model 3b is unnecessary, and Model 3a should be preferred.

Table 3.28: Maximum likelihood estimates of parameters from Model 3b, the Memory Tributary model. The estimate of ϕ_{D_{3T}, T_3}^T comes from $\hat{\phi}_{D_{3T}, T_3}^T = 1 - \hat{\phi}_{D_{3T}, D_{4B}}^T$.

Category	Parameter	Estimate	S.E.
Transition	ϕ_{R, T_0}	0.0130	0.0039
	$\phi_{R, D_{1B}}$	0.9645	0.0066
	$\phi_{T_0, D_{1B}}$	0.3643	0.1452
	$\phi_{D_{1B}, D_{1T}}$	0.9728	0.0075
	ϕ_{D_{1T}, T_1}	0.3679	0.0172
	ϕ_{D_{1T}, T_1}^T	0.4990	0.2498
	$\phi_{D_{1T}, D_{2T}}$	0.5371	0.0182
	$\phi_{D_{1T}, D_{2T}}^T$	0.2527	0.2190
	$\phi_{T_1, D_{2T}}$	0.1376	0.0202
	ϕ_{D_{2T}, T_2}	0.1545	0.0175
	ϕ_{D_{2T}, T_2}^T	0.2241	0.0658
	$\phi_{D_{2T}, D_{3T}}$	0.7603	0.0213
	$\phi_{D_{2T}, D_{3T}}^T$	0.7489	0.0693
	$\phi_{T_2, D_{3T}}$	0.0152	0.0150
	$\phi_{T_2, D_{3T}}^T$	0.2222	0.1385
	ϕ_{D_{3T}, T_3}	0.1240	0.0175
	ϕ_{D_{3T}, T_3}^T	0.3333	0.2721
	$\phi_{D_{3T}, D_{4B}}$	0.8136	0.0210
	$\phi_{D_{3T}, D_{4B}}^T$	0.6667	0.2721
	$\phi_{T_3, D_{4B}}$	0.1592	0.0552
	$\phi_{D_{4B}, D_{4T}}$	0.9742	0.0107
	ϕ_{D_{4T}, T_4}	0.5260	0.0298

Table 3.28 continued

Category	Parameter	Estimate	S.E.
Transition	ϕ_{D_{4T}, T_4}^T	0.1249	0.1165
	$\phi_{D_{4T}, D_{5B}}$	0.4037	0.0293
	$\phi_{D_{4T}, D_{5B}}^T$	0.7519	0.1536
	$\phi_{D_{5B}, D_{5T}}$	0.9614	0.0199
	ϕ_{D_{5T}, T_5}	0.3629	0.0448
	$\phi_{D_{5T}, D_{6B}}$	0.6025	0.0480
	$\phi_{T_5, D_{6B}}$	1.0036	0.0312
	$\phi_{D_{6B}, D_{7B}}$	0.9353	0.0378
	$\phi_{D_{6B}, D_{7B}}^T$	0.9283	0.0506
	$\phi_{D_{7B}, D_{7T}}$	0.8573	0.0354
	ϕ_{D_{7T}, T_7}	0.8161	0.0415
Detection	$p_{D_{1B}}$	0.9415	0.0084
	$p_{D_{1T}}$	0.8675	0.0127
	$p_{D_{2T}}$	0.8578	0.0169
	$p_{D_{3T}}$	0.9582	0.0109
	$p_{D_{4B}}$	0.9103	0.0168
	$p_{D_{4T}}$	0.9373	0.0147
	$p_{D_{5B}}$	0.9304	0.0237
	$p_{D_{5T}}$	0.8727	0.0318
	$p_{D_{6B}}$	0.6346	0.0472
	$p_{D_{7B}}$	0.9775	0.0157
	$p_{D_{7T}}$	0.9726	0.0191

3.8 Model 4: Fallback Model with Terminal Tributary Detections

This model and Models 5a, 5b, 5c, and 6 attempt to account for the effects of fallback on perceived survival. For the purposes of these models, “fallback” includes any travel directed downriver between two detection sites, as well as actual falling back over dams. Fish are classified as either fallback (equivalently, post-fallback) or non-fallback (equivalently, pre-fallback) fish. Once a fish has fallen back over a dam or otherwise swum downstream and has been detected again after the fallback, it is classified as a fallback (post-fallback) fish. Before the fallback occurs, the fish is a non-fallback (pre-fallback) fish, as are fish with no detected fallback. No attempt is made to model survival and movement during fallback; only pre-fallback and post-fallback transitions are modeled. Model 4 incorporates fallback into the terminal-tributary model (Model 2), while Models 5a, 5b, 5c, and 6 incorporate

fallback into the tributary models (Models 3a and 3b).

3.8.1 Data Description

The steps to simplify the data for Model 4 are those used for Model 2 (Terminal Tributary Model), but with an added fallback code, *FB*, placed between the last pre-fallback detection and the first post-fallback detection. The *FB* code represents not only the actual fallback and associated downriver travel, but also the upriver travel that was retraced during the fallback and that is removed from the detection history in the basic data simplification process described in Section 3.2; see Figures 3.3, 3.4, 3.5, 3.7, and 3.8 for examples of paths with fallback events removed. Thus, an *FB* code immediately preceding a detection at site i implies that the fish ended its (first) fallback at site i . This means that it must be obvious from the non-simplified data that the fish was either upriver of site i prior to the current detection at site i or had previously passed site i . The non-simplified data indicate this either via detections upriver from site i that occurred chronologically before the current detection, or by imputation, say from repeated top-of-dam detections. For example, a detection history $R D_{1T} D_{1T} D_{1T}$ implies that the fish ascended dam 1 (BON) at least three times, so it must have fallen back over the dam at least twice. This detection history is simplified to $R FB D_{1T}$ for Model 4. Note that for Model 2, this detection history would be reduced to $R D_{1T}$.

A fish may turn around and swim downriver from any point along its migration. All downriver travel is referred to as “fallback” here, not just descending over previously passed dams. Although a fish may turn around at any point, the placement of the fallback codes in the detection histories is restricted. In general, the *FB* code may come *after* any type of detection site except for the uppermost dam and the tributaries (only terminal tributary detections are considered here); *before* any type of detection site except for the release; and not between the base-of-dam and top-of-dam detections for the same dam. Using the detection site notation, the *FB* code may appear after the sites R , D_{kB} ($k = 1, \dots, K-1$), and D_{kT} ($k = 1, \dots, K-1$), and before the sites T_k ($k = 0, \dots, K-1$), D_{kB} ($k = 1, \dots, K$), and D_{kT} ($k = 1, \dots, K$), and not between the pair of detections D_{kB} and D_{kT} ($k =$

$1, \dots, K - 1$). The reason for this restriction is that in order for a fallback to have been observed from the radiotelemetry data between detections at sites D_{kB} and D_{kT} , the fish must have first passed the base of dam k going upriver and been detected there, then passed the top of dam k without being detected there, continued to upriver detection sites and been detected, turned around at some point above dam k , swum downriver past dam k , turned around again, and reascended dam k , this time without being detected at the base of dam k but with a detection at the top of dam k . Figure 3.11(a) shows an example of this type of path. Because only the post-fallback paths are used, the first ascent of dam k and the corresponding base-of-dam detection are removed from the simplified detection history as part of the pre-fallback path. Instead, the post-fallback ascent of dam k , with its missing detection at the base, is used in the reduced detection history. On the other hand, a fish with the migration path shown in Figure 3.11(b) reached the base of dam k and was detected there, then turned around and swam downriver, was detected downriver, and then turned around again and swam back upriver past dam k , with a detection at the top of dam k . This fish fell back between detections at the base of dam k and the top of dam k ; however, because only post-fallback paths are used, the detection at the base of dam k is not used in the simplified migration path, and the fallback event is seen to occur before reaching dam $k - 1$ on the post-fallback path. Thus, any reduced detection history with a base-of-dam detection (D_{kB}) followed by a top-of-dam detection for the same dam (D_{kT}) comes from a non-simplified detection history with no evidence of a fallback event between these two detections.

The second restriction on the placement of the code *FB* in the detection histories is that there must be at most a single *FB* code in each detection history. A fish that has been classified as a fallback fish keeps that classification throughout its detection history for Model 4, so no additional *FB* code is needed, even if the fish has multiple fallback events.

3.8.2 Notation

Model 4 is parameterized using transition parameters and detection parameters, following the pattern of the previous models. As usual, the index i indicates a site from which a

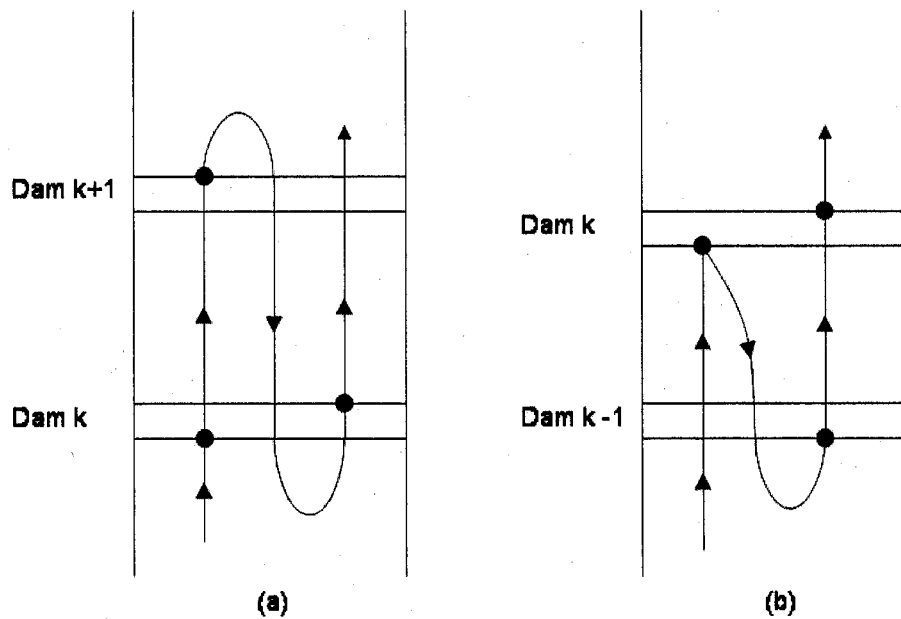


Figure 3.11: Two migration paths with fallback between detection at the base of dam k and detection at the top of dam k . In the first path (a), fallback occurs upstream of dam k . In the second path (b), fallback occurs downstream of dam k . In both cases, the reduced (i.e., simplified) migration path will include the detection at the top of dam k , but not the detection at the base of that dam.

transition is made, the index j indicates a site to which a transition is made, and K is the number of dams. The transition parameters are ϕ_{ij} and ϕ_{ij}^F , representing the probability of the transition (survival and movement) from site i to site j for fish who are and are not fallback fish, respectively:

$$\begin{aligned}\phi_{ij} &= Pr[\text{Survive and move from site } i \text{ to site } j \mid \text{Reach site } i, \text{ non-fallback fish}]; \\ \phi_{ij}^F &= Pr[\text{Survive and move from site } i \text{ to site } j \mid \text{Reach site } i, \text{ fallback fish}],\end{aligned}\quad (3.40)$$

where $i = R, D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}, D_{KT}$, and where

$$j = \begin{cases} D_{1B} \text{ or } T_0 & \text{for } i = R; \\ D_{kT} & \text{for } i = D_{kB}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = D_{kT}, k = 1, \dots, K-1; \\ T_k & \text{for } i = D_{kT}, k = 1, \dots, K. \end{cases}\quad (3.41)$$

As usual, p_i represents the probability of being detected at site i , conditional on reaching that site, and $q_i = 1 - p_i$ is the probability of not being detected at site i , conditional on reaching that site. It is assumed that the detection rate in the tributaries is 100%, i.e., $p_{T_k} = 1$ for $k = 0, \dots, K$. Detection parameters are the same for fallback and non-fallback fish.

This model incorporates the fallback (or equivalently, “post-fallback”) state as an absorbing state (“fallback fish” or “post-fallback fish”), with entry into that state possible between most pairs of detection sites (but see the restrictions described above). Before making the transition to the next detection site, a non-fallback fish at site i becomes a fallback fish via a Bernoulli trial with probability f_i . The parameter f_i is the probability of swimming upstream from site i , then turning around and swimming downstream, and finally being detected again upstream of site i , typically after turning around (so swimming upstream) again. A fish that falls back over a dam or swims downstream but is undetected after fallback is not observed to have fallen back, and so is not denoted a fallback fish. A

fish may be undetected after fallback if it does not turn around to swim upstream again, or if it does swim upstream again but evades detection. It is assumed that no non-detected fallback fish enter tributaries after fallback, because detection in the tributaries is assumed to be 100%.

Realistically, a fish becomes a fallback fish in the middle of the transition from site i to the next detection site (j) in the simplified detection history. Because the transition from site i to site j is different and possibly riskier for fish who become fallback fish (i.e., enter the post-fallback state) between these two sites than for fish who move directly from site i to site j , the event “becoming a fallback fish” is viewed as occurring before the transition from i to j . The exception to this is if i is a base-of-dam site, in which case it is assumed that the fish becomes a fallback fish after passing the corresponding top-of-dam site, whether or not it is detected there. For $i = D_{kB}$ for some k , the event “becoming a fallback fish” occurs in the middle of the transition to the next observed detection, which necessarily occurs upstream of site D_{kT} ; otherwise, the choice of entering the post-fallback state occurs before the transition between detection sites.

All fish are released as pre-fallback fish. This means that in order for a detection history to be parameterized with the transition parameter $\phi_{R,D_{1B}}^F$, the fish must have become a fallback fish between the release and reaching detection site D_{1B} . Thus, any detection history including the transition parameter $\phi_{R,D_{1B}}^F$ must also include the fallback parameter f_R as a factor. This is not the case for later transition parameters for fallback fish. For example, both a detection history showing that the fish became a post-fallback fish immediately after release (e.g., $R\ FB\ D_{1B}\ D_{1T}\ D_{2B}$) and a detection history showing that the fish became a post-fallback fish only after passing the top of the first dam (e.g., $R\ D_{1B}\ D_{1T}\ FB\ D_{2B}$) are parameterized with the transition parameter $\phi_{D_{1T},D_{2B}}^F$ as factors, but only the second detection history’s probability includes the fallback parameter $f_{D_{1T}}$ as a factor. It is possible to separately estimate the parameters $f_{D_{1T}}$ and $\phi_{D_{1T},D_{2B}}^F$ because some, but not all, detection history probabilities that include $\phi_{D_{1T},D_{2B}}^F$ do not also include $f_{D_{1T}}$. On the other hand, because all detection history probabilities that include $\phi_{R,D_{1B}}^F$ as a factor also include the factor f_R , it is not possible to separately estimate these two parameters. Instead, only their product may be estimated. Similarly, it is not possible to separately estimate the

parameters ϕ_{R,T_0}^F , $\phi_{R,D_{1B}}$, or ϕ_{R,T_0} . The estimable transition parameters corresponding to transitions originating at the release point are:

$$\begin{aligned}\Phi_{R,T_0} &= (1 - f_R)\phi_{R,T_0}; \\ \Phi_{R,D_{1B}} &= (1 - f_R)\phi_{R,D_{1B}}; \\ \Phi_{R,T_0}^F &= f_R\phi_{R,T_0}^F; \\ \Phi_{R,D_{1B}}^F &= f_R\phi_{R,D_{1B}}^F.\end{aligned}$$

The above discussion on entering the post-fallback state holds for actual transitions between sites, regardless of detection at the sites. However, because detection histories include only sites where the fish was detected, determining from the detection history where the fish entered the post-fallback state is more complicated. A detection history for Model 4 includes the *FB* code only if the detections indicate that the fish swam downriver at some point during sampling. This is indicated by repeated detections at a site, or by downriver detections chronologically following upriver detections. Such a detection history is simplified by removing the portion of the fish's migration path that was retraced by the fallback, and replacing this retraced portion with a shorter path that connects the last pre-fallback detection site to the lowest of the downriver sites where the fish was detected after fallback (e.g., see Figure 3.10 and 3.7). This "shorter path" that replaces the fallback path originates at the last detection site that occurs before the removed fallback path begins, whether or not the fish was detected at that site. This site will always be either the initial release site or a dam site, because only terminal tributary detections are included in Model 4. Because the base-of-dam and top-of-dam detection sites at a dam typically appear in pairs, the fallback replacement path (i.e., the heavy paths in Figures 3.10 and 3.7) will always begin at a top-of-dam site rather than at a base-of-dam site if (1) it begins at a dam (rather than the release site), and (2) detections are possible at the top of the dam. (In some cases, there may be no detection possible at the top of a dam, as for LMO in the 1996 Chinook data set analyzed in this chapter.) The location of the beginning of the short fallback replacement path in a detection history of a fallback fish is significant because

it indicates how to parameterize the probability of the detection history. In particular, it indicates at what site the fish becomes a fallback fish. As an example, consider a detection history that begins $R\ FB\ D_{2T} \dots$. A fish with this detection history was not detected between the initial release and the top of the second dam, although the FB code indicates that the fish was detected either multiple times at D_{2T} or at a site upriver of D_{2T} before being detected at D_{2T} again; Figure 3.12 shows these two possibilities, with the fallback path indicated by the dotted line and the fallback replacement path indicated by the curved heavy line. Although the fish was not detected at the first dam, it is apparent that the fish passed the first dam and that the fallback replacement path must begin at the top of the first dam. In other words, although the fish was not detected at D_{1T} , it must have entered the fallback state upon leaving that site. This means that the probability of this detection history begins:

$$Pr[R\ FB\ D_{2T} \dots] = \Phi_{R,D_{1B}} q_{D_{1B}} \phi_{D_{1B},D_{1T}} q_{D_{1T}} f_{D_{1T}} \phi_{D_{1T},D_{2B}}^F q_{D_{2B}} \phi_{D_{2B},D_{2T}}^F p_{D_{2T}} \dots \quad (3.42)$$

Because entering the post-fallback state is dependent on both fish movement and fish detection, it can occur only immediately before the detection site that follows the FB code in the detection history (with the restrictions on the placement of the FB code described above). Consider again the detection history beginning $R\ FB\ D_{2B} \dots$. If a fish with this detection history had entered the post-fallback state downriver from site D_{1T} , i.e., immediately after release, then this would be apparent in the detection history by a D_{1B} or D_{1T} detection coming immediately after the FB code. Without such a detection, there is no reason to suppose that the fish ended its fallback as far downriver as the first dam. As it is, there is reason to suppose that the fish ended its fallback no farther upriver than D_{2B} . It is possible that the fish actually fell back as far downriver as D_{1B} or D_{1T} , but the detection history gives no indication of this event, and the parameterization in Equation (3.42) is the only defensible parameterization. Based on the example parameterization above, a general rule for parameterizing detection histories with FB codes is to keep the fish in the pre-fallback state until it passes the top-of-dam site immediately before the detection site that follows

the *FB* code in the detection history, regardless of whether or not the fish was detected at that top-of-dam site.

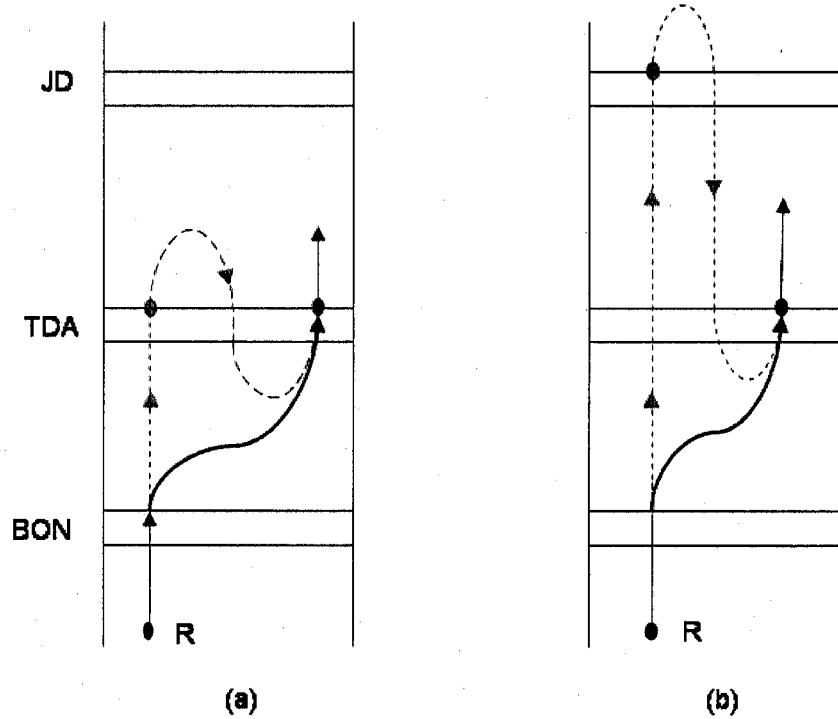


Figure 3.12: Two possible migration paths that simplify to the detection history beginning $R \text{ } FB \text{ } D_{2T} \dots$. Either (a) there were multiple detections at site D_{2T} , or (b) there were detections upstream of D_{2T} that occurred chronologically before the detection at D_{2T} . The dotted paths indicate the portion of the detection history removed due to the fallback or removal of the tributary visit; the heavy portion of the path replaces the dotted portion.

Define the parameters χ_i and χ_i^F as follows:

$$\chi_i = Pr[\text{Not detected after site } i \mid \text{Reach } i \text{ as a non-fallback fish}];$$

$$\chi_i^F = Pr[\text{Not detected after site } i \mid \text{Reach } i \text{ as a fallback fish}].$$

The χ_i^F parameters for fallback fish are analogous to the χ_i parameters in Model 2, but those for non-fallback fish must account for the possibility of becoming a fallback fish in the following reach. The χ_i^F parameters are expressed as:

$$\begin{aligned}
 \chi_{D_{kB}}^F &= 1 - \phi_{D_{kB}, D_{kT}}^F (1 - q_{D_{kT}} \chi_{D_{kT}}^F), & k = 1, \dots, K; \\
 \chi_{D_{kT}}^F &= 1 - \phi_{D_{kT}, T_k}^F - \phi_{D_{kT}, D_{k+1, B}}^F (1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}^F), & k = 1, \dots, K-1; \\
 \chi_{D_{KT}}^F &= 1 - \phi_{D_{KT}, T_K}^F; \\
 \chi_{T_k}^F &= 1, & k = 0, \dots, K.
 \end{aligned} \tag{3.43}$$

The χ_i parameters can be expressed as follows:

$$\begin{aligned}
 \chi_R &= 1 - \Phi_{R, T_0} - \Phi_{R, T_0}^F - \Phi_{R, D_{1B}} (1 - q_{D_{1B}} \chi_{D_{1B}}) - \\
 &\quad \Phi_{R, D_{1B}}^F \{1 - q_{D_{1B}} (1 - \phi_{D_{1B}, D_{1T}}^F p_{D_{1T}})\}; \\
 \chi_{D_{kB}} &= 1 - \phi_{D_{kB}, D_{kT}} + \phi_{D_{kB}, D_{kT}} q_{D_{kT}} \chi_{D_{kT}}, & k = 1, \dots, K; \\
 \chi_{D_{kT}} &= 1 - (1 - f_{D_{kT}}) \{ \phi_{D_{kT}, T_k} + \phi_{D_{kT}, D_{k+1, B}} (1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}) \} \\
 &\quad - f_{D_{kT}} \phi_{D_{kT}, T_k}^F \\
 &\quad - f_{D_{kT}} \phi_{D_{kT}, D_{k+1, B}}^F \{1 - q_{D_{k+1, B}} (1 - \phi_{D_{k+1, B}, D_{k+1, T}}^F p_{D_{k+1, T}})\}, & k = 1, \dots, K-1; \\
 \chi_{D_{KT}} &= 1 - \phi_{D_{KT}, T_K}; \\
 \chi_{T_k} &= 1, & k = 0, \dots, K.
 \end{aligned} \tag{3.44}$$

The parameters used in Model 4 are listed in Table 3.29.

Table 3.29: Parameters used in Model 4, the Fallback Terminal Tributary Model. The number of dams is K .

Parameter	Definition
Φ_{R, T_0}	Probability of surviving and moving from the release point directly to site T_0 without becoming a fallback fish;
$\Phi_{R, D_{1B}}$	Probability of surviving and moving from the release point directly to site D_{1B} without becoming a fallback fish;

Table 3.29 continued

Parameter	Definition
Φ_{R,T_0}^F	Probability of surviving, becoming a fallback fish, and then moving from the release point directly to site T_0 ;
$\Phi_{R,D_{1B}}^F$	Probability of surviving, becoming a fallback fish, and then moving from the release point directly to site D_{1B} ;
ϕ_{ij}	Probability of surviving and moving from site i directly to site j , given reaching site i and a non-fallback fish;
ϕ_{ij}^F	Probability of surviving and moving from site i directly to site j , given reaching site i and a fallback fish;
p_j	Probability of being detected at site j , given presence at site j ;
q_j	Probability of avoiding detection at site j , given presence at site j ; $= 1 - p_j$;
f_i	Probability of becoming a fallback fish between site i and the next detection site, given having reached site i as a non-fallback fish;
χ_i	Probability of not being detected after site i , given having reached site i as a non-fallback fish;
χ_i^F	Probability of not being detected after site i , given having reached site i as a fallback fish.

The parameters in Table 3.29 can be used to express the probabilities of all possible detection histories. For example, the probabilities of two detection histories are:

$$Pr[R FB D_{1B} D_{1T} D_{2T} T_2] = \Phi_{R,D_{1B}}^F p_{D_{1B}} \phi_{D_{1B},D_{1T}}^F p_{D_{1T}} \phi_{D_{1T},D_{2B}}^F q_{D_{2B}} \phi_{D_{2B},D_{2T}}^F \times p_{D_{2T}} \phi_{D_{2T},T_2}^F; \quad (3.45)$$

$$Pr[R D_{1B} D_{2B} FB D_{3T}] = \Phi_{R,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}} q_{D_{1T}} \phi_{D_{1T},D_{2B}} p_{D_{2B}} \phi_{D_{2B},D_{2T}} q_{D_{2T}} \times f_{D_{2T}} \phi_{D_{2T},D_{3B}}^F q_{D_{3B}} \phi_{D_{3B},D_{3T}}^F p_{D_{3T}} \chi_{D_{3T}}^F. \quad (3.46)$$

The fallback effect in both Equations (3.45) and (3.46) continues throughout the detection history. In Equation (3.45), the fish enters the post-fallback state during the transition from release to the base of the first dam, so the combination fallback-transition parameter $\Phi_{R,D_{1B}}^F$ is used. In Equation (3.46), the site from which the fish enters the post-fallback state (D_{2T}) is not observed but must be deduced from the site following the FB code (D_{3T}).

3.8.3 Likelihood

The likelihood for Model 4 is most easily expressed in terms of summary statistics, defined in Table 3.30. In addition to the number of fallback and non-fallback fish detected at each site (a_i^F and a_i , respectively) and the number of both of these also detected upstream in the same fallback state (b_i^F and b_i , respectively), it is also necessary to know the number of fish making the transition from non-fallback to fallback status after each detection (h_i) and the number of fish making that transition in each reach (t_k). Define “fallback reach k ” to be the river reach including sites T_{k-1} , D_{kB} , and D_{kT} . Then the summary statistic t_k is the number of fish entering the post-fallback state in fallback reach k . It is also useful to know the number of fish detected after each site, in both the fallback and non-fallback states (g_i^F and g_i , respectively). The statistic g_i is the number of fish detected after site i that were not fallback fish at site i . Because fish cannot enter the fallback state between sites D_{kB} and D_{kT} for any dam k (i.e., between the base and the top of a given dam), for $i = D_{kB}$ or D_{kT} , g_i is the number of fish detected after site i that were not fallback fish by the time they reached site D_{kB} . Because Model 4 assumes that the tributary sites are not visited by fish migrating on upriver, and because fish cannot become fallback fish between a tributary site and the following dam, then g_{T_k} is the number of fish detected after site T_k that were not fallback fish by the time they reached site $D_{k+1,B}$. On the other hand, $g_{T_k}^F$ is the number of fish detected upriver of site T_k that had fallen back by the time they passed site T_k . In other words, these fish were first detected as fallback fish before reaching site $D_{k+1,B}$. The g_i and g_i^F statistics can be expressed in terms of the other statistics as follows:

$$g_R = b_R + h_R;$$

$$g_R^F = 0;$$

$$g_{T_0} = g_R - a_{T_0} - t_1;$$

$$g_{T_0}^F = t_1 - a_{T_0}^F;$$

$$g_{T_k} = g_{D_{kT}} - a_{T_k} - t_{k+1},$$

$$k = 1, \dots, K-1;$$

$$g_{T_k}^F = g_{D_{kT}}^F - a_{T_k}^F + t_{k+1},$$

$$k = 1, \dots, K-1;$$

$$\begin{aligned}
g_{D_{kB}} &= g_{T_{k-1}} + b_{D_{kB}} + h_{D_{kB}} - a_{D_{kB}}, & k = 1, \dots, K; \\
g_{D_{kB}}^F &= g_{T_{k-1}}^F + b_{D_{kB}}^F - a_{D_{kB}}^F, & k = 1, \dots, K; \\
g_{D_{kT}} &= g_{D_{kB}} + b_{D_{kT}} + h_{D_{kT}} - a_{D_{kT}}, & k = 1, \dots, K; \\
g_{D_{kT}}^F &= g_{D_{kB}}^F + b_{D_{kT}}^F - a_{D_{kT}}^F, & k = 1, \dots, K.
\end{aligned}$$

The summary statistics are summarized in Table 3.30.

Table 3.30: Summary statistics for Model 4, the Fallback Terminal Tributary model. The number of dams is K .

Statistic	Definition
a_i	Number of non-fallback fish that were detected at site i , $i = R, T_0, D_{1B}, D_{1T}, T_1, \dots, T_k$;
a_i^F	Number of fallback fish that were detected at site i , $i = T_0, D_{1B}, D_{1T}, T_1, \dots, T_k$;
b_i	Number of fish detected at site i as non-fallback fish and detected upstream as non-fallback fish, $i = R, D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$;
b_i^F	Number of fish detected at site i as fallback fish and detected upstream (as fallback fish), $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$;
h_i	Number of fish detected at site i as non-fallback fish and next detected upstream as fallback fish, $i = R, D_{1B}, D_{1T}, D_{2B}, \dots, D_{K-1,T}$;
t_k	Number of fish detected as fallback fish first at site T_{k-1} , D_{kB} , or D_{kT} , $k = 1, \dots, K$;
g_i	Number of fish detected after site i that were not fallback fish at site i , $i = R, T_0, D_{1B}, D_{1T}, T_1, \dots, D_{KT}$;
g_i^F	Number of fish detected after site i that were fallback fish at site i , $i = T_0, D_{1B}, D_{1T}, T_1, \dots, D_{KT}$.

The minimal sufficient statistics are functions of the statistics listed in Table 3.30, and are listed in Table 3.31. For the full model with K dams, there are $9K + 1$ minimal sufficient statistics, and an equal number of parameters.

Table 3.31: Minimal sufficient statistics for Model 4, the Fallback Terminal Tributary model. The number of dams is K .

Statistic	Definition
a_{T_k}	Number of fish detected at site T_k as non-fallback fish, $k = 0, \dots, K - 1$;
$a_{T_k}^F$	Number of fish detected at site T_k as fallback fish, $k = 0, \dots, K - 1$;
$b_R + h_R$	Number of fish detected after the initial release;
t_k	Number of fish first detected as fallback fish at site T_{k-1} , D_{kB} , or D_{kT} , $k = 1, \dots, K$;
$a_{D_{kB}} - b_{D_{kB}} - h_{D_{kB}}$	Number of non-fallback fish detected for last time at site D_{kB} , $k = 1, \dots, K$;
$a_{D_{kT}} - b_{D_{kT}} - h_{D_{kT}}$	Number of non-fallback fish detected for last time at site D_{kT} , $k = 1, \dots, K$;
$a_{D_{kB}}^F - b_{D_{kB}}^F$	Number of fallback fish detected for last time at site D_{kB} , $k = 1, \dots, K$;
$a_{D_{kT}}^F - b_{D_{kT}}^F$	Number of fallback fish detected for last time at site D_{kT} , $k = 1, \dots, K$;
$a_{D_{kB}} + a_{D_{kB}}^F$	Number of fish detected at site D_{kB} , $k = 1, \dots, K$;
$a_{D_{kT}} + a_{D_{kT}}^F$	Number of fish detected at site D_{kT} , $k = 1, \dots, K$.

The likelihood for Model 4 can be expressed as follows:

$$\begin{aligned}
L \propto & \Phi_{R,T_0}^{a_{T_0}} \Phi_{R,D_{1B}}^{g_{T_0}} (\Phi_{R,T_0}^F)^{a_{T_0}^F} (\Phi_{R,D_{1B}}^F)^{g_{T_0}^F} \chi_R^{N-g_R} \\
& \times \prod_{k=1}^K \left\{ \phi_{D_{k-1},T,D_{kB}}^{g_{T_{k-1}}} (\phi_{D_{k-1},T,D_{kB}}^F)^{g_{T_{k-1}}^F} \phi_{D_{kB},D_{kT}}^{g_{D_{kB}}} (\phi_{D_{kB},D_{kT}}^F)^{g_{D_{kB}}^F} \phi_{D_{kT},T_k}^{a_{T_k}} (\phi_{D_{kT},T_k}^F)^{a_{T_k}^F} \right. \\
& \quad \times p_{D_{kB}}^{a_{D_{kB}} + a_{D_{kB}}^F} q_{D_{kB}}^{g_{T_{k-1}} + g_{T_{k-1}}^F - a_{D_{kB}} - a_{D_{kB}}^F} p_{D_{kT}}^{a_{D_{kT}} + a_{D_{kT}}^F} q_{D_{kT}}^{g_{D_{kB}} + g_{D_{kB}}^F - a_{D_{kT}} - a_{D_{kT}}^F} \\
& \quad \times \chi_{D_{kB}}^{a_{D_{kB}} - b_{D_{kB}} - h_{D_{kB}}} (\chi_{D_{kB}}^F)^{a_{D_{kB}}^F - b_{D_{kB}}^F} \chi_{D_{kT}}^{a_{D_{kT}} - b_{D_{kT}} - h_{D_{kT}}} (\chi_{D_{kT}}^F)^{a_{D_{kT}}^F - b_{D_{kT}}^F} \left. \right\} \\
& \times \prod_{k=1}^{K-1} \left\{ f_{D_{kT}}^{t_{k+1}} (1 - f_{D_{kT}})^{g_{D_{kT}} - t_{k+1}} \right\}, \tag{3.47}
\end{aligned}$$

where K is the number of dams and N is the size of the release group. Equation (3.47) may be tailored to a particular data set by specifying K , removing any extraneous parameters, and renaming parameters according to observed detections, if necessary. This is done for the 1996 Chinook salmon data set in the next section.

Maximum likelihood estimates from Model 3a may be modified to provide initial values for a numerical optimization routine used to fit Equation (3.47). For example, the maximum likelihood estimate of ϕ_{ij} from Model 3a may be used as the initial value for both ϕ_{ij} and ϕ_{ij}^F in Model 4. Fallback parameters f_i are likely to be low, so small initial values should be chosen for these parameters (say, 0.01); the optimization routine is unlikely to be sensitive to initial values of the f_i parameters. The transition parameters Φ_{R,T_0} , $\Phi_{R,D_{1B}}$, Φ_{R,T_0}^F , and $\Phi_{R,D_{1B}}^F$ must sum to < 1 . These parameters include the factors f_R or $(1 - f_R)$ and so have no counterparts in Model 3a. However, because Model 4 has an equal number of parameters and minimal sufficient statistics, the maximum likelihood estimates of Φ_{R,T_0} and Φ_{R,T_0}^F are easily derived from the minimal sufficient statistics:

$$\hat{\Phi}_{R,T_0} = a_{T_0}/N, \quad \hat{\Phi}_{R,T_0}^F = a_{T_0}^F/N. \quad (3.48)$$

Thus, Equation (3.48) provides initial values for Φ_{R,T_0} and Φ_{R,T_0}^F , and $1 - (\hat{\Phi}_{R,T_0} + \hat{\Phi}_{R,T_0}^F)$ may be split equally over the initial values for $\Phi_{R,D_{1B}}$ and $\Phi_{R,D_{1B}}^F$. Likewise, initial values for transition parameters from site D_{kT} must be such that neither $\chi_{D_{kT}}$ nor $\chi_{D_{kT}}^F$ is negative. The estimates for the 1996 Chinook salmon data set presented below were not sensitive to initial values.

3.8.4 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival, is S_{sys} , defined as follows:

$$S_{sys} = \eta_R,$$

where

$$\eta_R = \Phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \eta_{D_{1T}} + \Phi_{R,D_{1B}}^F \phi_{D_{1B},D_{1T}}^F \eta_{D_{1T}}^F,$$

$$\begin{aligned}
\eta_{D_{kT}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T} \\
&\quad + f_{D_{kT}} \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F, \quad k = 1, \dots, K-1; \\
\eta_{D_{KT}} &= 1; \\
\eta_{D_{kT}}^F &= \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F, \quad k = 1, \dots, K-1; \\
\eta_{D_{KT}}^F &= 1.
\end{aligned} \tag{3.49}$$

The variance estimator of \hat{S}_{sys} is defined in Appendix B.

In Model 4, the estimator for unaccountable loss excludes (i.e., accounts for) fallback that is followed by detection, (i.e., detection histories containing the code FB), because detection occurs only when fish are either passing a dam going upstream or entering or exiting a tributary. Thus, fallback followed by detection implies that the fish has turned around from its fallback and is once again headed upstream (or to a tributary). The f_i parameters represent the probability of entering the post-fallback state, so their use implies that the fish was last detected going upstream or to a tributary. Fish that fall back and do not subsequently turn around and swim back upstream are not detected during or after their fallback, so they should fall into the unaccountable loss category. All estimable transition parameters in Model 4 apply only to transitions directed upstream or to a tributary, so by default, the unaccountable loss estimator for Model 4 (and Models 5a, 5b, and 6) includes fish who fall back or otherwise swim downriver and do not subsequently reascend any dam or exit to a tributary. It is possible that some fish fall back or swim downriver and then turn around to swim upriver again, but evade detection at all subsequent dams. If this is the case, then the f_i parameters will be negatively biased. Because μ_R depends on both the factors f_i and $(1 - f_i)$, it is not obvious whether μ_R will be positively or negatively biased. If fallback does not affect subsequent survival, then μ_R will be unaffected if f_i is biased. As with Models 2, 3a, and 3b, if the assumption of 100% detection at the tributary antenna arrays is faulty, then the transitions ϕ_{D_{k+1}, T, T_k} and ϕ_{D_{k+1}, T, T_k}^F will be negatively biased, and so μ_R will be positively biased.

The probability of unaccountable loss for Model 4 is μ_R , defined as follows:

$$\begin{aligned}\mu_R = & 1 - \Phi_{R,T_0} - \Phi_{R,T_0}^F - \Phi_{R,D_{1B}}\phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}) \\ & - \Phi_{R,D_{1B}}^F\phi_{D_{1B},D_{1T}}^F(1 - \mu_{D_{1T}}^F),\end{aligned}\quad (3.50)$$

where

$$\begin{aligned}1 - \mu_{D_{kT}} = & (1 - f_{D_{kT}})\phi_{D_{kT},T_k} + f_{D_{kT}}\phi_{D_{kT},T_k}^F \\ & + (1 - f_{D_{kT}})\phi_{D_{kT},D_{k+1,B}}\phi_{D_{k+1,B},D_{k+1,T}}(1 - \mu_{D_{k+1,T}}) \\ & + f_{D_{kT}}\phi_{D_{kT},D_{k+1,B}}^F\phi_{D_{k+1,B},D_{k+1,T}}^F(1 - \mu_{D_{k+1,T}}^F), \quad k = 1, \dots, K-1; \\ 1 - \mu_{D_{kT}} = & 1, \quad k = K; \\ 1 - \mu_{D_{kT}}^F = & \phi_{D_{kT},T_k}^F + \phi_{D_{kT},D_{k+1,B}}^F\phi_{D_{k+1,B},D_{k+1,T}}^F(1 - \mu_{D_{k+1,T}}^F), \quad k = 1, \dots, K-1; \\ 1 - \mu_{D_{kT}}^F = & 1, \quad k = K.\end{aligned}$$

The variance estimator of $\hat{\mu}_R$ is defined in Appendix B.

3.8.5 1996 Chinook Data Set

The summary statistics for Model 4, observed from the full 1996 Chinook salmon data set, are presented in Table 3.32. Table 3.32 shows that no fish were detected at sites D_{2B} , D_{3B} , D_{6T} , or T_6 . With no detections at these sites, the transition parameters corresponding to these sites cannot be estimated. Instead, those transition parameters are replaced with the following:

$$\begin{aligned}\phi_{D_{1T},D_{2T}} &= \phi_{D_{1T},D_{2B}}\phi_{D_{2B},D_{2T}}; \\ \phi_{D_{1T},D_{2T}}^F &= \phi_{D_{1T},D_{2B}}^F\phi_{D_{2B},D_{2T}}^F; \\ \phi_{D_{2T},D_{3T}} &= \phi_{D_{2T},D_{3B}}\phi_{D_{3B},D_{3T}}; \\ \phi_{D_{2T},D_{3T}}^F &= \phi_{D_{2T},D_{3B}}^F\phi_{D_{3B},D_{3T}}^F;\end{aligned}$$

$$\begin{aligned}\phi_{D_{6B}, D_{7B}} &= \phi_{D_{6B}, D_{6T}} \phi_{D_{6T}, D_{7B}}; \\ \phi_{D_{6B}, D_{7B}}^F &= \phi_{D_{6B}, D_{6T}}^F \phi_{D_{6T}, D_{7B}}^F.\end{aligned}$$

Only a single fish (fallback) was detected at site T_5 ; the transition parameter ϕ_{D_{5T}, T_5} must be fixed to 0. Also, no fish were first detected as fallback fish after site D_{6B} , so $f_{D_{6B}}$ must be fixed to 0. Other parameters as described in Table 3.29 ($K = 7$) may be estimated.

The likelihood for Model 4, tailored to the 1996 Chinook salmon data set, is

$$\begin{aligned}L \propto & \chi_R^{N-g_R} \Phi_{R, T_0}^{a_{T_0}} \Phi_{R, D_{1B}}^{g_{T_0}} (\Phi_{R, T_0}^F)^{a_{T_0}^F} (\Phi_{R, D_{1B}}^F)^{g_{T_0}^F} p_{D_{1B}}^{a_{D_{1B}} + a_{D_{1B}}^F} q_{D_{1B}}^{g_{T_0} + g_{T_0}^F - a_{D_{1B}} - a_{D_{1B}}^F} \\ & \times \chi_{D_{1B}}^{a_{D_{1B}} - b_{D_{1B}} - h_{D_{1B}}} (\chi_{D_{1B}}^F)^{a_{D_{1B}}^F - b_{D_{1B}}^F} \phi_{D_{1B}, D_{1T}}^{g_{D_{1B}}} (\phi_{D_{1B}, D_{1T}}^F)^{g_{D_{1B}}^F} p_{D_{1T}}^{a_{D_{1T}} + a_{D_{1T}}^F} \\ & \times q_{D_{1T}}^{g_{D_{1B}} + g_{D_{1B}}^F - a_{D_{1T}} - a_{D_{1T}}^F} \chi_{D_{1T}}^{a_{D_{1T}} - b_{D_{1T}} - h_{D_{1T}}} (\chi_{D_{1T}}^F)^{a_{D_{1T}}^F - b_{D_{1T}}^F} f_{D_{1T}}^{t_2} (1 - f_{D_{1T}})^{g_{D_{1T}} - t_2} \\ & \times \phi_{D_{1T}, T_1}^{a_{T_1}} (\phi_{D_{1T}, T_1}^F)^{a_{T_1}^F} \phi_{D_{1T}, D_{2T}}^{g_{T_1}} (\phi_{D_{1T}, D_{2T}}^F)^{g_{T_1}^F} p_{D_{2T}}^{a_{D_{2T}} + a_{D_{2T}}^F} q_{D_{2T}}^{g_{T_1} + g_{T_1}^F - a_{D_{2T}} - a_{D_{2T}}^F} \\ & \times \chi_{D_{2T}}^{a_{D_{2T}} - b_{D_{2T}} - h_{D_{2T}}} (\chi_{D_{2T}}^F)^{a_{D_{2T}}^F - b_{D_{2T}}^F} f_{D_{2T}}^{t_3} (1 - f_{D_{2T}})^{g_{D_{2T}} - t_3} \phi_{D_{2T}, T_2}^{a_{T_2}} (\phi_{D_{2T}, T_2}^F)^{a_{T_2}^F} \\ & \times \phi_{D_{2T}, D_{3T}}^{g_{T_2}} (\phi_{D_{2T}, D_{3T}}^F)^{g_{T_2}^F} p_{D_{3T}}^{a_{D_{3T}} + a_{D_{3T}}^F} q_{D_{3T}}^{g_{T_2} + g_{T_2}^F - a_{D_{3T}} - a_{D_{3T}}^F} \chi_{D_{3T}}^{a_{D_{3T}} - b_{D_{3T}} - h_{D_{3T}}} \\ & \times (\chi_{D_{3T}}^F)^{a_{D_{3T}}^F - b_{D_{3T}}^F} f_{D_{3T}}^{t_4} (1 - f_{D_{3T}})^{g_{D_{3T}} - t_4} \phi_{D_{3T}, T_3}^{a_{T_3}} (\phi_{D_{3T}, T_3}^F)^{a_{T_3}^F} \phi_{D_{3T}, D_{4B}}^{g_{T_3}} (\phi_{D_{3T}, D_{4B}}^F)^{g_{T_3}^F} \\ & \times p_{D_{4B}}^{a_{D_{4B}} + a_{D_{4B}}^F} q_{D_{4B}}^{g_{T_3} + g_{T_3}^F - a_{D_{4B}} - a_{D_{4B}}^F} \chi_{D_{4B}}^{a_{D_{4B}} - b_{D_{4B}} - h_{D_{4B}}} (\chi_{D_{4B}}^F)^{a_{D_{4B}}^F - b_{D_{4B}}^F} \phi_{D_{4B}, D_{4T}}^{g_{D_{4B}}} \\ & \times (\phi_{D_{4B}, D_{4T}}^F)^{g_{D_{4B}}^F} p_{D_{4T}}^{a_{D_{4T}} + a_{D_{4T}}^F} q_{D_{4T}}^{g_{D_{4B}} + g_{D_{4B}}^F - a_{D_{4T}} - a_{D_{4T}}^F} \chi_{D_{4T}}^{a_{D_{4T}} - b_{D_{4T}} - h_{D_{4T}}} (\chi_{D_{4T}}^F)^{a_{D_{4T}}^F - b_{D_{4T}}^F} \\ & \times f_{D_{4T}}^{t_5} (1 - f_{D_{4T}})^{g_{D_{4T}} - t_5} \phi_{D_{4T}, T_4}^{a_{T_4}} (\phi_{D_{4T}, T_4}^F)^{a_{T_4}^F} \phi_{D_{4T}, D_{5B}}^{g_{T_4}} (\phi_{D_{4T}, D_{5B}}^F)^{g_{T_4}^F} p_{D_{5B}}^{a_{D_{5B}} + a_{D_{5B}}^F} \\ & \times q_{D_{5B}}^{g_{T_4} + g_{T_4}^F - a_{D_{5B}} - a_{D_{5B}}^F} \chi_{D_{5B}}^{a_{D_{5B}} - b_{D_{5B}} - h_{D_{5B}}} (\chi_{D_{5B}}^F)^{a_{D_{5B}}^F - b_{D_{5B}}^F} \phi_{D_{5B}, D_{5T}}^{g_{D_{5B}}} (\phi_{D_{5B}, D_{5T}}^F)^{g_{D_{5B}}^F} \\ & \times p_{D_{5T}}^{a_{D_{5T}} + a_{D_{5T}}^F} q_{D_{5T}}^{g_{D_{5B}} + g_{D_{5B}}^F - a_{D_{5T}} - a_{D_{5T}}^F} \chi_{D_{5T}}^{a_{D_{5T}} - b_{D_{5T}} - h_{D_{5T}}} (\chi_{D_{5T}}^F)^{a_{D_{5T}}^F - b_{D_{5T}}^F} f_{D_{5T}}^{t_6} \\ & \times (1 - f_{D_{5T}})^{g_{D_{5T}} - t_6} (\phi_{D_{5T}, T_5}^F)^{a_{T_5}^F} \phi_{D_{5T}, D_{6B}}^{g_{T_5}} (\phi_{D_{5T}, D_{6B}}^F)^{g_{T_5}^F} p_{D_{6B}}^{a_{D_{6B}} + a_{D_{6B}}^F} q_{D_{6B}}^{g_{T_5} + g_{T_5}^F - a_{D_{6B}} - a_{D_{6B}}^F} \\ & \times \chi_{D_{6B}}^{a_{D_{6B}} - b_{D_{6B}} - h_{D_{6B}}} (\chi_{D_{6B}}^F)^{a_{D_{6B}}^F - b_{D_{6B}}^F} f_{D_{6B}}^{t_7} (1 - f_{D_{6B}})^{g_{D_{6B}} - t_7} \phi_{D_{6B}, D_{7B}}^{g_{D_{6B}}} (\phi_{D_{6B}, D_{7B}}^F)^{g_{D_{6B}}^F} \\ & \times p_{D_{7B}}^{a_{D_{7B}} + a_{D_{7B}}^F} q_{D_{7B}}^{g_{D_{6B}} + g_{D_{6B}}^F - a_{D_{7B}} - a_{D_{7B}}^F} \chi_{D_{7B}}^{a_{D_{7B}} - b_{D_{7B}} - h_{D_{7B}}} (\chi_{D_{7B}}^F)^{a_{D_{7B}}^F - b_{D_{7B}}^F} \phi_{D_{7B}, D_{7T}}^{g_{D_{7B}}} \end{aligned}$$

$$\begin{aligned}
& \times (\phi_{D_{7B}, D_{7T}}^F)^{g_{D_{7B}}^F + a_{D_{7T}}^F + a_{D_{7T}}^F} p_{D_{7T}}^{g_{D_{7B}}^F + g_{D_{7B}}^F - a_{D_{7T}}^F - a_{D_{7T}}^F} q_{D_{7T}}^{a_{D_{7T}}^F - b_{D_{7T}}^F - h_{D_{7T}}^F} (\chi_{D_{7T}}^F)^{a_{D_{7T}}^F - b_{D_{7T}}^F} \\
& \times \phi_{D_{7T}, T_7}^{a_{T_7}} (\phi_{D_{7T}, T_7}^F)^{a_{T_7}^F}.
\end{aligned} \tag{3.51}$$

Because the data are sparse for dams 5 (IH), 6 (LMO), and 7 (LGR), it may be worthwhile to fit Model 4 to a reduced data set that includes only dams 1 (BON), 2 (TDA), 3 (JD), and 4 (MCN) (i.e., $K = 4$), along with the tributaries in the reaches immediately above and below these dams. Such a model is reasonable if the focus is on salmon returning to mid-Columbia spawning sites rather than to Snake River sites. Table 3.33 shows the observed summary statistics from the reduced 1996 data set including only the first 4 dams and their tributaries. Most statistics in Table 3.33 are the same as those in Table 3.32, with changes only in b_i , b_i^F , and h_i for upriver detection sites. As in the full model, it is necessary to use parameters $\phi_{D_{1T}, D_{2T}}$, $\phi_{D_{1T}, D_{2T}}^F$, $\phi_{D_{2T}, D_{3T}}$, and $\phi_{D_{2T}, D_{3T}}^F$ due to the lack of detections at sites D_{2B} and D_{3B} .

The likelihood for Model 4 for the reduced data 1996 set is

$$\begin{aligned}
L \propto & \chi_R^{N - g_R} \Phi_{R, T_0}^{a_{T_0}} \Phi_{R, D_{1B}}^{g_{T_0}} (\Phi_{R, T_0}^F)^{a_{T_0}^F} (\Phi_{R, D_{1B}}^F)^{g_{T_0}^F} p_{D_{1B}}^{a_{D_{1B}}^F + a_{D_{1B}}^F} q_{D_{1B}}^{g_{T_0}^F + g_{T_0}^F - a_{D_{1B}}^F - a_{D_{1B}}^F} \\
& \times \chi_{D_{1B}}^{a_{D_{1B}}^F - b_{D_{1B}}^F - h_{D_{1B}}^F} (\chi_{D_{1B}}^F)^{a_{D_{1B}}^F - b_{D_{1B}}^F} \phi_{D_{1B}, D_{1T}}^{g_{D_{1B}}^F} (\phi_{D_{1B}, D_{1T}}^F)^{g_{D_{1B}}^F} p_{D_{1T}}^{a_{D_{1T}}^F + a_{D_{1T}}^F} \\
& \times q_{D_{1T}}^{g_{D_{1B}}^F + g_{D_{1B}}^F - a_{D_{1T}}^F - a_{D_{1T}}^F} \chi_{D_{1T}}^{a_{D_{1T}}^F - b_{D_{1T}}^F - h_{D_{1T}}^F} (\chi_{D_{1T}}^F)^{a_{D_{1T}}^F - b_{D_{1T}}^F} f_{D_{1T}}^{t_2} (1 - f_{D_{1T}})^{g_{D_{1T}} - t_2} \\
& \times \phi_{D_{1T}, T_1}^{a_{T_1}} (\phi_{D_{1T}, T_1}^F)^{a_{T_1}^F} \phi_{D_{1T}, D_{2T}}^{g_{T_1}} (\phi_{D_{1T}, D_{2T}}^F)^{g_{T_1}^F} p_{D_{2T}}^{a_{D_{2T}}^F + a_{D_{2T}}^F} q_{D_{2T}}^{g_{T_1}^F + g_{T_1}^F - a_{D_{2T}}^F - a_{D_{2T}}^F} \\
& \times \chi_{D_{2T}}^{a_{D_{2T}}^F - b_{D_{2T}}^F - h_{D_{2T}}^F} (\chi_{D_{2T}}^F)^{a_{D_{2T}}^F - b_{D_{2T}}^F} f_{D_{2T}}^{t_3} (1 - f_{D_{2T}})^{g_{D_{2T}} - t_3} \phi_{D_{2T}, T_2}^{a_{T_2}} (\phi_{D_{2T}, T_2}^F)^{a_{T_2}^F} \\
& \times \phi_{D_{2T}, D_{3T}}^{g_{T_2}} (\phi_{D_{2T}, D_{3T}}^F)^{g_{T_2}^F} p_{D_{3T}}^{a_{D_{3T}}^F + a_{D_{3T}}^F} q_{D_{3T}}^{g_{T_2}^F + g_{T_2}^F - a_{D_{3T}}^F - a_{D_{3T}}^F} \chi_{D_{3T}}^{a_{D_{3T}}^F - b_{D_{3T}}^F - h_{D_{3T}}^F} \\
& \times (\chi_{D_{3T}}^F)^{a_{D_{3T}}^F - b_{D_{3T}}^F} f_{D_{3T}}^{t_4} (1 - f_{D_{3T}})^{g_{D_{3T}} - t_4} \phi_{D_{3T}, T_3}^{a_{T_3}} (\phi_{D_{3T}, T_3}^F)^{a_{T_3}^F} \phi_{D_{3T}, D_{4B}}^{g_{T_3}} (\phi_{D_{3T}, D_{4B}}^F)^{g_{T_3}^F} \\
& \times p_{D_{4B}}^{a_{D_{4B}}^F + a_{D_{4B}}^F} q_{D_{4B}}^{g_{T_3}^F + g_{T_3}^F - a_{D_{4B}}^F - a_{D_{4B}}^F} \chi_{D_{4B}}^{a_{D_{4B}}^F - b_{D_{4B}}^F - h_{D_{4B}}^F} (\chi_{D_{4B}}^F)^{a_{D_{4B}}^F - b_{D_{4B}}^F} \phi_{D_{4B}, D_{4T}}^{g_{D_{4B}}^F} \\
& \times (\phi_{D_{4B}, D_{4T}}^F)^{g_{D_{4B}}^F} p_{D_{4T}}^{a_{D_{4T}}^F + a_{D_{4T}}^F} q_{D_{4T}}^{g_{D_{4B}}^F + g_{D_{4B}}^F - a_{D_{4T}}^F - a_{D_{4T}}^F} \chi_{D_{4T}}^{a_{D_{4T}}^F - b_{D_{4T}}^F - h_{D_{4T}}^F} (\chi_{D_{4T}}^F)^{a_{D_{4T}}^F - b_{D_{4T}}^F} \\
& \times \phi_{D_{4T}, T_4}^{a_{T_4}} (\phi_{D_{4T}, T_4}^F)^{a_{T_4}^F}.
\end{aligned} \tag{3.52}$$

Table 3.33: Observed summary statistics for Model 4 (Fallback Terminal Tributary Model) from the 1996 Chinook salmon data set with $K = 4$ dams (BON, TDA, JD, and MCN). The release size is N . Descriptions of summary statistics are listed in Table 3.30

Statistic	Value	Statistic	Value	Statistic	Value	Statistic	Value	Statistic	Value	Statistic	Value
N	846			b_R	720			h_R	105		
a_{T0}	3	a_{T0}^F	4							t_1	105
a_{D1B}	674	a_{D1B}^F	98	b_{D1B}	641	b_{D1B}^F	94	h_{D1B}	6		
a_{D1T}	603	a_{D1T}^F	89	b_{D1T}	516	b_{D1T}^F	79	h_{D1T}	26		
a_{T1}	211	a_{T1}^F	43							t_2	30
a_{D2B}	0	a_{D2B}^F	0	b_{D2B}	0	b_{D2B}^F	0	h_{D2B}	0		
a_{D2T}	335	a_{D2T}^F	66	b_{D2T}	295	b_{D2T}^F	63	h_{D2T}	10		
a_{T2}	56	a_{T2}^F	16							t_3	12
a_{D3B}	0	a_{D3B}^F	0	b_{D3B}	0	b_{D3B}^F	0	h_{D3B}	0		
a_{D3T}	277	a_{D3T}^F	66	b_{D3T}	250	b_{D3T}^F	61	h_{D3T}	9		
a_{T3}	27	a_{T3}^F	10							t_4	9
a_{D4B}	220	a_{D4B}^F	54	b_{D4B}	212	b_{D4B}^F	45	h_{D4B}	0		
a_{D4T}	223	a_{D4T}^F	50	b_{D4T}	129	b_{D4T}^F	14	h_{D4T}	0		
a_{T4}	134	a_{T4}^F	16							t_5	4

3.8.6 Results

Program USER¹⁵ was used to fit Model 4 to the data via maximum likelihood. Maximum likelihood estimates from the full data set ($K = 7$ dams) are listed in Table 3.34. The log-likelihood was -3452.7375, with an AIC of 7007.475. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.1075$ ($\widehat{SE} = 0.0108$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2743$ ($\widehat{SE} = 0.0155$).

Model 4 is a modification of Model 2; it uses terminal tributary detections as in Model 2, but also accounts for fallback. In general, if the overall effect of fallback is to lower subsequent transition rates (i.e., $\phi_{ij}^F < \phi_{ij}$), and if fallback events are common (i.e., f_i are not small), then the perceived survival rate estimated from Model 4 should be less than that estimated by Model 2, while the opposite should be true for the unaccountable loss rate. However, if fallback events are uncommon and if $\hat{\phi}_{ij}$ for Model 4 is larger than $\hat{\phi}_{ij}$ for Model 2, then the estimated perceived survival rate may be greater, and the unaccountable loss rate smaller, for Model 4 than for Model 2, even if $\hat{\phi}_{ij}^F < \hat{\phi}_{ij}$ for Model 4. For the 1996 data set, although \hat{f}_i is small (≤ 0.05) for all sites, neither $\hat{\phi}_{ij}$ nor $\hat{\phi}_{ij}^F$ is consistently greater than the other for all sites i and j , and it is hard to predict how the estimates of perceived system survival and unaccountable loss rates will compare between Models 2 and 4. In fact, the estimate of perceived system survival is larger, and the estimate of unaccountable loss is smaller, for Model 4 than for Model 2. The benefit of Model 4 over Model 2 is more accurate estimates in the case of common fallback events.

Table 3.34: Maximum likelihood estimates of parameters from Model 4, the Fallback Terminal Tributary model, with $K = 7$ dams.

Category	Parameter	Estimate	S.E.
Transition	Φ_{R,T_0}	0.0035	0.0020
	Φ_{R,T_0}^F	0.0047	0.0024
	$\Phi_{R,D_{1B}}$	0.8495	0.0124
	$\Phi_{R,D_{1B}}^F$	0.1205	0.0113
	$\phi_{D_{1B},D_{1T}}$	0.9731	0.0079
	$\phi_{D_{1B},D_{1T}}^F$	0.9734	0.0213

¹⁵<http://www.cbr.washington.edu/paramEst/USER/>

Table 3.34 continued

Category	Parameter	Estimate	S.E.
Transition	ϕ_{D_{1T}, T_1}	0.3187	0.0183
	ϕ_{D_{1T}, T_1}^F	0.3166	0.0409
	$\phi_{D_{1T}, D_{2T}}$	0.5940	0.0200
	$\phi_{D_{1T}, D_{2T}}^F$	0.5709	0.0452
	ϕ_{D_{2T}, T_2}	0.1473	0.0182
	ϕ_{D_{2T}, T_2}^F	0.1831	0.0415
	$\phi_{D_{2T}, D_{3T}}$	0.7648	0.0226
	$\phi_{D_{2T}, D_{3T}}^F$	0.7735	0.0462
	ϕ_{D_{3T}, T_3}	0.0960	0.0176
	ϕ_{D_{3T}, T_3}^F	0.1302	0.0384
	$\phi_{D_{3T}, D_{4B}}$	0.8406	0.0223
	$\phi_{D_{3T}, D_{4B}}^F$	0.8126	0.0464
	$\phi_{D_{4B}, D_{4T}}$	0.9858	0.0093
	$\phi_{D_{4B}, D_{4T}}^F$	0.9355	0.0339
	ϕ_{D_{4T}, T_4}	0.5862	0.0327
	ϕ_{D_{4T}, T_4}^F	0.2549	0.0552
	$\phi_{D_{4T}, D_{5B}}$	0.3469	0.0316
	$\phi_{D_{4T}, D_{5B}}^F$	0.6548	0.0610
	$\phi_{D_{5B}, D_{5T}}$	0.9531	0.0269
	$\phi_{D_{5B}, D_{5T}}^F$	0.9774	0.0261
	ϕ_{D_{5T}, T_5}	0.0240	0.0235
	$\phi_{D_{5T}, D_{6B}}$	0.9602	0.0332
	$\phi_{D_{5T}, D_{6B}}^F$	0.9877	0.0446
	$\phi_{D_{6B}, D_{7B}}$	0.9584	0.0304
	$\phi_{D_{6B}, D_{7B}}^F$	0.8909	0.0614
	$\phi_{D_{7B}, D_{7T}}$	0.8995	0.0379
	$\phi_{D_{7B}, D_{7T}}^F$	0.7777	0.0706
	ϕ_{D_{7T}, T_7}	0.8155	0.0502
	ϕ_{D_{7T}, T_7}^F	0.8173	0.0737
Detection	$p_{D_{1B}}$	0.9407	0.0085
	$p_{D_{1T}}$	0.8665	0.0127
	$p_{D_{2T}}$	0.8518	0.0175
	$p_{D_{3T}}$	0.9571	0.0112
	$p_{D_{4B}}$	0.9171	0.0162
	$p_{D_{4T}}$	0.9369	0.0148
	$p_{D_{5B}}$	0.9302	0.0238
	$p_{D_{5T}}$	0.8725	0.0318
	$p_{D_{6B}}$	0.6413	0.0472
	$p_{D_{7B}}$	0.9775	0.0157
	$p_{D_{7T}}$	0.9726	0.0191

Table 3.34 continued

Category	Parameter	Estimate	S.E.
Fallback	$f_{D_{1T}}$	0.0534	0.0098
	$f_{D_{2T}}$	0.0330	0.0094
	$f_{D_{3T}}$	0.0331	0.0109
	$f_{D_{4T}}$	0.0190	0.0095
	$f_{D_{5T}}$	0.0201	0.0201

Maximum likelihood parameter estimates from the reduced data set ($K = 4$ dams [BON, TDA, JD, MCN]) are listed in Table 3.35. The log-likelihood was -3050.9398, with an AIC of 6163.880. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.3412$ ($\widehat{SE} = 0.0170$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2199$ ($\widehat{SE} = 0.0151$). This estimate of perceived system survival is larger than the analogous estimate when all 7 dams are considered because here, the “system” is considerably smaller, including only the first 4 dams: $\hat{S}_{sys,MCN} = 0.3412$ ($\widehat{SE} = 0.0170$) versus $\hat{S}_{sys,LGR} = 0.1075$ ($\widehat{SE} = 0.0108$). Likewise, the estimate of the unaccountable loss rate is smaller for the 4-dam system than for the 7-dam system: $\hat{\mu}_R = 0.2199$ ($\widehat{SE} = 0.0151$) for the 4-dam system, versus $\hat{\mu}_R = 0.2743$ ($\widehat{SE} = 0.0155$) for the 7-dam system. If the 4 dams chosen for the 4-dam analysis had been distributed throughout the larger system, with LGR among the 4 dams chosen, then the estimate of system survival and unaccountable loss rates should have been comparable for the smaller and larger systems.

Table 3.35: Maximum likelihood estimates of parameters from Model 4, the Fallback Terminal Tributary model, with $K = 4$ dams.

Category	Parameter	Estimate	S.E.
Transition	Φ_{R,T_0}	0.0035	0.0020
	Φ_{R,T_0}^F	0.0047	0.0024
	$\Phi_{R,D_{1B}}$	0.8495	0.0124
	$\Phi_{R,D_{1B}}^F$	0.1205	0.0113
	$\phi_{D_{1B},D_{1T}}$	0.9731	0.0079
	$\phi_{D_{1B},D_{1T}}^F$	0.9734	0.0213
	ϕ_{D_{1T},T_1}	0.3187	0.0183
	ϕ_{D_{1T},T_1}^F	0.3166	0.0409
	$\phi_{D_{1T},D_{2T}}$	0.5940	0.02000
	$\phi_{D_{1T},D_{2T}}^F$	0.5709	0.0452

Table 3.35 continued

Category	Parameter	Estimate	S.E.
Transition	ϕ_{D_{2T},T_2}	0.1473	0.0182
	ϕ_{D_{2T},T_2}^F	0.1831	0.0415
	$\phi_{D_{2T},D_{3T}}$	0.7648	0.0226
	$\phi_{D_{2T},D_{3T}}^F$	0.7740	0.0463
	ϕ_{D_{3T},T_3}	0.0961	0.0176
	ϕ_{D_{3T},T_3}^F	0.1299	0.0384
	$\phi_{D_{3T},D_{4B}}$	0.8423	0.0223
	$\phi_{D_{3T},D_{4B}}^F$	0.8033	0.0483
	$\phi_{D_{4B},D_{4T}}$	0.9826	0.0151
	$\phi_{D_{4B},D_{4T}}^F$	0.8699	0.0512
	ϕ_{D_{4T},T_4}	0.5761	0.0332
	ϕ_{D_{4T},T_4}^F	0.2977	0.0629
Detection	$p_{D_{1B}}$	0.9407	0.0085
	$p_{D_{1T}}$	0.8665	0.0127
	$p_{D_{2T}}$	0.8518	0.0175
	$p_{D_{3T}}$	0.9569	0.0113
	$p_{D_{4B}}$	0.9178	0.0164
	$p_{D_{4T}}$	0.9533	0.0172
Fallback	$f_{D_{1T}}$	0.0534	0.0098
	$f_{D_{2T}}$	0.0330	0.0094
	$f_{D_{3T}}$	0.0336	0.0111

3.9 Model 5: Fallback and Tributary Model

Models 5a and 5b incorporate both fallback and tributary visits. As with Model 4, the term “fallback” as used here includes any travel directed downriver between two detection sites, as well as actual falling back over dams. Model 5a accommodates fallback data in the same way as Model 4: fallback is assumed to have a permanent memory effect on subsequent transitions. Like Model 3a, Model 5a assumes that tributary detections have no effect on subsequent transition rates. Model 5b, on the other hand, accommodates tributary detections in the same way as Model 3b: a tributary visit is assumed to affect transitions in the reach following that tributary, but not later transitions. Model 5b accommodates fallback data in a slightly different manner than Model 4; Model 5b assumes only temporary fallback effects, and fallback effects may be extinguished by a tributary visit. Unlike Model 4, Models 5a and 5b allow for both terminal and non-terminal tributary detections. Individuals

are allowed to enter a tributary and then return to the river to continue migration (i.e., individuals may exhibit tributary visiting behavior). Unlike Models 3a and 3b, individuals may also fall back over dams they have already ascended or otherwise swim downriver. While travel during fallback is not explicitly modeled, the data note when a fish has fallen back and reascended (or entered a tributary), and the fish is known as a “fallback fish” thereafter. The model allows for individuals to become fallback fish between tributary and base-of-dam detection sites, and between top-of-dam and tributary detection sites. As in Model 4, individuals may not move from the non-fallback state to the fallback state between the base and top of a given dam. Like Model 3a, Model 5a allows for non-terminal tributary detections, but assumes that tributary behavior in one reach does not affect parameters in later reaches. Model 5b allows for tributary visits in one reach to affect fallback, survival, and tributary entry and exit rates in the following reach. Both Models 5a and 5b allow for fallback to affect survival and tributary entry and exit rates in the following reach. Model 5a extends this fallback effect throughout the remaining reaches, while Model 5b limits the effect to the reach following the fallback event. Thus, Model 5a incorporates a “permanent” memory effect in the same way as Model 4, while Model 5b incorporates a “temporary” memory effect. Also, Model 5a includes a memory effect for fallback but not for tributary visits, and Model 5b includes a memory effect for both fallback and tributary visits. Because of the different types of fallback effect uses, Models 5a and 5b are not nested. However, they use the same data format.

A model that includes the permanent memory effect of Model 4 and the temporary tributary effect of Model 3b is a logical continuation of the sequence of models. This is Model 5c.

3.9.1 Data Description

The data format used for Models 5a and 5b is the same as that used for Model 4, but with non-terminal tributary detections included. The fallback code (*FB*) may appear immediately after any other code in the detection histories, but not immediately before the final detection site (T_K) and not between the base-of-dam and top-of-dam detections for

the same dam (i.e., not between D_{kB} and D_{kT} , $k = 1, \dots, K$). As with Model 4, this last restriction arises from treating each dam's two detection sites as a pair when reducing the data to the post-fallback paths. Any pre-fallback detection at a base-of-dam detection site is ignored in favor of the post-fallback path past the dam.

Each of the detection histories considered in Sections 3.7 and 3.8 is also valid for Models 5a, 5b, and 5c. In addition, detection histories with both fallback and non-terminal tributaries are valid for Models 5a, 5b, and 5c. One example is the detection history $R \text{ } FB \text{ } T_0 \text{ } D_{1B} \text{ } D_{2T} \text{ } T_2 \text{ } D_{3T}$, implying that the fish visited tributary T_0 but fell back between release and reaching T_0 , then ascended dams 1 and 2, visited tributary T_2 , ascended dam 3, and was not detected above dam 3. A second example of a detection history is $R \text{ } D_{1B} \text{ } T_1 \text{ } FB \text{ } D_{2B} \text{ } T_3$. A fish with this detection history ascended dam 1 directly upon release, visited tributary T_1 , continued to ascend dam 2 after falling back between T_1 and dam 2, and finally entered tributary T_3 and was not detected again.

3.9.2 Model 5a: Fallback and Memory-Free Tributary Model

Model 5a assumes no effect of tributary behavior in reach k on survival, detection, or tributary parameters in reaches $k+1, \dots, K$ or in ascending dam $k+1$, for $k = 1, \dots, K-1$.

3.9.2.1 Notation

The same basic notation used in Model 4 may be used here. The index i indicates a site from which a transition is made, and the index j indicates a site to which a transition is made. The transition parameters ϕ_{ij} and ϕ_{ij}^F represent the probability of the transition (survival and movement) from site i to site j for fish who are and are not fallback fish, respectively:

$$\begin{aligned}\phi_{ij} &= Pr[\text{Survive and move from site } i \text{ to site } j \mid \text{Reach site } i, \text{ non-fallback fish}]; \\ \phi_{ij}^F &= Pr[\text{Survive and move from site } i \text{ to site } j \mid \text{Reach site } i, \text{ fallback fish}];\end{aligned}\quad (3.53)$$

where $i = R, T_0, D_{1B}, D_{1T}, T_1, \dots, T_{K-1}, D_{KB}, D_{KT}$, and where

$$j = \begin{cases} D_{1B} \text{ or } T_0 & \text{for } i = R; \\ D_{kT} & \text{for } i = D_{kB}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = D_{kT}, k = 1, \dots, K-1; \\ T_k & \text{for } i = D_{kT}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = T_k, k = 0, \dots, K-1. \end{cases} \quad (3.54)$$

Detection at site i occurs with probability p_i , conditional on reaching that site. The parameter $q_i = 1 - p_i$ is the probability of not being detected at site i , conditional on reaching that site. Detection rates in the tributaries are assumed to be 100%, i.e., $p_{T_k} = 1$ for $k = 0, \dots, K$. Detection parameters are the same regardless of previous fallback or tributary visiting behavior. As with Model 4, let f_i represent the probability of a non-fallback fish becoming a fallback fish immediately after passing site i . It is assumed that fallback occurs before the transition to the next observed site in the (simplified) detection history. The exception is for $i = D_{kB}$, a base-of-dam site, in which case it is assumed that the fish becomes a fallback fish after passing the corresponding top-of-dam site (D_{kT}), whether or not it is detected there.

The probability of not being detected after site i , given having reached that site as a fallback fish, is χ_i^F :

$$\begin{aligned} \chi_{D_{kB}}^F &= 1 - \phi_{D_{kB}, D_{kT}}^F + \phi_{D_{kB}, D_{kT}}^F q_{D_{kT}} \chi_{D_{kT}}^F, & k = 1, \dots, K; \\ \chi_{D_{kT}}^F &= 1 - \phi_{D_{kT}, T_k}^F - \phi_{D_{kT}, D_{k+1,B}}^F + \phi_{D_{kT}, D_{k+1,B}}^F q_{D_{k+1,B}} \chi_{D_{k+1,B}}^F, & k = 1, \dots, K-1; \\ \chi_{D_{KT}}^F &= 1 - \phi_{D_{KT}, T_K}^F; \\ \chi_{T_k}^F &= 1 - \phi_{T_k, D_{k+1,B}}^F + \phi_{T_k, D_{k+1,B}}^F q_{D_{k+1,B}} \chi_{D_{k+1,B}}^F, & k = 0, \dots, K-1. \end{aligned} \quad (3.55)$$

The probability of not being detected after site i , given having reached that site as a non-fallback fish, is χ_i :

$$\begin{aligned}
\chi_R &= 1 - \Phi_{R,T_0} - \Phi_{R,T_0}^F - \Phi_{R,D_{1B}}(1 - q_{D_{1B}}\chi_{D_{1B}}) \\
&\quad - \Phi_{R,D_{1B}}^F \{1 - q_{D_{1B}}(1 - \phi_{D_{1B},D_{1T}}^F p_{D_{1T}})\}; \\
\chi_{D_{kB}} &= 1 - \phi_{D_{kB},D_{kT}} + \phi_{D_{kB},D_{kT}} q_{D_{kT}} \chi_{D_{kT}}, \quad k = 1, \dots, K; \\
\chi_{D_{kT}} &= 1 - (1 - f_{D_{kT}}) \{ \phi_{D_{kT},T_k} + \phi_{D_{kT},D_{k+1,B}}(1 - q_{D_{k+1,B}}\chi_{D_{k+1,B}}) \} \\
&\quad - f_{D_{kT}} \phi_{D_{kT},T_k}^F \\
&\quad - f_{D_{kT}} \phi_{D_{kT},D_{k+1,B}}^F \left\{ 1 - q_{D_{k+1,B}}(1 - \phi_{D_{k+1,B},D_{k+1,T}}^F p_{D_{k+1,T}}) \right\}, \quad k = 1, \dots, K-1; \\
\chi_{D_{KT}} &= 1 - \phi_{D_{KT},T_K}; \\
\chi_{T_k} &= 1 - (1 - f_{T_k}) \phi_{T_k,D_{k+1,B}}(1 - q_{D_{k+1,B}}\chi_{D_{k+1,B}}) \\
&\quad - f_{T_k} \phi_{T_k,D_{k+1,B}}^F \left\{ 1 - q_{D_{k+1,B}}(1 - \phi_{D_{k+1,B},D_{k+1,T}}^F p_{D_{k+1,T}}) \right\}, \quad k = 0, \dots, K-1.
\end{aligned} \tag{3.56}$$

The parameters used in Model 5a are listed in Table 3.36.

Table 3.36: Parameters used in Model 5a, the Fallback and Memory-Free Tributary Model. The number of dams is K .

Parameter	Definition
Φ_{R,T_0}	Probability of surviving and moving from the release point directly to site T_0 without becoming a fallback fish;
$\Phi_{R,D_{1B}}$	Probability of surviving and moving from the release point directly to site D_{1B} without becoming a fallback fish;
Φ_{R,T_0}^F	Probability of surviving, becoming a fallback fish, and then moving from the release point directly to site T_0 ;
$\Phi_{R,D_{1B}}^F$	Probability of surviving, becoming a fallback fish, and then moving from the release point directly to site D_{1B} ;
ϕ_{ij}	Probability of surviving and moving from site i to site j , given having reached site i and a non-fallback fish, for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$ and j is as described in Equation (3.54);
ϕ_{ij}^F	Probability of surviving and moving from site i to site j , given having reached site i and a fallback fish, for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$ and j is as described in Equation (3.54);
p_i	Probability of being detected at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$;

Table 3.36 continued

Parameter	Definition
q_i	Probability of avoiding detection at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$; $= 1 - p_i$;
f_i	Probability of becoming a fallback fish upon leaving site i , given having reached site i as a non-fallback fish, for $i = T_0, D_{1T}, T_2, D_{2T}, \dots, T_{K-1}$;
χ_i	Probability of not being detected after site i , given having reached site i as a non-fallback fish, for $i = R, T_0, D_{1B}, \dots, D_{KT}$;
χ_i^F	Probability of not being detected after site i , given having reached site i as a fallback fish, for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$.

The parameters in Table 3.36 can be used to express the probabilities of the possible detection histories. For example, the probability of observing the detection history $R \text{ FB } T_0 \text{ } D_{1B} \text{ } D_{2T} \text{ } T_2 \text{ } D_{3T}$ is

$$\begin{aligned} Pr[R \text{ FB } T_0 \text{ } D_{1B} \text{ } D_{2T} \text{ } T_2 \text{ } D_{3T}] &= \Phi_{R,T_0}^F \phi_{T_0,D_{1B}}^F p_{D_{1B}} \phi_{D_{1B},D_{1T}}^F q_{D_{1T}} \phi_{D_{1T},D_{2B}}^F q_{D_{2B}} \phi_{D_{2B},D_{2T}}^F \\ &\times p_{D_{2T}} \phi_{D_{2T},T_2}^F \phi_{T_2,D_{3B}}^F q_{D_{3B}} \phi_{D_{3B},D_{3T}}^F p_{D_{3T}} \chi_{D_{3T}}^F. \end{aligned} \quad (3.57)$$

The probability of observing the detection history $R \text{ } D_{1B} \text{ } T_1 \text{ FB } D_{2B} \text{ } T_3$ is

$$\begin{aligned} Pr[R \text{ } D_{1B} \text{ } T_1 \text{ FB } D_{2B} \text{ } T_3] &= \Phi_{R,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}} q_{D_{1T}} (1 - f_{D_{1T}}) \phi_{D_{1T},T_1} f_{T_1} \phi_{T_1,D_{2B}}^F p_{D_{2B}} \\ &\times \phi_{D_{2B},D_{2T}}^F q_{D_{2T}} \phi_{D_{2T},D_{3B}}^F q_{D_{3B}} \phi_{D_{3B},D_{3T}}^F q_{D_{3T}} \phi_{D_{3T},T_3}^F \chi_{T_3}^F. \end{aligned} \quad (3.58)$$

The remaining detection histories can be expressed similarly.

3.9.2.2 Likelihood

The summary statistics used in the likelihood are similar to those used for Model 4: the number of non-fallback and fallback fish detected at each site (a_i and a_i^F , respectively); the number of fish detected at a site as non-fallback fish that are next detected as either non-fallback (b_i) or fallback (h_i) fish; and the number of fish detected at site i as fallback fish that are detected upstream (b_i^F). For Model 5, the statistics b_i , h_i , and b_i^F may be non-zero

for tributary sites as well as dam sites. Because fish may enter the post-fallback state upon leaving tributary sites as well as the release site and the top-of-dam sites, a modification of the statistic t_k from Model 4 is needed for Model 5a: define d_i to be the number of fish that are detected as fallback fish for the first time upon leaving site i , where i can be either a tributary site (T_k) or a top-of-dam site (D_{kT}). The statistic d_{T_k} is the number of fish detected at site T_k as non-fallback fish and next detected at either site $D_{k+1,B}$ or $D_{k+1,T}$ as fallback fish. The statistic $d_{D_{kT}}$ is the number of fish detected as fallback fish for the first time at sites T_k , $D_{k+1,B}$, or $D_{k+1,T}$, without being detected as non-fallback fish at site T_k . Also useful are the statistics g_i and g_i^F , representing the number of non-fallback and fallback fish, respectively, detected upstream of site i . These statistics can be expressed in terms of the other summary statistics as follows:

$$\begin{aligned}
g_R &= b_R + h_R; \\
g_R^F &= 0; \\
g_{T_0} &= g_R + b_{T_0} + h_{T_0} - a_{T_0} - d_R; \\
g_{T_0}^F &= b_{T_0}^F + d_R - a_{T_0}^F; \\
g_{T_k} &= g_{D_{kT}} + b_{T_k} + h_{T_k} - a_{T_k} - d_{D_{kT}}, & k = 1, \dots, K-1; \\
g_{T_k}^F &= g_{D_{kT}}^F + d_{D_{kT}} + b_{T_k}^F - a_{T_k}^F, & k = 1, \dots, K-1; \\
g_{D_{kB}} &= g_{T_{k-1}} - d_{T_{k-1}} + b_{D_{kB}} + h_{D_{kB}} - a_{D_{kB}}, & k = 1, \dots, K; \\
g_{D_{kB}}^F &= g_{T_{k-1}}^F + d_{T_{k-1}} + b_{D_{kB}}^F - a_{D_{kB}}^F, & k = 1, \dots, K; \\
g_{D_{kT}} &= g_{D_{kB}} + b_{D_{kT}} + h_{D_{kT}} - a_{D_{kT}}, & k = 1, \dots, K; \\
g_{D_{kT}}^F &= g_{D_{kB}}^F + b_{D_{kT}}^F - a_{D_{kT}}^F, & k = 1, \dots, K.
\end{aligned}$$

The summary statistics for Model 5a are listed in Table 3.37, and the minimal sufficient statistics are listed in Table 3.38. The full model has $12K + 1$ minimal sufficient statistics, and an equal number of parameters.

Table 3.37: Summary statistics for Model 5a, the Fallback and Memory-Free Tributary model. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i as non-fallback fish, for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}, T_K$;
a_i^F	Number of fish detected as fallback fish at site i , for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}, T_K$;
b_R	Number of fish first detected after the initial release as non-fallback fish;
b_i	Number of fish detected at site i as non-fallback fish and next detected upstream as non-fallback fish, for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$;
b_i^F	Number of fish detected at site i as fallback fish and detected upstream (as fallback fish), for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$;
h_R	Number of fish first detected after the initial release as fallback fish;
h_i	Number of fish detected at site i as non-fallback fish and next detected upstream as fallback fish, for $i = T_0, D_{1B}, D_{1T}, \dots, T_{K-1}$;
d_R	Number of fish detected as fallback fish for the first time at site T_0, D_{1B} , or D_{1T} , without being previously detected at site T_0 as non-fallback fish;
d_{T_k}	Number of fish detected at site T_k as non-fallback fish and next detected at site $D_{k+1,B}$ or $D_{k+1,T}$ as fallback fish, for $k = 0, \dots, K-1$;
$d_{D_{kT}}$	Number of fish detected as fallback fish for the first time at site $T_k, D_{k+1,B}$, or $D_{k+1,T}$ and not previously detected as non-fallback fish at site T_k , for $k = 1, \dots, K-1$;
g_i	Number of fish detected after site i that were not fallback fish at site i , for $i = R, T_0, D_{1B}, D_{1T}, \dots, D_{KT}$;
g_i^F	Number of fish detected after site i that were fallback fish at site i , for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$.

Table 3.38: Minimal sufficient statistics for Model 5a, the Fallback and Memory-Free Tributary model. The number of dams is K .

Statistic	Definition
a_{T_k}	Number of fish detected at site T_k as non-fallback fish, for $k = 0, \dots, K-1$;
$a_{T_k}^F$	Number of fish detected at site T_k as fallback fish, for $k = 0, \dots, K-1$;
$b_R + h_R$	Number of fish detected after the initial release;
d_R	Number of fish detected as fallback fish for the first time at site T_0, D_{1B} , or D_{1T} , without being previously detected at site T_0 as non-fallback fish;

Table 3.38 continued

Statistic	Definition
d_{T_k}	Number of fish detected at site T_k as non-fallback fish and next detected at site $D_{k+1,B}$ or $D_{k+1,T}$ as fallback fish, for $k = 0, \dots, K-1$;
$d_{D_{kT}}$	Number of fish detected as fallback fish for the first time at site T_k , $D_{k+1,B}$, or $D_{k+1,T}$ and not previously detected as non-fallback fish at site T_k , for $k = 1, \dots, K-1$;
$b_{T_k} + h_{T_k}$	Number of fish detected as non-fallback fish at site T_k and detected later upstream, for $k = 0, \dots, K-1$;
$b_{T_k}^F$	Number of fish detected as fallback fish at site T_k and detected later upstream, for $k = 0, \dots, K-1$;
$a_{D_{kB}} - b_{D_{kB}} - h_{D_{kB}}$ for	Number of non-fallback fish detected for last time at site D_{kB} , $k = 1, \dots, K$;
$a_{D_{kT}} - b_{D_{kT}} - h_{D_{kT}}$ for	Number of non-fallback fish detected for last time at site D_{kT} , $k = 1, \dots, K$;
$a_{D_{kB}}^F - b_{D_{kB}}^F$	Number of fallback fish detected for last time at site D_{kB} , for $k = 1, \dots, K$;
$a_{D_{kT}}^F - b_{D_{kT}}^F$	Number of fallback fish detected for last time at site D_{kT} , for $k = 1, \dots, K$;
$a_{D_{kB}} + a_{D_{kB}}^F$	Number of fish detected at site D_{kB} , $k = 1, \dots, K$; for
$a_{D_{kT}} + a_{D_{kT}}^F$	Number of fish detected at site D_{kT} , $k = 1, \dots, K$.

The likelihood for Model 5a can be expressed as follows:

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \Phi_{R,T_0}^{a_{T_0}} \Phi_{R,D_{1B}}^{g_R-d_R-a_{T_0}} (\Phi_{R,T_0}^F)^{a_{T_0}^F} (\Phi_{R,D_{1B}}^F)^{d_R-a_{T_0}^F} \prod_{k=0}^{K-1} \left[\chi_{T_k}^{a_{T_k}-b_{T_k}-h_{T_k}} \right. \\
& \times (\chi_{T_k}^F)^{a_{T_k}^F-b_{T_k}^F} f_{T_k}^{d_{T_k}} \left\{ (1-f_{T_k}) \phi_{T_k,D_{k+1,B}} \right\}^{b_{T_k}+h_{T_k}-d_{T_k}} (\phi_{T_k,D_{k+1,B}}^F)^{b_{T_k}^F+d_{T_k}^F} \Big] \\
& \times \prod_{k=1}^K \left\{ \phi_{D_{kB},D_{kT}}^{g_{D_{kB}},D_{kT}} (\phi_{D_{kB},D_{kT}}^F)^{g_{D_{kB}}^F,D_{kT}} \phi_{D_{kT},T_k}^{a_{T_k}} (\phi_{D_{kT},T_k}^F)^{a_{T_k}^F} p_{D_{kB}}^{a_{D_{kB}}+a_{D_{kB}}^F} \right. \\
& \times q_{D_{kB}}^{g_{T_{k-1}}+g_{T_{k-1}}^F-a_{D_{kB}}-a_{D_{kB}}^F} p_{D_{kT}}^{a_{D_{kT}}+a_{D_{kT}}^F} q_{D_{kT}}^{g_{D_{kB}}+g_{D_{kB}}^F-a_{D_{kT}}-a_{D_{kT}}^F} \\
& \times \chi_{D_{kB}}^{a_{D_{kB}}-b_{D_{kB}}-h_{D_{kB}}} (\chi_{D_{kB}}^F)^{a_{D_{kB}}^F-b_{D_{kB}}^F} \chi_{D_{kT}}^{a_{D_{kT}}-b_{D_{kT}}-h_{D_{kT}}} (\chi_{D_{kT}}^F)^{a_{D_{kT}}^F-b_{D_{kT}}^F} \Big\} \\
& \times \prod_{k=0}^{K-1} \left\{ f_{D_{kT}}^{d_{D_{kT}}} (1-f_{D_{kT}})^{g_{D_{kT}}-d_{D_{kT}}} \phi_{D_{kT},D_{k+1,B}}^{g_{D_{kT}}-d_{D_{kT}}-a_{T_k}} (\phi_{D_{kT},D_{k+1,B}}^F)^{g_{D_{kT}}^F+d_{D_{kT}}^F-a_{T_k}^F} \right\},
\end{aligned} \tag{3.59}$$

where K is the number of dams and N is the size of the release group. Equation (3.59) may be tailored to a particular data set by specifying K , removing any extraneous parameters, and renaming parameters according to observed detections, if necessary. This is done for the 1996 Chinook salmon data set in the next section.

Initial values for the optimization routine used to fit Equation (3.59) to data may be found from the initial values used for Models 3a and 4. For parameters common to both Models 5a and 4, the initial values from Model 4 may be used. For transition parameters from tributaries ($\phi_{T_k, D_{k+1}, B}$ and $\phi_{T_k, D_{k+1}, B}^F$), the initial value for $\phi_{T_k, D_{k+1}, B}$ from Model 3a may be used. Initial values for fallback parameters from tributaries (f_{T_k}) should be set to low values (say, 0.01) or to the ratio d_{T_k}/a_{T_k} .

3.9.2.3 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival, is S_{sys} , defined as follows:

$$S_{sys} = \eta_R,$$

where

$$\eta_R = \Phi_{R, T_0} \eta_{T_0} + \Phi_{R, T_0}^F \eta_{T_0}^F + \Phi_{R, D_{1B}} \phi_{D_{1B}, D_{1T}} \eta_{D_{1T}} + \Phi_{R, D_{1B}}^F \phi_{D_{1B}, D_{1T}}^F \eta_{D_{1T}}^F,$$

with

$$\begin{aligned} \eta_{D_{kT}} &= (1 - f_{D_{kT}}) \left(\phi_{D_{kT}, T_k} \eta_{T_k} + \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T} \right) \\ &\quad + f_{D_{kT}} \left(\phi_{D_{kT}, T_k}^F \eta_{T_k}^F + \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F \right), \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}} &= 1; \\ \eta_{D_{kT}}^F &= \phi_{D_{kT}, T_k}^F \eta_{T_k}^F + \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F, \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}}^F &= 1; \end{aligned} \tag{3.60}$$

$$\begin{aligned}
\eta_{T_k} &= (1 - f_{T_k})\phi_{T_k, D_{k+1}, B}\phi_{D_{k+1}, B, D_{k+1}, T}\eta_{D_{k+1}, T} \\
&\quad + f_{T_k}\phi_{T_k, D_{k+1}, B}^F\phi_{D_{k+1}, B, D_{k+1}, T}^F\eta_{D_{k+1}, T}^F, \quad k = 0, \dots, K-1; \\
\eta_{T_k}^F &= \phi_{T_k, D_{k+1}, B}^F\phi_{D_{k+1}, B, D_{k+1}, T}^F\eta_{D_{k+1}, T}^F, \quad k = 0, \dots, K-1.
\end{aligned}$$

The variance estimator of \hat{S}_{sys} is defined in Appendix B.

Models 5a and 5b incorporate both fallback and tributary detections, including non-terminal tributary detections. Non-fallback fish may or may not become post-fallback fish upon returning from a tributary, and this possibility must be accounted for in defining unaccountable loss. If it is assumed that survival from each tributary to the next dam upriver is 100% (as in Models 3a and 3b), then for Model 5a, the probability of a non-fallback fish returning to the river from tributary T_k is $(1 - f_{T_k})\phi_{T_k, D_{k+1}, B} + f_{T_k}\phi_{T_k, D_{k+1}, B}^F$. The comparable probability for fish that entered tributary T_k as post-fallback fish is $\phi_{T_k, D_{k+1}, B}^F$. The probability of unaccountable loss from the release is defined as follows for Model 5a:

$$\begin{aligned}
\mu_R &= 1 - \Phi_{R, T_0}(1 - \mu_{T_0}) - \Phi_{R, T_0}^F(1 - \mu_{T_0}^F) - \Phi_{R, D_{1B}}\phi_{D_{1B}, D_{1T}}(1 - \mu_{D_{1T}}) \\
&\quad - \Phi_{R, D_{1B}}^F\phi_{D_{1B}, D_{1T}}^F(1 - \mu_{D_{1T}}^F), \quad (3.61)
\end{aligned}$$

where

$$\begin{aligned}
1 - \mu_{T_k} &= 1 - (1 - f_{T_k})\phi_{T_k, D_{k+1}, B}\{1 - \phi_{D_{k+1}, B, D_{k+1}, T}(1 - \mu_{D_{k+1}, T})\} \\
&\quad - f_{T_k}\phi_{T_k, D_{k+1}, B}^F\{1 - \phi_{D_{k+1}, B, D_{k+1}, T}^F(1 - \mu_{D_{k+1}, T}^F)\}, \quad k = 0, \dots, K-1; \\
1 - \mu_{T_k}^F &= 1 - \phi_{T_k, D_{k+1}, B}^F + \phi_{T_k, D_{k+1}, B}^F\phi_{D_{k+1}, B, D_{k+1}, T}^F(1 - \mu_{D_{k+1}, T}^F), \quad k = 0, \dots, K-1; \\
1 - \mu_{D_{kT}} &= (1 - f_{D_{kT}})\phi_{D_{kT}, T_k}(1 - \mu_{T_k}) + f_{D_{kT}}\phi_{D_{kT}, T_k}^F(1 - \mu_{T_k}^F) \\
&\quad + (1 - f_{D_{kT}})\phi_{D_{kT}, D_{k+1}, B}\phi_{D_{k+1}, B, D_{k+1}, T}(1 - \mu_{D_{k+1}, T}) \\
&\quad + f_{D_{kT}}\phi_{D_{kT}, D_{k+1}, B}^F\phi_{D_{k+1}, B, D_{k+1}, T}^F(1 - \mu_{D_{k+1}, T}^F), \quad k = 1, \dots, K-1; \\
1 - \mu_{D_{kT}} &= 1, \quad k = K; \\
1 - \mu_{D_{kT}}^F &= \phi_{D_{kT}, T_k}^F(1 - \mu_{T_k}^F) + \phi_{D_{kT}, D_{k+1}, B}^F\phi_{D_{k+1}, B, D_{k+1}, T}^F(1 - \mu_{D_{k+1}, T}^F), \quad k = 1, \dots, K-1;
\end{aligned}$$

$$1 - \mu_{D_{kT}}^F = 1,$$

$$k = K.$$

The variance estimator of $\hat{\mu}_R$ is defined in Appendix B.

3.9.2.4 1996 Chinook Data Set

The summary statistics for the full 1996 Chinook salmon data set ($K = 7$) are given in Table 3.39. Table 3.39 shows that no fish were detected at sites D_{2B} , D_{3B} , D_{6T} , or T_6 . With no detections at these sites, the transition parameters corresponding to these sites cannot be estimated. Instead, those transition parameters are replaced with the following:

$$\begin{aligned} \phi_{D_{1T}, D_{2T}} &= \phi_{D_{1T}, D_{2B}} \phi_{D_{2B}, D_{2T}} & \phi_{D_{1T}, D_{2T}}^F &= \phi_{D_{1T}, D_{2B}}^F \phi_{D_{2B}, D_{2T}}^F \\ \phi_{T_1, D_{2T}} &= \phi_{T_1, D_{2B}} \phi_{D_{2B}, D_{2T}} & \phi_{T_1, D_{2T}}^F &= \phi_{T_1, D_{2B}}^F \phi_{D_{2B}, D_{2T}}^F \\ \phi_{D_{2T}, D_{3T}} &= \phi_{D_{2T}, D_{3B}} \phi_{D_{3B}, D_{3T}} & \phi_{D_{2T}, D_{3T}}^F &= \phi_{D_{2T}, D_{3B}}^F \phi_{D_{3B}, D_{3T}}^F \\ \phi_{T_2, D_{3T}} &= \phi_{T_2, D_{3B}} \phi_{D_{3B}, D_{3T}} & \phi_{T_2, D_{3T}}^F &= \phi_{T_2, D_{3B}}^F \phi_{D_{3B}, D_{3T}}^F \\ \phi_{D_{6B}, D_{7B}} &= \phi_{D_{6B}, D_{6T}} \phi_{D_{6T}, D_{7B}} & \phi_{D_{6B}, D_{7B}}^F &= \phi_{D_{6B}, D_{6T}}^F \phi_{D_{6T}, D_{7B}}^F. \end{aligned}$$

The fallback parameter $f_{D_{6T}}$ should be replaced with $f_{D_{6B}}$. Table 3.39 also shows that no fish detected at sites T_0 , T_1 , T_2 , T_4 , T_5 , or D_{6T} (equivalently, D_{6B}) as non-fallback fish were detected as fallback fish at the next upstream dam sites (i.e., $d_{T_0} = d_{T_1} = d_{T_2} = d_{T_4} = d_{T_5} = d_{D_{6T}} = 0$). The parameters f_{T_0} , f_{T_1} , f_{T_2} , f_{T_4} , f_{T_5} , and $f_{D_{6T}}$ must be fixed to 0. No fish detected at T_4 were detected again upstream ($b_{T_4} + h_{T_4} = b_{T_4}^F = 0$), and no fish detected as fallback fish at site T_0 were detected again upstream ($b_{T_0}^F = 0$). Thus, the parameters $\phi_{T_0, D_{1B}}^F$, $\phi_{T_4, D_{5B}}$, and $\phi_{T_4, D_{5B}}^F$ must be fixed to 0, giving $\chi_{T_4} = \chi_{T_4}^F = \chi_{T_0}^F = 1$. Finally, all non-fallback fish detected at site T_5 were detected again upstream ($a_{T_5} - b_{T_5} - h_{T_5} = 0$), indicating that $\phi_{T_5, D_{6B}}$ should be fixed to 1. This gives $\chi_{T_5} = q_{D_{6B}} \chi_{D_{6B}}$. Other transition parameters as described in Table 3.36 may be estimated for $K = 7$.

The likelihood for Model 5a, tailored to the 1996 Chinook Salmon data set, is

$$\begin{aligned}
L \propto & \chi^{N-g_R} \Phi_{R,T_0}^{a_{T_0}} \Phi_{R,D_{1B}}^{g_R-d_r-a_{T_0}} (\Phi_{R,T_0}^F)^{a_{T_0}^F} (\Phi_{R,D_{1B}}^F)^{d_R-a_{T_0}^F} \chi_{T_0}^{a_{T_0}-b_{T_0}-h_{T_0}} \phi_{T_0,D_{1B}}^{b_{T_0}+h_{T_0}} p_{D_{1B}}^{a_{D_{1B}}+a_{D_{1B}}^F} \\
& \times q_{D_{1B}}^{g_{T_0}+g_{T_0}^F-a_{D_{1B}}-a_{D_{1B}}^F} \chi_{D_{1B}}^{a_{D_{1B}}-b_{D_{1B}}-h_{D_{1B}}} (\chi_{D_{1B}}^F)^{a_{D_{1B}}^F-b_{D_{1B}}^F} \phi_{D_{1B},D_{1T}}^{g_{D_{1B}}} (\phi_{D_{1B},D_{1T}}^F)^{g_{D_{1B}}^F} \\
& \times p_{D_{1T}}^{a_{D_{1T}}+a_{D_{1T}}^F} q_{D_{1T}}^{g_{D_{1B}}+g_{D_{1B}}^F-a_{D_{1T}}-a_{D_{1T}}^F} \chi_{D_{1T}}^{a_{D_{1T}}-b_{D_{1T}}-h_{D_{1T}}} (\chi_{D_{1T}}^F)^{a_{D_{1T}}^F-b_{D_{1T}}^F} f_{D_{1T}}^{d_{D_{1T}}} \\
& \times (1-f_{D_{1T}})^{g_{D_{1T}}-d_{D_{1T}}} \phi_{D_{1T},T_1}^{a_{T_1}} (\phi_{D_{1T},T_1}^F)^{a_{T_1}^F} \phi_{D_{1T},D_{2T}}^{g_{D_{1T}}-d_{D_{1T}}-a_{T_1}} (\phi_{D_{1T},D_{2T}}^F)^{g_{D_{1T}}^F+d_{D_{1T}}-a_{T_1}^F} \\
& \times \chi_{T_1}^{a_{T_1}-b_{T_1}-h_{T_1}} (\chi_{T_1}^F)^{a_{T_1}^F-b_{T_1}^F} \phi_{T_1,D_{2T}}^{b_{T_1}+h_{T_1}} (\phi_{T_1,D_{2T}}^F)^{b_{T_1}^F} p_{D_{2T}}^{a_{D_{2T}}+a_{D_{2T}}^F} q_{D_{2T}}^{g_{T_1}+g_{T_1}^F-a_{D_{2T}}-a_{D_{2T}}^F} \\
& \times \chi_{D_{2T}}^{a_{D_{2T}}-b_{D_{2T}}-h_{D_{2T}}} (\chi_{D_{2T}}^F)^{a_{D_{2T}}^F-b_{D_{2T}}^F} f_{D_{2T}}^{d_{D_{2T}}} (1-f_{D_{2T}})^{g_{D_{2T}}-d_{D_{2T}}} \phi_{D_{2T},T_2}^{a_{T_2}} (\phi_{D_{2T},T_2}^F)^{a_{T_2}^F} \\
& \times \phi_{D_{2T},D_{3T}}^{g_{D_{2T}}-d_{D_{2T}}-a_{T_2}} (\phi_{D_{2T},D_{3T}}^F)^{g_{D_{2T}}^F+d_{D_{2T}}-a_{T_2}^F} \chi_{T_2}^{a_{T_2}-b_{T_2}-h_{T_2}} (\chi_{T_2}^F)^{a_{T_2}^F-b_{T_2}^F} \phi_{T_2,D_{3T}}^{b_{T_2}+h_{T_2}} \\
& \times (\phi_{T_2,D_{3T}}^F)^{b_{T_2}^F} p_{D_{3T}}^{a_{D_{3T}}+a_{D_{3T}}^F} q_{D_{3T}}^{g_{T_2}+g_{T_2}^F-a_{D_{3T}}-a_{D_{3T}}^F} \chi_{D_{3T}}^{a_{D_{3T}}-b_{D_{3T}}-h_{D_{3T}}} (\chi_{D_{3T}}^F)^{a_{D_{3T}}^F-b_{D_{3T}}^F} f_{D_{3T}}^{d_{D_{3T}}} \\
& \times (1-f_{D_{3T}})^{g_{D_{3T}}-d_{D_{3T}}} \phi_{D_{3T},T_3}^{a_{T_3}} (\phi_{D_{3T},T_3}^F)^{a_{T_3}^F} \phi_{D_{3T},D_{4B}}^{g_{D_{3T}}-d_{D_{3T}}-a_{T_3}} (\phi_{D_{3T},D_{4B}}^F)^{g_{D_{3T}}^F+d_{D_{3T}}-a_{T_3}^F} \\
& \times \chi_{T_3}^{a_{T_3}-b_{T_3}-h_{T_3}} (\chi_{T_3}^F)^{a_{T_3}^F-b_{T_3}^F} f_{T_3}^{d_{T_3}} \{(1-f_{T_3})\phi_{T_3,D_{4B}}\}^{b_{T_3}+h_{T_3}-d_{T_3}} (\phi_{T_3,D_{4B}}^F)^{b_{T_3}^F+d_{T_3}} \\
& \times p_{D_{4B}}^{a_{D_{4B}}+a_{D_{4B}}^F} q_{D_{4B}}^{g_{T_3}+g_{T_3}^F-a_{D_{4B}}-a_{D_{4B}}^F} \chi_{D_{4B}}^{a_{D_{4B}}-b_{D_{4B}}-h_{D_{4B}}} (\chi_{D_{4B}}^F)^{a_{D_{4B}}^F-b_{D_{4B}}^F} \phi_{D_{4B},D_{4T}}^{g_{D_{4B}}} \\
& \times (\phi_{D_{4B},D_{4T}}^F)^{g_{D_{4B}}^F} p_{D_{4T}}^{a_{D_{4T}}+a_{D_{4T}}^F} q_{D_{4T}}^{g_{D_{4B}}+g_{D_{4B}}^F-a_{D_{4T}}-a_{D_{4T}}^F} \chi_{D_{4T}}^{a_{D_{4T}}-b_{D_{4T}}-h_{D_{4T}}} (\chi_{D_{4T}}^F)^{a_{D_{4T}}^F-b_{D_{4T}}^F} \\
& \times f_{D_{4T}}^{d_{D_{4T}}} (1-f_{D_{4T}})^{g_{D_{4T}}-d_{D_{4T}}} \phi_{D_{4T},T_4}^{a_{T_4}} (\phi_{D_{4T},T_4}^F)^{a_{T_4}^F} \phi_{D_{4T},D_{5B}}^{g_{D_{4T}}-d_{D_{4T}}-a_{T_4}} \\
& \times (\phi_{D_{4T},D_{5B}}^F)^{g_{D_{4T}}^F+d_{D_{4T}}-a_{T_4}^F} p_{D_{5B}}^{a_{D_{5B}}+a_{D_{5B}}^F} q_{D_{5B}}^{g_{T_4}+g_{T_4}^F-a_{D_{5B}}-a_{D_{5B}}^F} \chi_{D_{5B}}^{a_{D_{5B}}-b_{D_{5B}}-h_{D_{5B}}} \\
& \times (\chi_{D_{5B}}^F)^{a_{D_{5B}}^F-b_{D_{5B}}^F} \phi_{D_{5B},D_{5T}}^{g_{D_{5B}}} (\phi_{D_{5B},D_{5T}}^F)^{g_{D_{5B}}^F} p_{D_{5T}}^{a_{D_{5T}}+a_{D_{5T}}^F} q_{D_{5T}}^{g_{D_{5B}}+g_{D_{5B}}^F-a_{D_{5T}}-a_{D_{5T}}^F} \\
& \times \chi_{D_{5T}}^{a_{D_{5T}}-b_{D_{5T}}-h_{D_{5T}}} (\chi_{D_{5T}}^F)^{a_{D_{5T}}^F-b_{D_{5T}}^F} f_{D_{5T}}^{d_{D_{5T}}} (1-f_{D_{5T}})^{g_{D_{5T}}-d_{D_{5T}}} \phi_{D_{5T},T_5}^{a_{T_5}} (\phi_{D_{5T},T_5}^F)^{a_{T_5}^F} \\
& \times \phi_{D_{5T},D_{6B}}^{g_{D_{5T}}-d_{D_{5T}}-a_{T_5}} (\phi_{D_{5T},D_{6B}}^F)^{g_{D_{5T}}^F+d_{D_{5T}}-a_{T_5}^F} (\chi_{T_5}^F)^{a_{T_5}^F-b_{T_5}^F} (\phi_{T_5,D_{6B}}^F)^{b_{T_5}^F} p_{D_{6B}}^{a_{D_{6B}}+a_{D_{6B}}^F} \\
& \times q_{D_{6B}}^{g_{T_5}+g_{T_5}^F-a_{D_{6B}}-a_{D_{6B}}^F} \chi_{D_{6B}}^{a_{D_{6B}}-b_{D_{6B}}-h_{D_{6B}}} (\chi_{D_{6B}}^F)^{a_{D_{6B}}^F-b_{D_{6B}}^F} \phi_{D_{6B},D_{7B}}^{g_{D_{6B}}} (\phi_{D_{6B},D_{7B}}^F)^{g_{D_{6B}}^F} \\
& \times p_{D_{7B}}^{a_{D_{7B}}+a_{D_{7B}}^F} q_{D_{7B}}^{g_{D_{6B}}+g_{D_{6B}}^F-a_{D_{7B}}-a_{D_{7B}}^F} \chi_{D_{7B}}^{a_{D_{7B}}-b_{D_{7B}}-h_{D_{7B}}} (\chi_{D_{7B}}^F)^{a_{D_{7B}}^F-b_{D_{7B}}^F} \phi_{D_{7B},D_{7T}}^{g_{D_{7B}}}
\end{aligned}$$

$$\begin{aligned}
& \times (\phi_{D_{7B}, D_{7T}}^F)^{g_{D_{7B}}^F} p_{D_{7T}}^{a_{D_{7T}} + a_{D_{7T}}^F} q_{D_{7T}}^{g_{D_{7B}} + g_{D_{7B}}^F - a_{D_{7T}} - a_{D_{7T}}^F} \chi_{D_{7T}}^{a_{D_{7T}} - b_{D_{7T}} - h_{D_{7T}}} (\chi_{D_{7T}}^F)^{a_{D_{7T}}^F - b_{D_{7T}}^F} \\
& \times \phi_{D_{7T}, T_7}^{a_{T_7}} (\phi_{D_{7T}, T_7}^F)^{a_{T_7}^F}.
\end{aligned} \tag{3.62}$$

As with Model 4, Model 5a was fit to a reduced data set with only the first 4 dams (i.e., BON, TDA, JD, and MCN), and the tributaries in the reaches immediately above and below these dams. Using this restricted data set is reasonable if the focus is on salmon returning to Mid-Columbia spawning sites rather than to Snake River sites. Table 3.40 shows the observed summary statistics from the reduced 1996 data set including only the first 4 dams and their tributaries. Most statistics in Table 3.40 are the same as those in Table 3.39, with changes only in b_i , b_i^F , and h_i for upriver detection sites. As in the full model, it is necessary to use parameters $\phi_{D_{1T}, D_{2T}}$, $\phi_{D_{1T}, D_{2T}}^F$, $\phi_{T_1, D_{2T}}$, $\phi_{T_1, D_{2T}}^F$, $\phi_{D_{2T}, D_{3T}}$, $\phi_{D_{2T}, D_{3T}}^F$, $\phi_{T_2, D_{3T}}$, and $\phi_{T_2, D_{3T}}^F$ due to the lack of detections at sites D_{2B} and D_{3B} . Also, it is necessary to fix to 0 the parameters f_{T_0} , f_{T_1} , f_{T_2} , and $\phi_{T_0, D_{1B}}^F$.

Table 3.40: Observed summary statistics for Model 5a (Fallback and Memory-Free Tributary Model) from the 1996 Chinook salmon data set with $K = 4$ dams (BON, TDA, JD, and MCN). The release size is N . Descriptions of summary statistics are listed in Table 3.37

Statistic	Value	Statistic	Value	Statistic	Value	Statistic	Value	Statistic	Value	Statistic	Value
N	846	b_R	720	h_R	105	d_R	105				
a_{T0}	7	b_{T0}	4	b_{T0}^F	0	d_{T0}	0				
a_{D1B}	674	b_{D1B}	641	b_{D1B}^F	94	h_{D1B}	6				
a_{D1T}	603	b_{D1T}	516	b_{D1T}^F	79	h_{D1T}	26	d_{D1T}	30		
a_{T1}	240	b_{T1}	29	b_{T1}^F	11	d_{T1}	0				
a_{D2B}	0	b_{D2B}	0	b_{D2B}^F	0	h_{D2B}	0				
a_{D2T}	335	b_{D2T}	295	b_{D2T}^F	63	h_{D2T}	10	d_{D2T}	12		
a_{T2}	58	b_{T2}	2	b_{T2}^F	1	d_{T2}	0				
a_{D3B}	0	b_{D3B}	0	b_{D3B}^F	0	h_{D3B}	0				
a_{D3T}	277	b_{D3T}	250	b_{D3T}^F	61	h_{D3T}	9	d_{D3T}	9		
a_{T3}	30	b_{T3}	2	b_{T3}^F	5	d_{T3}	1				
a_{D4B}	219	b_{D4B}	211	b_{D4B}^F	44	h_{D4B}	0				
a_{D4T}	222	b_{D4T}	129	b_{D4T}^F	14	h_{D4T}	0				
a_{T4}	134	b_{T4}	16								

The likelihood for Model 5a for the reduced data 1996 set is

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \Phi_{R,T_0}^{a_{T_0}} \Phi_{R,D_{1B}}^{g_R-d_R-a_{T_0}} (\Phi_{R,T_0}^F)^{a_{T_0}^F} (\Phi_{R,D_{1B}}^F)^{d_R-a_{T_0}^F} \chi_{T_0}^{a_{T_0}-b_{T_0}} \phi_{T_0,D_{1B}}^{b_{T_0}} p_{D_{1B}}^{a_{D_{1B}}+a_{D_{1B}}^F} \\
& \times q_{D_{1B}}^{g_{T_0}+g_{T_0}^F-a_{D_{1B}}-a_{D_{1B}}^F} \chi_{D_{1B}}^{a_{D_{1B}}-b_{D_{1B}}-h_{D_{1B}}} (\chi_{D_{1B}}^F)^{a_{D_{1B}}^F-b_{D_{1B}}^F} \phi_{D_{1B},D_{1T}}^{g_{D_{1B}}} (\phi_{D_{1B},D_{1T}}^F)^{g_{D_{1B}}^F} \\
& \times p_{D_{1T}}^{a_{D_{1T}}+a_{D_{1T}}^F} q_{D_{1T}}^{g_{D_{1B}}+g_{D_{1B}}^F-a_{D_{1T}}-a_{D_{1T}}^F} \chi_{D_{1T}}^{a_{D_{1T}}-b_{D_{1T}}-h_{D_{1T}}} (\chi_{D_{1T}}^F)^{a_{D_{1T}}^F-b_{D_{1T}}^F} f_{D_{1T}}^{d_{D_{1T}}} \\
& \times (1-f_{D_{1T}})^{g_{D_{1T}}-d_{D_{1T}}} \phi_{D_{1T},T_1}^{a_{T_1}} (\phi_{D_{1T},T_1}^F)^{a_{T_1}^F} \phi_{D_{1T},D_{2T}}^{g_{D_{1T}}-d_{D_{1T}}-a_{T_1}} (\phi_{D_{1T},D_{2T}}^F)^{g_{D_{1T}}^F+d_{D_{1T}}-a_{T_1}^F} \\
& \times \chi_{T_1}^{a_{T_1}-b_{T_1}} (\chi_{T_1}^F)^{a_{T_1}^F-b_{T_1}^F} \phi_{T_1,D_{2T}}^{b_{T_1}} (\phi_{T_1,D_{2T}}^F)^{b_{T_1}^F} p_{D_{2T}}^{a_{D_{2T}}+a_{D_{2T}}^F} q_{D_{2T}}^{g_{T_2}+g_{T_2}^F-a_{D_{2T}}-a_{D_{2T}}^F} \\
& \times \chi_{D_{2T}}^{a_{D_{2T}}-b_{D_{2T}}-h_{D_{2T}}} (\chi_{D_{2T}}^F)^{a_{D_{2T}}^F-b_{D_{2T}}^F} f_{D_{2T}}^{d_{D_{2T}}} (1-f_{D_{2T}})^{g_{D_{2T}}-d_{D_{2T}}} \phi_{D_{2T},T_2}^{a_{T_2}} (\phi_{D_{2T},T_2}^F)^{a_{T_2}^F} \\
& \times \phi_{D_{2T},D_{3T}}^{g_{D_{2T}}-d_{D_{2T}}-a_{T_2}} (\phi_{D_{2T},D_{3T}}^F)^{g_{D_{2T}}^F+d_{D_{2T}}-a_{T_2}^F} \chi_{T_2}^{a_{T_2}-b_{T_2}} (\chi_{T_2}^F)^{a_{T_2}^F-b_{T_2}^F} \phi_{T_2,D_{3T}}^{b_{T_2}} \\
& \times (\phi_{T_2,D_{3T}}^F)^{b_{T_2}^F} p_{D_{3T}}^{a_{D_{3T}}+a_{D_{3T}}^F} q_{D_{3T}}^{g_{T_2}+g_{T_2}^F-a_{D_{3T}}-a_{D_{3T}}^F} \chi_{D_{3T}}^{a_{D_{3T}}-b_{D_{3T}}-h_{D_{3T}}} (\chi_{D_{3T}}^F)^{a_{D_{3T}}^F-b_{D_{3T}}^F} f_{D_{3T}}^{d_{D_{3T}}} \\
& \times (1-f_{D_{3T}})^{g_{D_{3T}}-d_{D_{3T}}} \phi_{D_{3T},T_3}^{a_{T_3}} (\phi_{D_{3T},T_3}^F)^{a_{T_3}^F} \phi_{D_{3T},D_{4B}}^{g_{D_{3T}}-d_{D_{3T}}-a_{T_3}} (\phi_{D_{3T},D_{4B}}^F)^{g_{D_{3T}}^F+d_{D_{3T}}-a_{T_3}^F} \\
& \times \chi_{T_3}^{a_{T_3}-b_{T_3}-h_{T_3}} (\chi_{T_3}^F)^{a_{T_3}^F-b_{T_3}^F} f_{T_3}^{d_{T_3}} \{(1-f_{T_3})\phi_{T_3,D_{4B}}\}^{b_{T_3}+h_{T_3}-d_{T_3}} (\phi_{T_3,D_{4B}}^F)^{b_{T_3}^F+d_{T_3}^F} \\
& \times p_{D_{4B}}^{a_{D_{4B}}+a_{D_{4B}}^F} q_{D_{4B}}^{g_{T_3}+g_{T_3}^F-a_{D_{4B}}-a_{D_{4B}}^F} \chi_{D_{4B}}^{a_{D_{4B}}-b_{D_{4B}}-h_{D_{4B}}} (\chi_{D_{4B}}^F)^{a_{D_{4B}}^F-b_{D_{4B}}^F} p_{D_{4T}}^{a_{D_{4T}}+a_{D_{4T}}^F} \\
& \times q_{D_{4T}}^{g_{D_{4B}}+g_{D_{4B}}^F-a_{D_{4T}}-a_{D_{4T}}^F} \chi_{D_{4T}}^{a_{D_{4T}}-b_{D_{4T}}-h_{D_{4T}}} (\chi_{D_{4T}}^F)^{a_{D_{4T}}^F-b_{D_{4T}}^F} \phi_{D_{4T},T_4}^{a_{T_4}} (\phi_{D_{4T},T_4}^F)^{a_{T_4}^F}. \quad (3.63)
\end{aligned}$$

3.9.2.5 Results

Program USER¹⁶ was used to fit Model 5a to the data via maximum likelihood. Maximum likelihood estimates from the full data set ($K = 7$ dams) are listed in Table 3.41. The log-likelihood was -3744.8799, with an AIC of 7611.780. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.1073$ ($\widehat{SE} = 0.0108$) and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2763$ ($\widehat{SE} = 0.0156$).

Model 5a is a modification of Model 3a; both models use all tributary detections, but Model 5a accounts for the effect of fallback on transition rates. The relationship between

¹⁶<http://www.cbr.washington.edu/paramEst/USER/>

Models 5a and 3a is the same as that between Models 4 and 2. As with Model 4, for Model 5a there is no consistency in which of $\hat{\phi}_{ij}$ or $\hat{\phi}_{ij}^F$ is larger, although in general, $\hat{\phi}_{ij}^F > \hat{\phi}_{ij}$ for downriver sites while $\hat{\phi}_{ij} > \hat{\phi}_{ij}^F$ for upriver sites for Model 5a. Just as the estimate of perceived system survival is larger for Model 4 than for Model 2, so it is larger for Model 5a than for Model 3a ($\hat{S}_{sys} = 0.1073$, $\widehat{SE} = 0.0108$ for Model 5a versus $\hat{S}_{sys} = 0.1057$, $\widehat{SE} = 0.0106$ for Model 3a). Likewise, the estimate of the unaccountable loss rate is smaller for Model 5a ($\hat{\mu}_R = 0.2763$, $\widehat{SE} = 0.0156$) than for Model 3a ($\hat{\mu}_R = 0.2803$, $\widehat{SE} = 0.0156$).

Model 5a is also a modification of Model 4; both models account for fallback, but Model 5a uses all tributary detections while Model 4 uses only terminal tributary detections. The relationship between Models 5a and 4 is the same as that between Models 3a and 2. However, whereas both \hat{S}_{sys} and $\hat{\mu}_R$ were larger for Model 3a than for Model 2, they are approximately equal for Models 5 and 4, with \hat{S}_{sys} slightly smaller for Model 5a ($\hat{S}_{sys} = 0.1075$, $\widehat{SE} = 0.0108$ for Model 4), and $\hat{\mu}_R$ slightly larger for Model 5a ($\hat{\mu}_R = 0.2743$, $\widehat{SE} = 0.0155$ for Model 4). It is reasonable that the unaccountable loss estimate is larger for the Model 5a than for Model 4, because fish that enter tributaries in Model 5a are not necessarily accounted for, as they are in Model 4. In general, the extra tributary detections in Model 5a are preferable to the terminal tributary detections in Model 4 because the extra detections may provide more information on fallback events; however, the additional information gleaned from the current data set is minimal.

Table 3.41: Maximum likelihood estimates of parameters from Model 5a, the Fallback Memory-Free Tributary model, with $K = 7$ dams.

Category	Parameter	Estimate	S.E.
Transition	Φ_{R,T_0}	0.0083	0.0031
	Φ_{R,T_0}^F	0.0047	0.0024
	$\Phi_{R,D_{1B}}$	0.8448	0.0126
	$\Phi_{R,D_{1B}}^F$	0.1205	0.0113
	$\phi_{T_0,D_{1B}}$	0.5728	0.1876
	$\phi_{D_{1B},D_{1T}}$	0.9731	0.0079
	$\phi_{D_{1B},D_{1T}}^F$	0.9734	0.0213
	ϕ_{D_{1T},T_1}	0.3622	0.0189
	ϕ_{D_{1T},T_1}^F	0.3993	0.0435
	$\phi_{D_{1T},D_{2T}}$	0.5490	0.0201

Table 3.41 continued

Category	Parameter	Estimate	S.E.
Transition	$\phi_{D_{1T}, D_{2T}}^F$	0.4877	0.0451
	$\phi_{T_1, D_{2T}}$	0.1224	0.0213
	$\phi_{T_1, D_{2T}}^F$	0.2051	0.0552
	ϕ_{D_{2T}, T_2}	0.1526	0.0185
	ϕ_{D_{2T}, T_2}^F	0.1945	0.0424
	$\phi_{D_{2T}, D_{3T}}$	0.7596	0.0228
	$\phi_{D_{2T}, D_{3T}}^F$	0.7618	0.0470
	$\phi_{T_2, D_{3T}}$	0.0346	0.0240
	$\phi_{T_2, D_{3T}}^F$	0.0590	0.0573
	ϕ_{D_{3T}, T_3}	0.1067	0.0184
	ϕ_{D_{3T}, T_3}^F	0.1954	0.0453
	$\phi_{D_{3T}, D_{4B}}$	0.8301	0.0228
	$\phi_{D_{3T}, D_{4B}}^F$	0.7474	0.0511
	$\phi_{T_3, D_{4B}}$	0.0742	0.0510
	$\phi_{T_3, D_{4B}}^F$	0.3354	0.1225
	$\phi_{D_{4B}, D_{4T}}$	0.9856	0.0094
	$\phi_{D_{4B}, D_{4T}}^F$	0.9360	0.0336
	ϕ_{D_{4T}, T_4}	0.5888	0.0328
	ϕ_{D_{4T}, T_4}^F	0.2510	0.0544
	$\phi_{D_{4T}, D_{5B}}$	0.3440	0.0317
	$\phi_{D_{4T}, D_{5B}}^F$	0.6603	0.0603
	$\phi_{D_{5B}, D_{5T}}$	0.9525	0.0272
	$\phi_{D_{5B}, D_{5T}}^F$	0.9779	0.0255
	ϕ_{D_{5T}, T_5}	0.3052	0.0545
	ϕ_{D_{5T}, T_5}^F	0.4582	0.0760
	$\phi_{D_{5T}, D_{6B}}$	0.6473	0.0587
	$\phi_{D_{5T}, D_{6B}}^F$	0.5354	0.0805
	$\phi_{T_5, D_{6B}}^F$	0.9895	0.0559
	$\phi_{D_{6B}, D_{7B}}$	0.9636	0.0269
	$\phi_{D_{6B}, D_{7B}}^F$	0.8948	0.0593
	$\phi_{D_{7B}, D_{7T}}$	0.8960	0.0389
	$\phi_{D_{7B}, D_{7T}}^F$	0.7901	0.0675
	ϕ_{D_{7T}, T_7}	0.8266	0.0498
	ϕ_{D_{7T}, T_7}^F	0.7955	0.0743
Detection	$p_{D_{1B}}$	0.9407	0.0085
	$p_{D_{1T}}$	0.8665	0.0127
	$p_{D_{2T}}$	0.8528	0.0174
	$p_{D_{3T}}$	0.9571	0.0112
	$p_{D_{4B}}$	0.9102	0.0168
	$p_{D_{4T}}$	0.9369	0.0148

Table 3.41 continued

Category	Parameter	Estimate	S.E.
Detection	$p_{D_{5B}}$	0.9302	0.0238
	$p_{D_{5T}}$	0.8725	0.0318
	$p_{D_{6B}}$	0.6349	0.0471
	$p_{D_{7B}}$	0.9775	0.0157
	$p_{D_{7T}}$	0.9726	0.0191
Fallback	$f_{D_{1T}}$	0.0526	0.0096
	$f_{D_{2T}}$	0.0330	0.0094
	$f_{D_{3T}}$	0.0331	0.0109
	f_{T_3}	0.1005	0.1052
	$f_{D_{4T}}$	0.0191	0.0095
	$f_{D_{5T}}$	0.0336	0.0235

Maximum likelihood parameter estimates from the reduced data set ($K = 4$ dams) are listed in Table 3.42. The log-likelihood was -3267.0957, with an AIC of 6612.191. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.3408$ ($\widehat{SE} = 0.0169$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2211$ ($\widehat{SE} = 0.0151$).

As for the 7-dam analysis, the estimate of perceived system survival is slightly smaller for Model 5a than for Model 4 ($\hat{S}_{sys} = 0.3408$, $\widehat{SE} = 0.0169$ for Model 5a versus $\hat{S}_{sys} = 0.3412$, $\widehat{SE} = 0.0170$ for Model 4), and the estimate of unaccountable loss is slightly larger for Model 5a than for Model 4 ($\hat{\mu}_R = 0.2211$, $\widehat{SE} = 0.0151$ for Model 5a versus $\hat{\mu}_R = 0.2199$, $\widehat{SE} = 0.0151$ for Model 4). The differences are very small. As expected, system survival is estimated to be larger for the smaller system ($\hat{S}_{sys,LGR} = 0.1073$, $\widehat{SE} = 0.0108$ for the 7-dam system), and the unaccountable loss rate is estimated to be smaller for the smaller system ($\hat{\mu}_R = 0.2763$, $\widehat{SE} = 0.0156$ for the 7-dam system).

Table 3.42: Maximum likelihood estimates of parameters from Model 5a, the Fallback Memory-Free Tributary model, with $K = 4$ dams.

Category	Parameter	Estimate	S.E.
Transition	Φ_{R,T_0}	0.0083	0.0031
	Φ_{R,T_0}^F	0.0047	0.0024
	$\Phi_{R,D_{1B}}$	0.8448	0.0126
	$\Phi_{R,D_{1B}}^F$	0.1205	0.0113
	$\phi_{T_0,D_{1B}}$	0.5728	0.1875

Table 3.42 continued

Category	Parameter	Estimate	S.E.
Transition	$\phi_{D_{1B}, D_{1T}}$	0.9731	0.0079
	$\phi_{D_{1B}, D_{1T}}^F$	0.9734	0.0213
	ϕ_{D_{1T}, T_1}	0.3622	0.0189
	ϕ_{D_{1T}, T_1}^F	0.3993	0.0435
	$\phi_{D_{1T}, D_{2T}}$	0.5490	0.0201
	$\phi_{D_{1T}, D_{2T}}^F$	0.4877	0.0451
	$\phi_{T_1, D_{2T}}$	0.1224	0.0213
	$\phi_{T_1, D_{2T}}^F$	0.2051	0.0552
	ϕ_{D_{2T}, T_2}	0.1526	0.0185
	ϕ_{D_{2T}, T_2}^F	0.1945	0.0424
	$\phi_{D_{2T}, D_{3T}}$	0.7596	0.0228
	$\phi_{D_{2T}, D_{3T}}^F$	0.7623	0.0470
	$\phi_{T_2, D_{3T}}$	0.0346	0.0240
	$\phi_{T_2, D_{3T}}^F$	0.0590	0.0572
	ϕ_{D_{3T}, T_3}	0.1067	0.0184
	ϕ_{D_{3T}, T_3}^F	0.1949	0.0452
	$\phi_{D_{3T}, D_{4B}}$	0.8318	0.0229
	$\phi_{D_{3T}, D_{4B}}^F$	0.7382	0.0527
	$\phi_{T_3, D_{4B}}$	0.0743	0.0511
	$\phi_{T_3, D_{4B}}^F$	0.3381	0.1237
	$\phi_{D_{4B}, D_{4T}}$	0.9821	0.0152
	$\phi_{D_{4B}, D_{4T}}^F$	0.8717	0.0508
	ϕ_{D_{4T}, T_4}	0.5787	0.0332
	ϕ_{D_{4T}, T_4}^F	0.2920	0.0620
Detection	$p_{D_{1B}}$	0.9407	0.0085
	$p_{D_{1T}}$	0.8665	0.0127
	$p_{D_{2T}}$	0.8528	0.0174
	$p_{D_{3T}}$	0.9570	0.0113
	$p_{D_{4B}}$	0.9107	0.0170
	$p_{D_{4T}}$	0.9533	0.0172
Fallback	$f_{D_{1T}}$	0.0526	0.0096
	$f_{D_{2T}}$	0.0330	0.0094
	$f_{D_{3T}}$	0.0336	0.0111
	f_{T_3}	0.1001	0.1056

3.9.3 Model 5b: Short-term Fallback and Tributary Memory Model

Model 5b includes memory effects of both fallback and tributary entry and exit. It assumes that entering and exiting a tributary may affect survival and tributary behavior only in

the following reach. Because migrating individuals may enter a tributary to determine if it leads to their spawning grounds, it may be that these individuals are more likely to fall back in the reach upstream of the tributary, as well. Therefore, Model 5b allows for a differential probability of fallback in the reach following a given tributary, for non-fallback fish who entered the tributary. As with Model 3b, the reach immediately following tributary k extends from the base of dam $k+1$ to the base of dam $k+2$ (without including dam $k+2$) for $k = 0, \dots, K-2$, and from the base of dam K to tributary T_K for $k = K-1$. Detection rates at the dams are unaffected by tributary visits or fallback, and detection rates in the tributaries are assumed to be 100%.

To simplify Model 5b, the memory effect of only one “anomalous” action (fallback or tributary visit) acts at a time. In particular, the most recent anomalous action from the previous reach affects survival and transition probabilities, with no added effect of earlier anomalous actions. Thus, if a fish falls back between a top-of-dam site and the subsequent tributary, the tributary effect has precedent over the fallback effect because the fish experienced the tributary after falling back. If the fallback event occurs between the tributary and the next base-of-dam site, then the fallback effect has precedent. If the fish has neither fallen back nor entered the tributary in the previous reach, then neither effect applies.

Using effects of only the most recent anomalous event assumes that effects of fallback are temporary, even in the event of bypassing tributaries, rather than permanent as in Models 4 and 5a. Temporary (single-period) memory effects have been used elsewhere, e.g. Cormack (1989) and Brownie et al. (1993). With temporary fallback effects, if the fallback event occurs during the transition from either the top of dam k (site D_{kT}) or the tributary between dams k and $k+1$ (site T_k) to the base of dam $k+1$ (site $D_{k+1,B}$), then the memory effect of fallback extends through the transitions ending at the base of dam $k+2$ (site $D_{k+2,B}$). Any transition originating at or upstream of site $D_{k+2,B}$ has no memory effect of fallback. Likewise, if the fallback event occurs during the transition between the initial release and the base of the first dam, then the memory effect extends only through transitions to the base of the second dam; all transitions originating at the base of the second dam are free of the fallback effect. In general, fallback effects extend only through the following reach, where the reach immediately following the top of dam k extends from tributary T_k to the

base of dam $k + 2$ (without including dam $k + 2$) for $k = 1, \dots, K - 2$, and from tributary $K - 1$ to tributary T_K for $k = K - 1$. The definition of “reach” following a top-of-dam site for fallback effects is larger than the “reach” following a tributary for tributary effects. For simplicity, a “fallback fish” is a fish that fell back in the preceding reach, without having entered a tributary after falling back, while a “non-fallback fish” is a fish that either did not fall back in the preceding reach, or possibly fell back in that reach but subsequently entered a tributary after fallback. Unlike Models 4 and 5a, Model 5b does not treat the fallback state as absorbing.

The assumption of temporary fallback effects together with simplified data that include only the first fallback event is tantamount to assuming that each fish falls back at most once during their upstream migration. Models 4 and 5a assume that once a fish has fallen back, it remains a “fallback fish,” with the implicit assumption that subsequent fallbacks have no significant added impact on survival and transition probabilities. Model 5b allows fallback fish to return to the pre-fallback state after a single reach or after entering and leaving a tributary, and then does not allow them to fall back again. Thus, Model 5b assumes either that no subsequent fallbacks occur, or that they have no effect relative to the original pre-fallback state. The difference between the earlier models and Model 5b is that the earlier models assume no effect of subsequent fallback on post-fallback transitions, while Model 5b assumes no effect of subsequent fallback on pre-fallback transitions. While the assumption of Models 4 and 5a is perhaps more tenable, the assumption of Model 5b is necessary to make the model tractable.

3.9.3.1 Notation

The notation used for Model 5b is a mixture of that used for Models 3b and 4, the Memory Tributary Model and the Fallback Model, respectively. Some notation is the same as that used in Model 5a. The transition parameters ϕ_{ij} and ϕ_{ij}^F are defined as for Model 5a for the cases where $i = R$ and $i = T_0$. For other values of i , define the transition parameters

ϕ_{ij} , ϕ_{ij}^F , ϕ_{ij}^T , and ϕ_{ij}^{TF} as follows:

$\phi_{ij} = Pr[\text{Survive and move directly from site } i \text{ to site } j \mid \text{Neither fell back nor entered the tributary in the reach immediately preceding site } i];$

$\phi_{ij}^T = Pr[\text{Survive and move directly from site } i \text{ to site } j \mid \text{Entered the tributary in the reach immediately preceding site } i \text{ and did not fall back between that tributary and site } i];$

$\phi_{ij}^F = Pr[\text{Survive and move from site } i \text{ to site } j \mid \text{Either fall back during transition from site } i \text{ to site } j, \text{ or fell back in the reach immediately preceding site } i \text{ without entering a tributary between fallback and site } i];$

$\phi_{ij}^{FT} = Pr[\text{Survive and move from site } i \text{ to site } j \mid \text{Entered tributary in the reach immediately preceding site } i, \text{ and fall back during the transition from site } i \text{ to site } j];$

where $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$, and where

$$j = \begin{cases} D_{kT} & \text{for } i = D_{kB}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = D_{kT}, k = 1, \dots, K-1; \\ T_k & \text{for } i = D_{kT}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = T_k, k = 0, \dots, K-1. \end{cases} \quad (3.64)$$

As usual, p_i and q_i represent the conditional detection and non-detection rates, respectively, at site i , with $q_i = 1 - p_i$. The probability of becoming a fallback fish after site i is f_i for fish who did not enter the tributary in the reach preceding site i , and is f_i^T for fish who did enter that tributary.

As described above, two types of temporary memory effect are used in Model 5b: the fallback effect and the tributary effect. Only a single type of memory effect acts on any given parameter, with the most recent effect taking precedent. While the parameter ϕ_{ij}^{FT} appears

to include both types of memory effect, it actually includes only the tributary effect; the fallback notation F in the superscript denotes that the transition from i to j is a fallback transition, and does not refer to a fallback memory effect. Thus, ϕ_{ij}^{FT} is used only during the transition that includes the fallback event, and always follows the parameter f_i^T in detection history probabilities. The superscript F in the parameter ϕ_{ij}^F , on the other hand, denotes either that the transition from i to j includes fallback (if ϕ_{ij}^F follows f_i), or that the memory effect of fallback applies. For simplicity, the same parameter is used in both cases.

For example, consider the simplified migration path in Figure 3.13(a). A fish following this path moved from the release point to tributary T_1 , returned to the river and swam upstream past TDA and JD, fell back over both JD and TDA, and then reascended TDA and JD. The corresponding (simplified) detection history is $R T_1 FB D_{2B} D_{2T} D_{3T} \dots$. The portion of the history's probability that relates to the return to the river from T_1 , fallback, and subsequent transitions is

$$\dots f_{T_1} \phi_{T_1, D_{2B}}^F p_{D_{2B}} \phi_{D_{2B}, D_{2T}}^F p_{D_{2T}} \phi_{D_{2T}, D_{3B}}^F q_{D_{3B}} \phi_{D_{3B}, D_{3T}} p_{D_{3T}} \dots \quad (3.65)$$

The transition between site T_1 and D_{2B} is the fallback transition, requiring $\phi_{T_1, D_{2B}}^F$. The transitions between D_{2B} and D_{3B} are not fallback transitions, but they include the memory effect of the fallback (but not of tributary T_1). The fallback memory effect ends at D_{3B} , and transitions there and upstream no longer include the fallback notation. Because the fallback occurs between leaving the tributary T_1 and ascending dam D_2 (TDA), there is no memory effect of tributary visits on the transition from D_{2B} and D_{2T} : $\phi_{D_{2B}, D_{2T}}^F$ is used instead of $\phi_{D_{2B}, D_{2T}}^T$. Had the migration path included tributary T_0 but was otherwise identical (i.e., simplified detection history $R T_0 T_1 FB D_{2B} D_{2T} D_{3T} \dots$), then $f_{T_1}^T \phi_{T_1, D_{2B}}^{FT}$ would replace $f_{T_1} \phi_{T_1, D_{2B}}^F$ in Equation (3.65), but otherwise the same parameters would be used.

The path in Figure 3.13(b) shows a case in which the fallback event occurs before the tributary event. In this case, the fish fell back between sites D_{1T} (BON) and T_1 , then returned to the river, and continued migrating upstream past TDA and JD. The portion of the simplified detection history shown in Figure 3.13(b) is $R D_{1T} FB T_1 D_{2T} D_{3T} \dots$.

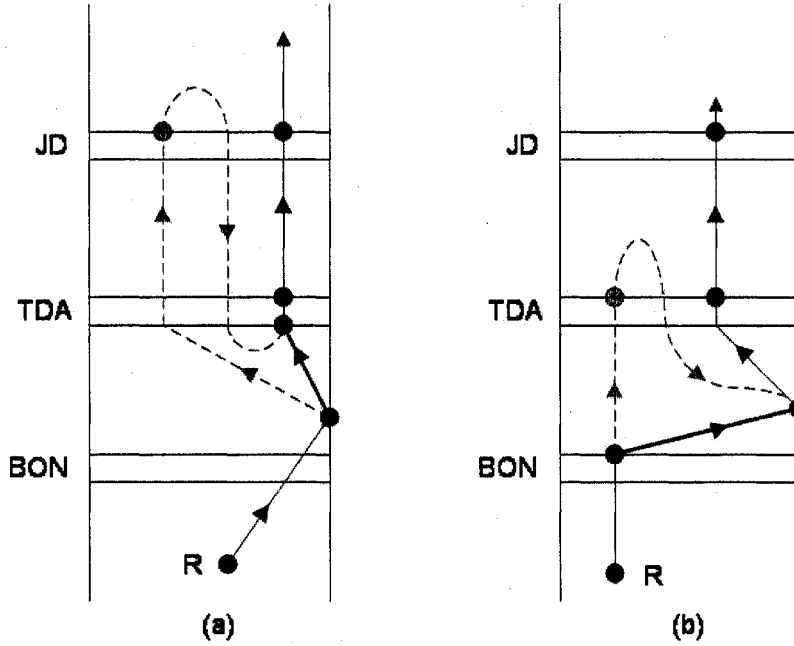


Figure 3.13: Two migration paths for consideration in developing Model 5b. In one path (a), the fish falls back over dams JD and TDA after visiting tributary T_1 . In the other path (b), the fish falls back over dam TDA before visiting tributary T_1 . The dotted paths indicate the portion of the detection history removed due to the fallback; the heavy portions replace the dotted portions.

The probability of the fallback and subsequent transitions is

$$\dots f_{D_{1T}} \phi_{D_{1T}, T_1}^F \phi_{T_1, D_{2B}}^F q_{D_{2B}} \phi_{D_{2B}, D_{2T}}^T p_{D_{2B}} \phi_{D_{2T}, D_{3B}}^T q_{D_{3B}} \phi_{D_{3B}, D_{3T}} p_{D_{3T}} \dots \quad (3.66)$$

The parameter ϕ_{D_{1T}, T_1}^F represents the fallback transition, and the parameter $\phi_{T_1, D_{2B}}^F$ includes the fallback memory effect. The transitions originating at dam 2 (TDA) include the tributary effect rather than the fallback effect, because the fish visited the tributary more recently than it fell back. The tributary effect ends at the third dam (JD), and

transitions originating at or upstream of JD have no memory effect. Had the fish visited the tributary below BON (site T_0), then $f_{D_{1T}}^T \phi_{D_{1T}, T_1}^{FT} \phi_{T_1, D_{2B}}^F q_{D_{2B}}$ would be used in place of $f_{D_{1T}} \phi_{D_{1T}, T_1}^F \phi_{T_1, D_{2B}}^F q_{D_{2B}}$ in Equation (3.66). In that case, the fallback effect takes precedent over the effect of visiting tributary T_0 on the transition from T_1 to D_{2B} : $\phi_{T_1, D_{2B}}^F$ is used instead of $\phi_{T_1, D_{2B}}^T$.

Several types of χ_i parameters are needed in Model 5b, each representing the probability of not being detected after site i , conditional on reaching site i , and each for a particular group of fish. For fish who never fell back, the parameters χ_i and χ_i^T are appropriate, where χ_i is used for fish who did not enter the tributary in the reach immediately preceding site i (if it exists), and χ_i^T is used for fish who did enter that tributary. Because χ_i and χ_i^T are used for fish who never fell back, they account for the possibility of falling back upon leaving site i . The parameter χ_i^F is appropriate for fish who fell back in the previous reach and did not enter a tributary between falling back and reaching site i . Fish that fell back in an earlier reach, or that entered a tributary since falling back, are assumed not to fall back again, so a new type of χ parameter is necessary for these fish: χ_i^f is used for fish that fell back but not within the previous reach and that did not enter the tributary in the previous reach, while χ_i^{fT} is used for fish that entered the tributary in the previous reach and also fell back some time before entering that tributary. Expressions for the different types of χ parameters are given below.

The probability of not being detected after site i , conditional upon reaching it without having fallen back or entering the tributary in the preceding reach, is χ_i :

$$\begin{aligned}
 \chi_R &= 1 - \Phi_{R, T_0} - \Phi_{R, T_0}^F - \Phi_{R, D_{1B}}(1 - q_{D_{1B}} \chi_{D_{1B}}) \\
 &\quad - \Phi_{R, D_{1B}}^F(p_{D_{1B}} + q_{D_{1B}} \phi_{D_{1B}, D_{1T}}^F p_{D_{1T}}); \\
 \chi_{D_{kB}} &= 1 - \phi_{D_{kB}, D_{kT}}(1 - q_{D_{kT}} \chi_{D_{kT}}), & k = 1, \dots, K; \\
 \chi_{D_{kT}} &= 1 - (1 - f_{D_{kT}}) \{ \phi_{D_{kT}, T_k} + \phi_{D_{kT}, D_{k+1, B}}(1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}) \} \\
 &\quad - f_{D_{kT}} \phi_{D_{kT}, T_k}^F \\
 &\quad - f_{D_{kT}} \phi_{D_{kT}, D_{k+1, B}}^F(p_{D_{k+1, B}} + q_{D_{k+1, B}} \phi_{D_{k+1, B}, D_{k+1, T}}^F p_{D_{k+1, T}}), & k = 1, \dots, K-1;
 \end{aligned} \tag{3.67}$$

$$\chi_{D_{KT}} = 1 - \phi_{D_{KT}, T_K};$$

$$\begin{aligned} \chi_{T_k} &= 1 - (1 - f_{T_k}) \phi_{T_k, D_{k+1}, B} (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^T) \\ &\quad - f_{T_k} \phi_{T_k, D_{k+1}, B}^F (p_{D_{k+1}, B} + q_{D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^F p_{D_{k+1}, T}), \quad k = 0, \dots, K-1. \end{aligned}$$

The probability of not being detected after site i , given having reached that site after entering the tributary in the reach immediately preceding site i but without having fallen back, is χ_i^T :

$$\begin{aligned} \chi_{D_{kB}}^T &= 1 - \phi_{D_{kB}, D_{kT}}^T (1 - q_{D_{kT}} \chi_{D_{kT}}^T), \quad k = 1, \dots, K; \\ \chi_{D_{kT}}^T &= 1 - (1 - f_{D_{kT}}^T) \left\{ \phi_{D_{kT}, T_k}^T + \phi_{D_{kT}, D_{k+1}, B}^T (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^T) \right\}, \\ &\quad - f_{D_{kT}}^T \phi_{D_{kT}, T_k}^{FT}, \quad (3.68) \\ &\quad - f_{D_{kT}}^T \phi_{D_{kT}, D_{k+1}, B}^{FT} (p_{D_{k+1}, B} + q_{D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^F p_{D_{k+1}, T}), \quad k = 1, \dots, K-1; \\ \chi_{D_{KT}}^T &= 1 - \phi_{D_{KT}, T_K}^T; \\ \chi_{T_k}^T &= 1 - (1 - f_{T_k}^T) \phi_{T_k, D_{k+1}, B}^T (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^T) \\ &\quad - f_{T_k}^T \phi_{T_k, D_{k+1}, B}^{FT} (p_{D_{k+1}, B} + q_{D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^F p_{D_{k+1}, T}), \quad k = 1, \dots, K-1. \end{aligned}$$

The probability of not being detected after site i , conditional on reaching that site after falling back in the previous reach and without entering a tributary in between falling back and reaching site i , is χ_i^F :

$$\begin{aligned} \chi_{D_{kB}}^F &= 1 - \phi_{D_{kB}, D_{kT}}^F (1 - q_{D_{kT}} \chi_{D_{kT}}^F), \quad k = 1, \dots, K; \\ \chi_{D_{kT}}^F &= 1 - \phi_{D_{kT}, T_k}^F - \phi_{D_{kT}, D_{k+1}, B}^F (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^f), \quad k = 1, \dots, K-1; \\ \chi_{D_{KT}}^F &= 1 - \phi_{D_{KT}, T_K}^F; \quad (3.69) \\ \chi_{T_k}^F &= 1 - \phi_{T_k, D_{k+1}, B}^F (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^{fT}), \quad k = 0, \dots, K-1. \end{aligned}$$

The parameters χ_i^f and χ_i^{fT} are appropriate for fish that fell back previously but no longer experience the effects of fallback. The probability of not being detected after site i , conditional on reaching that site after having fallen back but not within the previous reach, and

without entering the tributary in the preceding reach, is χ_i^f :

$$\begin{aligned}
\chi_{D_{kB}}^f &= 1 - \phi_{D_{kB}, D_{kT}} (1 - q_{D_{kT}} \chi_{D_{kT}}^f), & k &= 2, \dots, K; \\
\chi_{D_{kT}}^f &= 1 - \phi_{D_{kT}, T_k} - \phi_{D_{kT}, D_{k+1, B}} (1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}^f), & k &= 2, \dots, K-1; \\
\phi_{D_{KT}}^f &= 1 - \phi_{D_{KT}, T_K}; & & \\
\phi_{T_k}^f &= 1 - \phi_{T_k, D_{k+1, B}} (1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}^{fT}), & k &= 2, \dots, K-1.
\end{aligned} \tag{3.70}$$

The probability of not being detected after site i , conditional on reaching that site after entering the preceding tributary and having fallen back before entering that tributary, is χ_i^{fT} :

$$\begin{aligned}
\chi_{D_{kB}}^{fT} &= 1 - \phi_{D_{kB}, D_{kT}}^T (1 - q_{D_{kT}} \chi_{D_{kT}}^{fT}), & k &= 1, \dots, K; \\
\chi_{D_{kT}}^{fT} &= 1 - \phi_{D_{kT}, T_k}^T - \phi_{D_{kT}, D_{k+1, B}}^T (1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}^f), & k &= 1, \dots, K-1; \\
\chi_{D_{KT}}^{fT} &= 1 - \phi_{D_{KT}, T_K}^T; & & \\
\chi_{T_k}^{fT} &= 1 - \phi_{T_k, D_{k+1, B}}^T (1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}^{fT}), & k &= 1, \dots, K-1.
\end{aligned} \tag{3.71}$$

The parameters used in Model 5b are listed in Table 3.43.

Table 3.43: Parameters used in Model 5b, the Fallback and Memory Tributary Model. The number of dams is K .

Parameter	Definition
Φ_{R, T_0}	Probability of surviving and moving from the release point directly to site T_0 without becoming a fallback fish;
$\Phi_{R, D_{1B}}$	Probability of surviving and moving from the release point directly to site D_{1B} without becoming a fallback fish;
Φ_{R, T_0}^F	Probability of surviving, becoming a fallback fish, and then moving from the release point directly to site T_0 ;
$\Phi_{R, D_{1B}}^F$	Probability of surviving, becoming a fallback fish, and then moving from the release point directly to site D_{1B} ;
ϕ_{ij}	Probability of surviving and moving from site i to site j as a non-fallback fish, given reaching site i without entering the tributary (if any) in the reach immediately preceding site i , for $i = T_0, D_{1B}, D_{1T}, T_1, \dots, D_{KT}$ and j as in Equation (3.64);

Table 3.43 continued

Parameter	Definition
ϕ_{ij}^T	Probability of surviving and moving from site i to site j as a non-fallback fish, given reaching site i after entering the tributary in the reach immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, T_K$ and j as in Equation (3.64);
ϕ_{ij}^F	Probability of surviving and moving from site i to site j , given either (a) having reached site i after falling back in the previous reach but without entering the tributary in that reach, or (b) having reached site i after both entering the preceding tributary and then falling back before site i , or (c) falling back during the transition from i to j , having not entered the tributary in the previous reach, for
ϕ_{ij}^{FT}	$i = T_0, D_{1B}, D_{1T}, T_1, \dots, D_{KT}$ and j as in Equation (3.64); Probability of surviving and moving from site i to site j , conditional on falling back during that transition and on having reached site i after entering the tributary in the reach immediately preceding site i , for $i = D_{1T}, T_1, D_{2T}, \dots, D_{KT}$ and j as in Equation (3.64);
p_i	Probability of being detected at site j , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$;
q_i	Probability of avoiding detection at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$; $= 1 - p_i$;
f_i	Probability of becoming a post-fallback fish between site i and the next detection site, given having reached site i as a non-fallback fish without entering the tributary in the reach immediately preceding site i , for $i = T_0, D_{1T}, T_1, D_{2T}, \dots, T_{K-1}$;
f_i^T	Probability of becoming a post-fallback fish between site i and the next detection site, given having reached site i as a non-fallback fish after entering the tributary in the reach immediately preceding site i , for $i = D_{1T}, T_1, D_{2T}, T_2, \dots, T_{K-1}$;
χ_i	Probability of not being detected after site i , given having reached site i without having ever fallen back and without having entered the tributary (if any)
χ_i^T	in the reach immediately preceding site i , for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$; Probability of not being detected after site i , given having reached site i without having ever fallen back, and after entering the tributary in the reach
χ_i^F	immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$; Probability of not being detected after site i , given having reached site i after falling back within the previous reach but without having entered the tributary (if any) between falling back and reaching site i , for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$;
χ_i^f	Probability of not being detected after site i , given having reached site i after falling back at least two reaches previously, and without

Table 3.43 continued

Parameter	Definition
χ_i^{fT}	having entered the tributary in the reach immediately preceding site i , for $i = D_{2B}, D_{2T}, T_2, \dots, D_{KT}$; Probability of not being detected after site i , given having reached site i after entering the tributary in the reach immediately preceding site i , and having fallen back prior to entering that tributary, for $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$.

The parameters in Table 3.43 can be used to express the probabilities of the possible detection histories. For example, the probability of observing the detection history $R \text{ FB } T_0 \text{ } D_{1B} \text{ } D_{2T} \text{ } T_2 \text{ } D_{3T}$ is

$$Pr[R \text{ FB } T_0 \text{ } D_{1B} \text{ } D_{2T} \text{ } T_2 \text{ } D_{3T}] = \Phi_{R,T_0}^F \phi_{T_0,D_{1B}}^F p_{D_{1B}} \phi_{D_{1B},D_{1T}}^T q_{D_{1T}} \phi_{D_{1T},D_{2B}}^T q_{D_{2B}} \phi_{D_{2B},D_{2T}} \\ \times p_{D_{2T}} \phi_{D_{2T},T_2} \phi_{T_2,D_{3B}}^T q_{D_{3B}} \phi_{D_{3B},D_{3T}}^T p_{D_{3T}} \chi_{D_{3T}}^{fT}. \quad (3.72)$$

The probability of observing the detection history $R \text{ } D_{1B} \text{ } T_1 \text{ FB } D_{2B} \text{ } T_3$ is

$$Pr[R \text{ } D_{1B} \text{ } T_1 \text{ FB } D_{2B} \text{ } T_3] = \Phi_{R,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}} q_{D_{1T}} (1 - f_{D_{1T}}) \phi_{D_{1T},T_1} f_{T_1} \phi_{T_1,D_{2B}}^F p_{D_{2B}} \\ \times \phi_{D_{2B},D_{2T}}^F q_{D_{2T}} \phi_{D_{2T},D_{3B}}^F q_{D_{3B}} \phi_{D_{3B},D_{3T}} q_{D_{3T}} \\ \times \phi_{D_{3T},T_3}^f \chi_{T_3}^f. \quad (3.73)$$

A slightly different detection history, $R \text{ } T_0 \text{ } D_{1B} \text{ } T_1 \text{ FB } D_{2B} \text{ } T_3$, has probability

$$Pr[R \text{ } T_0 \text{ } D_{1B} \text{ } T_1 \text{ FB } D_{2B} \text{ } T_3] = \Phi_{R,T_0} \phi_{T_0,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}}^T q_{D_{1T}} (1 - f_{D_{1T}}^T) \phi_{D_{1T},T_1}^T f_{T_1}^T \\ \times \phi_{T_1,D_{2B}}^{FT} p_{D_{2B}} \phi_{D_{2B},D_{2T}}^F q_{D_{2T}} \phi_{D_{2T},D_{3B}}^F q_{D_{3B}} \phi_{D_{3B},D_{3T}} q_{D_{3T}} \\ \times \phi_{D_{3T},T_3}^f \chi_{T_3}^f. \quad (3.74)$$

In the first detection history (Equation (3.72)), the fallback occurs before the visit to tributary T_0 , at which point the tributary effect overrides the fallback effect. The tributary effect ends after reaching dam 2, and another tributary effect begins after the visit to site T_2 . The final parameter $\chi_{D_{3T}}^{fT}$ indicates that the tributary effect is current, and that the

fish has already fallen back and is assumed not to fall back again. The second two detection histories (Equations (3.73) and (3.74)) are very similar, with the only difference being that that the latter one includes a visit to tributary T_0 . In both of these detection histories, the effect of visiting tributary T_1 is not apparent in the parameterization due to the fallback that occurs upon leaving site T_1 . Unlike Equation (3.73), Equation (3.74) includes the effect of visiting tributary T_0 on the fallback parameters ($f_{D_{1T}}^T$ and $f_{T_1}^T$) and on the fallback transition parameter ($\phi_{T_1, D_{2B}}^{FT}$).

3.9.3.2 Likelihood

The sufficient statistics used in Model 5b are essentially the same type as those used in previous models: the number detected at a site (a), the number detected at a site and again later as either fallback or non-fallback fish (h or b , respectively), and the number that become fallback fish upon leaving a site (d). As in previous models, the number of fish detected upstream of a particular site (g) is also used, and is expressed in terms of the other statistics. With both fallback and tributary memory effects, these statistics must be defined separately for several different groups of fish, each corresponding to a particular type of memory effect, indicated by the superscript on the statistic. Using the number detected at site i as an example, the necessary categories are:

1. Fish that have not fallen back and did not visit the tributary in the previous reach (a_i);
2. Fish that have not fallen back and did visit the tributary in the previous reach (a_i^T);
3. Fish that fell back before the previous reach, and did not visit the tributary in the previous reach (a_i^f);
4. Fish that visited the tributary in the previous reach and fell back prior to visiting that tributary (a_i^{fT});
5. Fish that fell back in the previous reach, and did not visit the tributary in that reach between falling back and reaching site i (a_i^F).

Fish that never fall back, or do not fall back before reaching site i , are accounted for by a_i and a_i^T . Fish that fall back before site i are accounted for by a_i^f , a_i^{fT} , and a_i^F , depending on where they fell back and whether they visited certain tributaries. If i is a dam site, then these three fallback categories are sufficient. If i is a tributary site, then the last category, a_i^F , must be subdivided into subcategories, as follows; Figure 3.14 is provided for reference. Let $a_i^{F(j)}$ represent the number of fish detected at site i that became fallback fish upon leaving site j (downstream of i), and that did *not* visit the tributary immediately downstream of site j . Let $a_i^{F(j)T}$ represent the comparable number of fish that did visit that tributary. For example, $a_{T_k}^{F(D_kT)}$ is the number of fish detected as fallback fish at site T_k that became fallback fish upon leaving the top of the previous dam, and that did not visit the tributary T_{k-1} before falling back (see Figure 3.14 for reference). The statistic $a_{T_k}^{F(D_kT)T}$ is the number of fish detected as fallback fish at site T_k that visited tributary T_{k-1} and then became fallback fish upon leaving dam k . Both $a_{T_k}^{F(D_kT)}$ and $a_{T_k}^{F(D_kT)T}$ are necessary statistics. Another necessary statistic is the number of fish detected as fallback fish at site T_k that fell back within the previous reach, but did not visit the previous tributary before falling back, denoted $a_{T_k}^{FNT}$, where

$$a_{T_k}^{FNT} = a_{T_k}^{F(D_kT)} + a_{T_k}^{F(T_{k-1})} + a_{T_k}^{F(T_{k-1})T} + a_{T_k}^{F(D_{k-1,T})} + a_{T_k}^{F(D_{k-1,T})T}, \quad (3.75)$$

for $k = 1, \dots, K - 1$. Equation (3.75) indicates that the fish included in $a_{T_k}^{FNT}$ are those that fell back at either dam site $D_{k-1,T}$ or tributary site T_{k-1} (regardless of having visited tributary T_{k-2}), or at dam site D_{kT} without having visited tributary T_{k-1} . The same categories of fallback fish are needed for the b statistics for $i = T_k$: $b_{T_k}^{F(D_kT)}$, $b_{T_k}^{F(D_kT)T}$, and $b_{T_k}^{FNT}$.

For the case where i is a dam site ($i = D_{kB}$ or $i = D_{kT}$), it is not necessary to subdivide the category of fallback fish as done for $i = T_k$. For the cases where i is a dam site, define a_i^F to be the number of fish detected at site i that fell back in the previous reach, regardless

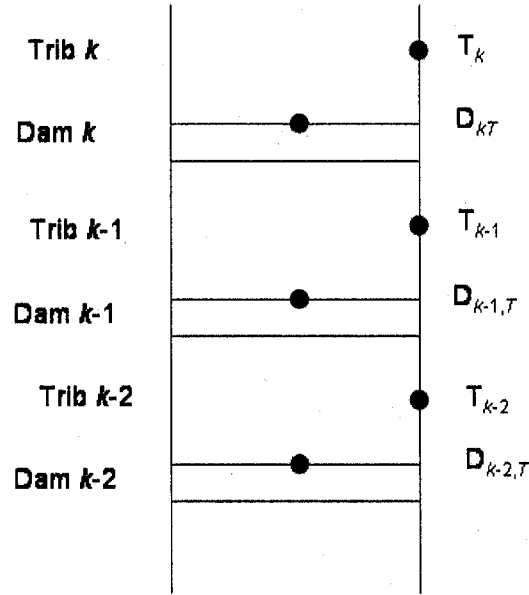


Figure 3.14: Dams $k-2$, $k-1$, and k , and tributaries $k-2$, $k-1$, and k , along with detection sites $D_{k-2,T}$, T_{k-2} , $D_{k-1,T}$, T_{k-1} , D_{kT} , and T_k .

of having visited the tributary before the fallback site:

$$a_{D_{kB}}^F = \begin{cases} a_{D_{1B}}^{F(R)} + a_{D_{1B}}^{F(T_0)} & \text{for } k = 1; \\ a_{D_{kB}}^{F(D_{k-1,T})} + a_{D_{kB}}^{F(D_{k-1,T})T} + a_{D_{kB}}^{F(T_{k-1})} + a_{D_{kB}}^{F(T_{k-1})T} & \text{for } k = 2, \dots, K. \end{cases} \quad (3.76)$$

The definitions in Equation (3.76) are also valid if D_{kB} is replaced by D_{kT} ; the statistics $b_{D_{kB}}^F$ and $b_{D_{kT}}^F$ are defined analogously.

The statistics a_i^f , a_i^{fT} , b_i^f , and b_i^{fT} account for fish detected at site i that fell back before site i and that are not accounted for by the statistics a_i^F and b_i^F statistics described above.

Finally, to simplify the presentation of the minimal sufficient statistics and the likelihood, define the following statistics to be 0: $a_{D_{1B}}^f$, $a_{D_{1T}}^f$, $a_{T_1}^f$, $b_{D_{1B}}^f$, $b_{D_{1T}}^f$, $b_{T_1}^f$, $b_{T_0}^{fT}$, and $b_{T_0}^{FT}$. The g statistics can be expressed in terms of the other summary statistics as follows:

$$\begin{aligned}
g_R &= b_R + h_R; \\
g_{T_0} &= g_R - d_R - (a_{T_0} - b_{T_0} - h_{T_0}); \\
g_{T_k} &= g_{D_{kT}} - d_{D_{kT}} - (a_{T_k} - b_{T_k} - h_{T_k}) && \text{for } k = 1, \dots, K-1; \\
g_{T_0}^T &= 0; \\
g_{T_0}^T &= g_{D_{kT}}^T - d_{D_{kT}}^T - (a_{T_k}^T - b_{T_k}^T - h_{T_k}^T) && \text{for } k = 1, \dots, K-1; \\
g_{T_k}^f &= 0 && \text{for } k = 0, 1; \\
g_{T_k}^f &= g_{D_{kT}}^f - (a_{T_k}^f - b_{T_k}^f) && \text{for } k = 2, \dots, K-1; \\
g_{T_0}^{fT} &= 0; \\
g_{T_0}^{fT} &= g_{D_{kT}}^{fT} - (a_{T_k}^{fT} - b_{T_k}^{fT}) && \text{for } k = 1, \dots, K-1; \\
g_{T_0}^F &= d_R - (a_{T_0}^F - b_{T_0}^F); \\
g_{T_k}^F &= g_{D_{kT}}^F + d_{kT} + d_{kT}^T - (a_{T_k}^{FNT} + a_{T_k}^{F(D_{kT})T}) \\
&\quad + (b_{T_k}^{FNT} + b_{T_k}^{F(D_{kT})T}) && \text{for } k = 1, \dots, K-1; \\
G_{T_0} &= g_{T_0} + g_{T_0}^F; \\
G_{T_1} &= g_{T_1} + g_{T_1}^T + g_{T_1}^{fT} + g_{T_1}^F; \\
G_{T_k} &= g_{T_k} + g_{T_k}^T + g_{T_k}^f + g_{T_k}^{fT} + g_{T_k}^F && \text{for } k = 2, \dots, K-1; \\
g_{D_{1B}} &= g_{T_0} - b_{T_0} - h_{T_0} - (a_{D_{1B}} - b_{D_{1B}} - h_{D_{1B}}); \\
g_{D_{kB}} &= g_{T_{k-1}} + g_{T_{k-1}}^T - (b_{T_{k-1}} + h_{T_{k-1}}) - (b_{T_{k-1}}^T + h_{T_{k-1}}^T) \\
&\quad - (a_{D_{kB}} - b_{D_{kB}} - h_{D_{kB}}) && \text{for } k = 2, \dots, K; \\
g_{D_{1B}}^T &= b_{T_0} + h_{T_0} - d_{T_0} - (a_{D_{1B}}^T - b_{D_{1B}}^T - h_{D_{1B}}^T); \\
g_{D_{kB}}^T &= b_{T_{k-1}} + h_{T_{k-1}} - d_{T_{k-1}} + b_{T_{k-1}}^T + h_{T_{k-1}}^T - d_{T_{k-1}}^T \\
&\quad - (a_{D_{kB}}^T - b_{D_{kB}}^T - h_{D_{kB}}^T) && \text{for } k = 2, \dots, K;
\end{aligned}$$

$$\begin{aligned}
g_{D_{1B}}^f &= 0; \\
g_{D_{kB}}^f &= g_{T_{k-1}}^F + g_{T_{k-1}}^f + g_{T_{k-1}}^{fT} - d_{D_{k-1},T} - d_{D_{k-1},T}^T - b_{T_{k-1}}^{FNT} \\
&\quad - b_{D_{k-1}}^{F(D_{k-1},T)T} - b_{T_{k-1}}^f - b_{T_{k-1}}^{fT} + b_{T_{k-1}}^{F(D_{k-1},T)} + b_{T_{k-1}}^{F(D_{k-1},T)T} \\
&\quad - (a_{D_{kB}}^f - b_{D_{kB}}^f) \quad \text{for } k = 2, \dots, K; \\
g_{D_{1B}}^{fT} &= b_{T_0}^F - (a_{D_{1B}}^{fT} - b_{D_{1B}}^{fT}); \\
g_{D_{kB}}^{fT} &= b_{T_{k-1}}^{FNT} + b_{D_{k-1}}^{F(D_{k-1},T)T} + b_{T_{k-1}}^f + b_{T_{k-1}}^{fT} - (a_{D_{kB}}^{fT} - b_{D_{kB}}^{fT}) \quad \text{for } k = 2, \dots, K; \\
g_{D_{1B}}^F &= d_R + d_{T_0} - a_{T_0}^F - (a_{D_{1B}}^F - b_{D_{1B}}^F); \\
g_{D_{kB}}^F &= d_{D_{k-1},T} + d_{D_{k-1},T}^T + d_{T_{k-1}} + d_{T_{k-1}}^T - a_{T_{k-1}}^{F(D_{k-1},T)} \\
&\quad - a_{T_{k-1}}^{F(D_{k-1},T)T} - (a_{D_{kB}}^F - b_{D_{kB}}^F) \quad \text{for } k = 2, \dots, K; \\
G_{D_{1B}} &= g_{D_{1B}} + g_{D_{1B}}^T + g_{D_{1B}}^{fT} + g_{D_{1B}}^F; \\
G_{D_{kB}} &= g_{D_{kB}} + g_{D_{kB}}^T + g_{D_{kB}}^f + g_{D_{kB}}^{fT} + g_{D_{kB}}^F \quad \text{for } k = 2, \dots, K; \\
g_{D_{kT}} &= g_{D_{kB}} - (a_{D_{kT}} - b_{D_{kT}} - h_{D_{kT}}) \quad \text{for } k = 1, \dots, K; \\
g_{D_{kT}}^T &= g_{D_{kB}}^T - (a_{D_{kT}}^T - b_{D_{kT}}^T - h_{D_{kT}}^T) \quad \text{for } k = 1, \dots, K; \\
g_{D_{1T}}^f &= 0; \\
g_{D_{kT}}^f &= g_{D_{kB}}^f - (a_{D_{kT}}^f - b_{D_{kT}}^f) \quad \text{for } k = 2, \dots, K; \\
g_{D_{kT}}^{fT} &= g_{D_{kB}}^{fT} - (a_{D_{kT}}^{fT} - b_{D_{kT}}^{fT}) \quad \text{for } k = 1, \dots, K; \\
g_{D_{kT}}^F &= g_{D_{kB}}^F - (a_{D_{kT}}^F - b_{D_{kT}}^F) \quad \text{for } k = 1, \dots, K.
\end{aligned}$$

The summary statistics used in Model 5b are listed in Table 3.44.

The minimal sufficient statistics corresponding to dam sites are the numbers of fish in the various tributary and fallback categories that are seen for the last time at those sites ($a - b - h$), and the number of fish that become fallback fish upon leaving those sites (d). Generally, the minimal sufficient statistics for tributary sites are the number of fish detected at those sites (a), the number detected there and again upstream (b , h), and the number that fall back upon leaving those sites (d), each in the various tributary and fallback categories. Minimal sufficient statistics for Model 5b are listed in Table 3.45. For a study with K dams, there are $29K - 14$ minimal sufficient statistics in the full model, with $21K - 6$ parameters.

Thus, numerical methods must be used to fit the model via maximum likelihood.

Table 3.44: Summary statistics for Model 5b, the Fallback and Tributary model with short-term memory. The number of dams is K .

Statistic	Definition
a_i	Number of fish detected at site i that had not fallen back before site i and had not visited the tributary (if any) in the reach immediately preceding site i , for $i = T_0, D_{1B}, D_{1T}, T_1, \dots, T_K$;
a_i^T	Number of fish detected at site i that had not fallen back before site i and had visited the tributary in the reach immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, T_K$;
a_i^f	For $i = D_{kB}, D_{kT}$, or T_k , the number of fish detected at site i that had fallen back before reaching dam $k - 1$ and had not visited tributary T_{k-1} , for $k = 2, \dots, K$;
a_i^{fT}	For $i = D_{kB}, D_{kT}$, or T_k , the number of fish detected at site i that had visited site T_{k-1} and had fallen back before reaching that site, for $k = 1, \dots, K$;
a_i^F	For $i = D_{1B}$ or D_{1T} , the number of fish detected at site i that either had fallen back upon leaving the initial release site (R) without subsequently visiting site T_0 , or else had fallen back upon leaving site T_0 ;
	For $i = D_{kB}$ or D_{kT} with $k = 2, \dots, K$, the number of fish detected at site i that either had fallen back upon leaving dam $k - 1$ without subsequently visiting site T_{k-1} , or else had fallen back upon leaving site T_{k-1} ;
A_i	For $i = D_{kB}$ or D_{kT} , the number of fish detected at site i , for $k = 1, \dots, K$; $= a_i + a_i^T + a_i^f + a_i^{fT} + a_i^F$;
$a_{T_0}^{F(R)}$	Number of fish detected at site T_0 as fallback fish;
$a_{T_k}^{FNT}$	For $k = 1$, the number of fish detected at site T_1 that either had fallen back upon leaving dam 1 without having first visited site T_0 , or else had fallen back upon leaving either site R or site T_0 ;
	For $k = 2, \dots, K$, the number of fish detected at site T_k that either had fallen back upon leaving dam k without having first visited site T_{k-1} , or else had fallen back upon leaving either site T_{k-1} or dam $k - 1$;
$a_{T_k}^{F(D_{kT})}$	Number of fish detected at site T_k that had fallen back upon leaving dam k without having first visited site T_{k-1} , for $k = 1, \dots, K$;
$a_{T_k}^{F(D_{kT})T}$	Number of fish detected at site T_k that had fallen back upon leaving dam k after visiting site T_{k-1} , for $k = 1, \dots, K$;
b_i	Number of fish detected both at site i and upstream of site i without

Table 3.44 continued

Statistic	Definition
	having fallen back or having visited the tributary (if any) in the reach immediately preceding site i , for $i = R, T_0, D_{1B}, D_{1T}, T_1, \dots, D_{KT}$;
b_i^T	Number of fish detected both at site i and upstream of site i without having fallen back but had visited the tributary in the reach immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$;
b_i^f	For $i = D_{kB}, D_{kT}$, or T_k , the number of fish detected at site i and again upstream that had fallen back before reaching dam $k - 1$ and had not visited site T_{k-1} , for $k = 2, \dots, K$ for $i = D_{kB}$ or D_{kT} , and $k = 2, \dots, K - 1$ for $i = T_k$;
b_i^{fT}	For $i = D_{kB}, D_{kT}$, or T_k , the number of fish detected at site i and again upstream of site i that had visited site T_{k-1} and had fallen back before reaching site T_{k-1} , for $k = 1, \dots, K$ for $i = D_{kB}$ or D_{kT} , and $k = 1, \dots, K - 1$ for $i = T_k$;
b_i^F	For $i = D_{1B}$ or D_{1T} , the number of fish detected at site i and again upstream that either had fallen back upon leaving site R without subsequently visiting site T_0 , or else had fallen back upon leaving site T_0 ;
	For $i = D_{kB}$ or D_{kT} with $k = 2, \dots, K$, the number of fish detected at site i and again upstream that either had fallen back upon leaving dam $k - 1$ without subsequently visiting site T_{k-1} , or else had fallen back upon leaving site T_{k-1} ;
$b_{T_0}^{F(R)}$	Number of fish detected as fallback fish at site T_0 and detected again upstream;
$b_{T_k}^{FNT}$	For $k = 1$, the number of fish detected at site T_1 and again upstream that either had fallen back upon leaving dam 1 without first visiting site T_0 , or else had fallen back upon leaving either site R or T_0 ;
	For $k = 2, \dots, K - 1$, the number of fish detected at site T_k and again upstream that either had fallen back upon leaving dam k without having first visited site T_{k-1} , or else had fallen back upon leaving either site T_{k-1} or dam $k - 1$;
$b_{T_k}^{F(D_{kT})}$	Number of fish detected at site T_k and again upstream that had fallen back upon leaving dam k without having first visited site T_{k-1} , for $k = 1, \dots, K - 1$;
$b_{T_k}^{F(D_{kT})T}$	Number of fish detected at site T_k and again upstream that had fallen back upon leaving dam k after visiting site T_{k-1} , for $k = 1, \dots, K - 1$;
h_i	Number of fish detected at site i that had neither fallen back before

Table 3.44 continued

Statistic	Definition
	reaching site i , nor visited the tributary in the reach immediately preceding site i , and that were next detected as fallback fish upstream of site i , for $i = R, T_0, D_{1T}, T_1, D_{2T}, \dots, T_K$;
h_i^T	Number of fish detected at site i that had not fallen back before reaching site i but had visited the tributary in the reach immediately preceding site i , and that were next detected as fallback fish upstream of site i , for $i = D_{1T}, T_1, D_{2T}, \dots, T_K$;
d_R	Number of fish first detected as fallback fish either at site T_0 , or at dam 1 without having visited T_0 first as non-fallback fish;
d_{T_k}	Number of fish detected at site T_k as non-fallback fish and subsequently detected at dam $k + 1$ as fallback fish, that did not visit tributary T_{k-1} (if it exists), for $k = 0, 1, \dots, K - 1$;
$d_{T_k}^T$	Number of fish detected at site T_k as non-fallback fish and subsequently detected at dam $k + 1$ as fallback fish, that did visit tributary T_{k-1} , for $k = 1, \dots, K - 1$;
$d_{D_{kT}}$	Number of fish detected as fallback fish for the first time at either site T_k or dam $k + 1$ that had visited neither T_k nor T_{k-1} (if it exists) as non-fallback fish, for $k = 1, \dots, K - 1$;
$d_{D_{kT}}^T$	Number of fish detected as fallback fish for the first time at either site T_k or dam $k + 1$ that had visited site T_{k-1} but not site T_k as non-fallback fish, for $k = 1, \dots, K - 1$;
g_i	Number of fish detected after site i that had neither fallen back before reaching site i nor had visited the tributary in the reach immediately preceding site i (if any), for $i = R, T_0, D_{1B}, D_{1T}, \dots, D_{KT}$;
g_i^T	Number of fish detected after site i that had not fallen back before reaching site i and had visited the tributary in the reach immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$;
g_i^f	For $i = D_{kB}, D_{kT}$, or T_k , the number of fish detected after site i that had fallen back before reaching dam $k - 1$ and had not been detected at site T_{k-1} , for $k = 2, \dots, K$ for $i = D_{kB}$ or D_{kT} , and $k = 2, \dots, K - 1$ for $i = T_k$;
g_i^{fT}	For $i = D_{kB}, D_{kT}$, or T_k , the number of fish detected after site i that visited site T_{k-1} and had fallen back before reaching site T_{k-1} , for $k = 1, \dots, K$ for $i = D_{kB}$ or D_{kT} , and $k = 1, \dots, K - 1$ for $i = T_k$;
g_i^F	For $i = D_{1B}$ or D_{1T} , the number of fish detected after site i that either had fallen back upon leaving the release site (R) without subsequently visiting site T_0 , or else had fallen back upon leaving site T_0 ;
	For $i = D_{kB}$ or D_{kT} with $k = 2, \dots, K$, the number of fish detected after site i that either had fallen back upon leaving dam $k - 1$ without subsequently visiting site T_{k-1} , or else had fallen back upon leaving site

Table 3.44 continued

Statistic	Definition
	T_{k-1} ;
g_i^F	For $i = T_1$, the number of fish detected after site i that had fallen back upon leaving either site R , site T_0 , or dam 1, without visiting site T_0 after falling back;
	For $i = T_k$ with $k = 2, \dots, K - 1$, the number of fish detected after site i that had fallen back upon leaving either dam k , tributary T_{k-1} , or dam $k - 1$, without visiting tributary T_{k-1} after falling back;
G_i	Number of fish detected after site i , for $i = T_k$ ($k = 0, \dots, K - 1$) or $i = D_{kB}$ ($k = 1, \dots, K$).

Table 3.45: Minimal sufficient statistics for Model 5b, the Fallback and Tributary model with short-term memory. The number of dams is K .

Statistic	Definition
a_{T_k}	Number of fish detected at site T_k that had neither fallen back before reaching site i nor visited tributary T_{k-1} (if it exists), for $k = 0, 1, \dots, K - 1$;
$a_{T_k}^T$	Number of fish detected at site T_k that had not fallen back before reaching site i and had visited tributary T_{k-1} $k = 1, \dots, K - 1$;
$a_{T_k}^f$	The number of fish detected at site T_k that had fallen back before reaching dam $k - 1$ and had not visited tributary T_{k-1} , for $k = 2, \dots, K - 1$;
$a_{T_k}^{fT}$	The number of fish detected at site T_k that had visited tributary T_{k-1} and had fallen back downstream of site T_{k-1} , for $k = 1, \dots, K - 1$;
$a_{T_0}^{F(R)}$	Number of fish detected at site T_0 as fallback fish;
$a_{T_k}^{FNT}$	For $k = 1$, the number of fish detected at site T_1 that either had fallen back upon leaving dam 1 without having first visited site T_0 , or else had fallen back upon leaving either site R or site T_0 ;
	For $k = 2, \dots, K - 1$, the number of fish detected at site T_k that either had fallen back upon leaving dam k without having first visited site T_{k-1} , or else had fallen back upon leaving either site T_{k-1} or dam $k - 1$;
$a_{T_k}^{F(D_kT)}$	Number of fish detected at site T_k that had fallen back upon leaving

Table 3.45 continued

Statistic	Definition
$a_{T_k}^{F(D_{kT})T}$	dam k without having first visited site T_{k-1} , for $k = 1, \dots, K - 1$; Number of fish detected at site T_k that had fallen back upon leaving dam k after visiting site T_{k-1} , for $k = 1, \dots, K - 1$;
A_i	Number of fish detected at site i , for $i = D_{kB}$ or $i = D_{kT}$ with $k = 1, \dots, K$; $= a_i + a_i^T + a_i^f + a_i^{fT} + a_i^F$;
$b_R + h_R$	Number of fish detected after the initial release;
$b_{T_k} + h_{T_k}$	Number of fish detected both at site T_k and again upstream that had neither fallen back before reaching site T_k nor visited site T_{k-1} (if it exists), for $k = 0, 1, \dots, K - 1$;
$b_{T_k}^T + h_{T_k}^T$	Number of fish detected both at site T_k and again upstream that had not fallen back before reaching site T_k and had visited site T_{k-1} , for $k = 1, \dots, K - 1$;
$b_{T_k}^f$	The number of fish detected at site T_k and again upstream that had fallen back before reaching dam $k - 1$ and had not visited site T_{k-1} , for $k = 2, \dots, K - 1$;
$b_{T_k}^{fT}$	The number of fish detected at site T_k and again upstream that had visited site T_{k-1} and had fallen back before reaching T_{k-1} , for $k = 1, \dots, K - 1$;
$b_{T_0}^{F(R)}$	Number of fish detected as fallback fish at site T_0 and detected again upstream;
$b_{T_k}^{FNT}$	For $k = 1$, the number of fish detected at site T_1 and again upstream that either had fallen back upon leaving dam 1 without first visiting site T_0 , or else had fallen back upon leaving either site R or T_0 ; For $k = 2, \dots, K - 1$, the number of fish detected at site T_k and again upstream that either had fallen back upon leaving dam k without having first visited site T_{k-1} , or else had fallen back upon leaving either site T_{k-1} or dam $k - 1$;
$b_{T_k}^{F(D_{kT})}$	Number of fish detected at site T_k and again upstream that had fallen back upon leaving dam k without have first visited site T_{k-1} , for $k = 1, \dots, K - 1$;
$b_{T_k}^{F(D_{kT})T}$	Number of fish detected at site T_k and again upstream that had fallen back upon leaving dam k after visiting site T_{k-1} , for $k = 1, \dots, K - 1$;
d_R	Number of fish first detected as fallback fish either at site T_0 , or at dam 1 without having visited T_0 first as non-fallback fish;
d_{T_k}	Number of fish detected at site T_k as non-fallback fish and

Table 3.45 continued

Statistic	Definition
$d_{T_k}^T$	subsequently detected at dam $k + 1$ as fallback fish, that did not visit site T_{k-1} (if it exists), for $k = 0, 1, \dots, K - 1$; Number of fish detected at site T_k as non-fallback fish and subsequently detected at dam $k + 1$ as fallback fish, that did visit site T_{k-1} , for $k = 1, \dots, K - 1$;
$d_{D_{kT}}$	Number of fish detected as fallback fish for the first time at either site T_k or dam $k + 1$ that had visited neither T_k nor T_{k-1} (if it exists) as non-fallback fish, for $k = 1, \dots, K - 1$;
$d_{D_{kT}}^T$	Number of fish detected as fallback fish for the first time at either site T_k or dam $k + 1$ that had visited site T_{k-1} but not site T_k as non-fallback fish, for $k = 1, \dots, K - 1$;
$a_i - b_i - h_i$	Number of fish detected for the last time at site i that had not fallen back before reaching site i and had not visited the tributary in the reach immediately below site i , for $i = D_{kB}$ or D_{kT} with $k = 1, \dots, K$;
$a_i^T - b_i^T - h_i^T$	Number of fish detected for the last time at site i that had not fallen back before reaching site i and had visited the tributary in the reach immediately below site i , for $i = D_{kB}$ or D_{kT} with $k = 1, \dots, K$;
$a_i^f - b_i^f$	For $i = D_{kB}$ or D_{kT} , the number of fish detected for the last time at site i that had fallen back before reaching dam $k - 1$ and had not visited site T_{k-1} , for $k = 2, \dots, K$;
$a_i^{fT} - b_i^{fT}$	For $i = D_{kB}$ or D_{kT} , the number of fish detected for the last time at site i that had visited site T_{k-1} and had fallen back before reaching site T_{k-1} , for $k = 1, \dots, K$;
$a_i^F - b_i^F$	For $i = D_{kB}$ or D_{kT} , the number of fish detected for the last time at site i that either had fallen back upon leaving dam $k - 1$ without subsequently visiting site T_{k-1} , or else had fallen back upon leaving site T_{k-1} , for $k = 1, \dots, K$.

The likelihood for Model 5b can be expressed as follows:

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \Phi_{R,T_0}^{a_{T_0}} \Phi_{R,D_{1B}}^{g_{T_0}-b_{T_0}-h_{T_0}} (\Phi_{R,T_0}^F)^{a_{T_0}^{F(R)}} (\Phi_{R,D_{1B}}^F)^{d_R-a_{T_0}^{F(R)}} \\
& \times (\chi_{T_0}^F)^{a_{T_0}^{F(R)}-b_{T_0}^{F(R)}} (\phi_{T_0,D_{1B}}^F)^{d_{T_0}+b_{T_0}^{F(R)}} \\
& \times \prod_{k=0}^{K-1} \left\{ \chi_{T_k}^{a_{T_k}-b_{T_k}-h_{T_k}} f_{T_k}^{d_{T_k}} (1-f_{T_k})^{b_{T_k}+h_{T_k}-d_{T_k}} \phi_{T_k,D_{k+1,B}}^{b_{T_k}+h_{T_k}-d_{T_k}+b_{T_k}^f} \right\} \\
& \times \prod_{k=1}^K \left\{ \phi_{D_{kB},D_{kT}}^{g_{D_{kB}}+g_{D_{kT}}^f} (\phi_{D_{kB},D_{kT}}^T)^{g_{D_{kB}}+g_{D_{kT}}^{fT}} (\phi_{D_{kB},D_{kT}}^F)^{g_{D_{kB}}^F} \phi_{D_{kT},T_k}^{a_{T_k}+a_{T_k}^f} (\phi_{D_{kT},T_k}^T)^{a_{T_k}^T+a_{T_k}^{fT}} \right\}
\end{aligned}$$

$$\begin{aligned}
& \times (\phi_{D_{kT}, T_k}^F)^{a_{T_k}^{FNT}} p_{D_{kB}}^{A_{D_{kB}}} q_{D_{kB}}^{G_{T_{k-1}} - A_{D_{kB}}} p_{D_{kT}}^{A_{D_{kT}}} q_{D_{kT}}^{G_{D_{kB}} - A_{D_{kT}}} \chi_{D_{kB}}^{a_{D_{kB}} - b_{D_{kB}} - h_{D_{kB}}} \\
& \times (\chi_{D_{kB}}^T)^{a_{D_{kB}}^T - b_{D_{kB}}^T - h_{D_{kB}}^T} (\chi_{D_{kB}}^{fT})^{a_{D_{kB}}^{fT} - b_{D_{kB}}^{fT}} (\chi_{D_{kB}}^F)^{a_{D_{kB}}^F - b_{D_{kB}}^F} \chi_{D_{kT}}^{a_{D_{kT}} - b_{D_{kT}} - h_{D_{kT}}} \\
& \times (\chi_{D_{kT}}^T)^{a_{D_{kT}}^T - b_{D_{kT}}^T - h_{D_{kT}}^T} (\chi_{D_{kT}}^{fT})^{a_{D_{kT}}^{fT} - b_{D_{kT}}^{fT}} (\chi_{D_{kT}}^F)^{a_{D_{kT}}^F - b_{D_{kT}}^F} \Big\} \\
& \times \prod_{k=1}^{K-1} \left\{ f_{D_{kT}}^{d_{D_{kT}}} (1 - f_{D_{kT}})^{g_{D_{kT}} - d_{D_{kT}}} (f_{D_{kT}}^T)^{d_{D_{kT}}^T} (1 - f_{D_{kT}}^T)^{g_{D_{kT}}^T - d_{D_{kT}}^T} (\phi_{D_{kT}, T_k}^{FT})^{a_{T_k}^{FT}} \right. \\
& \quad \times \phi_{D_{kT}, D_{k+1}, B}^{g_{T_k} + g_{T_k}^f - (b_{T_k} + h_{T_k} + b_{T_k}^f)} (\phi_{D_{kT}, D_{k+1}, B}^T)^{g_{T_k}^T + g_{T_k}^{fT} - (b_{T_k}^T + h_{T_k}^T + b_{T_k}^{fT})} \\
& \quad \times (\phi_{D_{kT}, D_{k+1}, B}^F)^{g_{D_{kT}}^F + d_{D_{kT}} - a_{T_k}^{FNT}} (\phi_{D_{kT}, D_{k+1}, B}^{FT})^{d_{D_{kT}}^T - a_{T_k}^{F(D_{kT})T}} (f_{T_k}^T)^{d_{T_k}^T} \\
& \quad \times (1 - f_{T_k}^T)^{b_{T_k}^T + h_{T_k}^T - d_{T_k}^T} (\phi_{T_k, D_{k+1}, B}^T)^{b_{T_k}^T + h_{T_k}^T - d_{T_k}^T + b_{T_k}^{fT}} \\
& \quad \times (\phi_{T_k, D_{k+1}, B}^F)^{d_{T_k} + b_{T_k}^{FNT} + b_{T_k}^{F(D_{kT})T}} (\phi_{T_k, D_{k+1}, B}^{FT})^{d_{T_k}^T} (\chi_{T_k}^T)^{a_{T_k}^T - b_{T_k}^T - h_{T_k}^T} (\chi_{T_k}^{fT})^{a_{T_k}^{fT} - b_{T_k}^{fT}} \\
& \quad \times (\chi_{T_k}^F)^{a_{T_k}^{FNT} + a_{T_k}^{F(D_{kT})T} - b_{T_k}^{FNT} - b_{T_k}^{F(D_{kT})T}} \Big\} \\
& \times \prod_{k=2}^K \left\{ (\chi_{D_{kB}}^f)^{a_{D_{kB}}^f - b_{D_{kB}}^f} (\chi_{D_{kT}}^f)^{a_{D_{kT}}^f - b_{D_{kT}}^f} \right\} \prod_{k=2}^{K-1} (\chi_{T_k}^f)^{a_{T_k}^f - b_{T_k}^f}, \tag{3.77}
\end{aligned}$$

where N is the size of the initial release and K is the number of dams. Equation (3.77) may be tailored to a particular data set by specifying K , removing any extraneous parameters, and renaming parameters according to observed detections, if necessary. This is done for the 1996 Chinook salmon data set below.

The initial values used for Models 3b, 4, and 5a may be used for Model 5b. The values from the previous models may need to be modified to ensure that all derived parameters (e.g., χ_i , χ_i^T , and χ_i^F) are between 0 and 1.

3.9.3.3 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival, is S_{sys} , defined as follows:

$$S_{sys} = \eta_R,$$

where

$$\eta_R = \Phi_{R,T_0} \eta_{T_0} + \Phi_{R,T_0}^F \eta_{T_0}^F + \Phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \eta_{D_{1T}} + \Phi_{R,D_{1B}}^F \phi_{D_{1B},D_{1T}}^F \eta_{D_{1T}}^F,$$

with

$$\begin{aligned} \eta_{D_{kT}} &= (1 - f_{D_{kT}}) \{ \phi_{D_{kT},T_k} \eta_{T_k} + \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}} \} \\ &\quad + f_{D_{kT}} \{ \phi_{D_{kT},T_k}^F \eta_{T_k}^F + \phi_{D_{kT},D_{k+1,B}}^F \phi_{D_{k+1,B},D_{k+1,T}}^F \eta_{D_{k+1,T}}^F \}, \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}} &= 1; \\ \eta_{D_{kT}}^T &= (1 - f_{D_{kT}}^T) \{ \phi_{D_{kT},T_k}^T \eta_{T_k}^T + \phi_{D_{kT},D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}} \} \\ &\quad + f_{D_{kT}}^T \{ \phi_{D_{kT},T_k}^{FT} \eta_{T_k}^F + \phi_{D_{kT},D_{k+1,B}}^{FT} \phi_{D_{k+1,B},D_{k+1,T}}^F \eta_{D_{k+1,T}}^F \}, \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}}^T &= 1; \\ \eta_{D_{kT}}^f &= \phi_{D_{kT},T_k} \eta_{T_k}^f + \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}}^f, \quad k = 2, \dots, K-1; \\ \eta_{D_{KT}}^f &= 1; \\ \eta_{D_{kT}}^{fT} &= \phi_{D_{kT},T_k}^T \eta_{T_k}^{fT} + \phi_{D_{kT},D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}}^f, \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}}^{fT} &= 1; \\ \eta_{D_{kT}}^F &= \phi_{D_{kT},T_k}^F \eta_{T_k}^F + \phi_{D_{kT},D_{k+1,B}}^F \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}}^f, \quad k = 1, \dots, K-1; \\ \eta_{D_{KT}}^F &= 1; \\ \eta_{T_k} &= (1 - f_{T_k}) \phi_{T_k,D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}}^T \eta_{D_{k+1,T}}^T \\ &\quad + f_{T_k} \phi_{T_k,D_{k+1,B}}^F \phi_{D_{k+1,B},D_{k+1,T}}^F \eta_{D_{k+1,T}}^F, \quad k = 0, \dots, K-1; \\ \eta_{T_k}^T &= (1 - f_{T_k}^T) \phi_{T_k,D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}}^T \eta_{D_{k+1,T}}^T \\ &\quad + f_{T_k}^T \phi_{T_k,D_{k+1,B}}^{FT} \phi_{D_{k+1,B},D_{k+1,T}}^F \eta_{D_{k+1,T}}^F, \quad k = 1, \dots, K-1; \\ \eta_{T_k}^f &= \phi_{T_k,D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}}^T \eta_{D_{k+1,T}}^{fT}, \quad k = 2, \dots, K-1; \\ \eta_{T_k}^{fT} &= \phi_{T_k,D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}}^T \eta_{D_{k+1,T}}^{fT}, \quad k = 1, \dots, K-1; \\ \eta_{T_k}^F &= \phi_{T_k,D_{k+1,B}}^F \phi_{D_{k+1,B},D_{k+1,T}}^T \eta_{D_{k+1,T}}^{fT}, \quad k = 0, \dots, K-1. \end{aligned} \tag{3.78}$$

The variance estimator of \hat{S}_{sys} is defined in Appendix B.

The probability of unaccountable loss, μ_R , is defined for Model 5b as follows:

$$\begin{aligned}\mu_R = 1 - \Phi_{R,T_0}(1 - \mu_{T_0}) - \Phi_{R,T_0}^F(1 - \mu_{T_0}^F) - \Phi_{R,D_{1B}}\phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}) \\ - \Phi_{R,D_{1B}}^F\phi_{D_{1B},D_{1T}}^F(1 - \mu_{D_{1T}}^F),\end{aligned}\quad (3.79)$$

where

$$\begin{aligned}1 - \mu_{T_k} &= 1 - (1 - f_{T_k})\phi_{T_k,D_{k+1,B}} \left\{ 1 - \phi_{D_{k+1,B},D_{k+1,T}}^T(1 - \mu_{D_{k+1,T}}^T) \right\} \\ &\quad - f_{T_k}\phi_{T_k,D_{k+1,B}}^F \left\{ 1 - \phi_{D_{k+1,B},D_{k+1,T}}^F(1 - \mu_{D_{k+1,T}}^F) \right\}, \quad k = 0, \dots, K-1; \\ 1 - \mu_{T_k}^T &= 1 - (1 - f_{T_k}^T)\phi_{T_k,D_{k+1,B}}^T \left\{ 1 - \phi_{D_{k+1,B},D_{k+1,T}}^T(1 - \mu_{D_{k+1,T}}^T) \right\} \\ &\quad - f_{T_k}^T\phi_{T_k,D_{k+1,B}}^{FT} \left\{ 1 - \phi_{D_{k+1,B},D_{k+1,T}}^F(1 - \mu_{D_{k+1,T}}^F) \right\}, \quad k = 1, \dots, K-1; \\ 1 - \mu_{T_k}^f &= 1 - \phi_{T_k,D_{k+1,B}} + \phi_{T_k,D_{k+1,B}}\phi_{D_{k+1,B},D_{k+1,T}}^T(1 - \mu_{D_{k+1,T}}^{fT}), \quad k = 2, \dots, K-1; \\ 1 - \mu_{T_k}^{fT} &= 1 - \phi_{T_k,D_{k+1,B}}^T + \phi_{T_k,D_{k+1,B}}^T\phi_{D_{k+1,B},D_{k+1,T}}^T(1 - \mu_{D_{k+1,T}}^{fT}), \quad k = 1, \dots, K-1; \\ 1 - \mu_{T_k}^F &= 1 - \phi_{T_k,D_{k+1,B}}^F + \phi_{T_k,D_{k+1,B}}^F\phi_{D_{k+1,B},D_{k+1,T}}^T(1 - \mu_{D_{k+1,T}}^{fT}), \quad k = 0, \dots, K-1; \\ 1 - \mu_{D_{kT}} &= (1 - f_{D_{kT}})\phi_{D_{kT},T_k}(1 - \mu_{T_k}) + f_{D_{kT}}\phi_{D_{kT},T_k}^F(1 - \mu_{T_k}^F) \\ &\quad + (1 - f_{D_{kT}})\phi_{D_{kT},D_{k+1,B}}\phi_{D_{k+1,B},D_{k+1,T}}(1 - \mu_{D_{k+1,T}}) \\ &\quad + f_{D_{kT}}\phi_{D_{kT},D_{k+1,B}}^F\phi_{D_{k+1,B},D_{k+1,T}}^F(1 - \mu_{D_{k+1,T}}^F), \quad k = 1, \dots, K-1; \\ 1 - \mu_{D_{kT}} &= 1, \quad k = K; \\ 1 - \mu_{D_{kT}}^T &= (1 - f_{D_{kT}}^T)\phi_{D_{kT},T_k}^T(1 - \mu_{T_k}^T) + f_{D_{kT}}^T\phi_{D_{kT},T_k}^{FT}(1 - \mu_{T_k}^F) \\ &\quad + (1 - f_{D_{kT}}^T)\phi_{D_{kT},D_{k+1,B}}^T\phi_{D_{k+1,B},D_{k+1,T}}(1 - \mu_{D_{k+1,T}}) \\ &\quad + f_{D_{kT}}^T\phi_{D_{kT},D_{k+1,B}}^{FT}\phi_{D_{k+1,B},D_{k+1,T}}^F(1 - \mu_{D_{k+1,T}}^F), \quad k = 1, \dots, K-1; \\ 1 - \mu_{D_{kT}}^T &= 1, \quad k = K; \\ 1 - \mu_{D_{kT}}^f &= \phi_{D_{kT},T_k}(1 - \mu_{T_k}^f) + \phi_{D_{kT},D_{k+1,B}}\phi_{D_{k+1,B},D_{k+1,T}}(1 - \mu_{D_{k+1,T}}^f), \quad k = 2, \dots, K-1; \\ 1 - \mu_{D_{kT}}^f &= 1, \quad k = K; \\ 1 - \mu_{D_{kT}}^{fT} &= \phi_{D_{kT},T_k}^T(1 - \mu_{T_k}^{fT}) + \phi_{D_{kT},D_{k+1,B}}^T\phi_{D_{k+1,B},D_{k+1,T}}(1 - \mu_{D_{k+1,T}}^f), \quad k = 1, \dots, K-1; \\ 1 - \mu_{D_{kT}}^{fT} &= 1, \quad k = K;\end{aligned}$$

$$\begin{aligned}
1 - \mu_{D_{kT}}^F &= \phi_{D_{kT}, T_k}^F (1 - \mu_{T_k}^F) + \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}^f), & k = 1, \dots, K-1; \\
1 - \mu_{D_{kT}}^F &= 1, & k = K.
\end{aligned}$$

The variance estimator of $\hat{\mu}_R$ is defined in Appendix B.

3.9.3.4 1996 Chinook Data Set

Model 5b is a complicated model with many parameters and minimal sufficient statistics. While there are enough minimal sufficient statistics to estimate all parameters in the general model, it is likely that many minimal sufficient statistics will be 0 and many parameters will be inestimable for a particular data set. This is the case for the 1996 Chinook data set, as is shown by the summary statistics for the full data set ($K = 7$) given in Table 3.46.

As usual, no fish were detected at sites D_{2B} , D_{3B} , D_{6T} , or T_6 , so modifications must be made to the parameters estimated by the likelihood. The parameters ϕ_{ij} and ϕ_{ij}^T are easily modified in the case where either site i or site j is never detected (see Equation (3.80)). Because the memory effect of fallback is temporary, the modification of the ϕ_{ij}^F parameters is not as simple. Consider $\phi_{D_{1T}, D_{2T}}^F$. The superscript F indicates that either the fish fell back during the transition from D_{1T} to D_{2B} , or else that the fish fell back before site D_{1T} and the memory effect still applies during the transition from D_{1T} to D_{2B} . In the former case, the combined transition between D_{1T} and D_{2T} should be $\phi_{D_{1T}, D_{2T}}^F = \phi_{D_{1T}, D_{2B}}^F \phi_{D_{2B}, D_{2T}}^F$. In the latter case, the combined transition between D_{1T} and D_{2T} should be $\phi_{D_{1T}, D_{2T}}^F = \phi_{D_{1T}, D_{2B}}^F \phi_{D_{2B}, D_{2T}}^F$, because the memory effect of the earlier fallback does not apply once the fish reaches site D_{2B} . Similar considerations apply to $\phi_{T_1, D_{2T}}^F$, $\phi_{D_{2T}, D_{3T}}^F$, $\phi_{T_2, D_{3T}}^F$, $\phi_{D_{6B}, D_{7B}}^F$, and $\phi_{D_{6B}, D_{7B}}^{FT}$.

It is possible to express the likelihood in terms of transitions starting and ending at sites D_{2B} and D_{3B} , even though there are no detections at these sites. However, such a model is unstable, and results in highly uncertain parameter estimates. For the 1996 Chinook salmon data set, it is necessary to fix $\phi_{D_{kB}, D_{kT}}^F = \phi_{D_{kB}, D_{kT}}^T = \phi_{D_{kB}, D_{kT}}$ for $k = 2, 3$ in order to fit such a model. This restriction is tantamount to defining $\phi_{D_{1T}, D_{2T}}^F = \phi_{D_{1T}, D_{2B}}^F \phi_{D_{2B}, D_{2T}}^F$ and $\phi_{T_1, D_{2T}}^F = \phi_{T_1, D_{2B}}^F \phi_{D_{2B}, D_{2T}}^F$, with comparable definitions for transitions to D_{3T} (see

Equation (3.81)). Thus, the combination parameters shown in Equations (3.80) and (3.81) are used to fit Model 5b to the 1996 Chinook salmon data set. (Note: Examination of the sufficient statistics (below) leads to removal from the likelihood of several of the transition parameters involving these missing detection sites, either because they cannot be estimated for this data set or because they are unnecessary. The parameters to be removed from Equations (3.80) and (3.81) are $\phi_{D_{1T}, D_{2T}}^{FT}$, $\phi_{T_1, D_{2T}}^T$, $\phi_{T_1, D_{2T}}^{FT}$, $\phi_{D_{2T}, D_{3T}}^{FT}$, $\phi_{T_2, D_{3T}}^F$, $\phi_{T_2, D_{3T}}^{FT}$, $\phi_{D_{6B}, D_{7B}}^F$, and $\phi_{D_{6B}, D_{7B}}^{FT}$. Also, because no fish fell back upon leaving site T_1 , the transition parameter $\phi_{T_1, D_{2T}}^F$ must equal $\phi_{T_1, D_{2B}}^F \phi_{D_{2B}, D_{2T}}^T$.)

The approach taken above to dealing with the missing detection sites results in estimating only the composite transition parameters (given in Equations (3.80) and (3.81)) for those sites. Thus, the actual definitions of those composite transition parameters in terms of the underlying inestimable parameters do not affect the results, although they may affect the interpretation of the results. As for fitting the model, using the composite parameters is equivalent to the simpler alternative of ignoring the missing detection sites, and simply treating dams 2, 3, and 6 as if they each had only a single detection site, with characteristics of both base-of-dam and top-of-dam sites. In particular, these single dam sites would act as the upper limits of both fallback and tributary memory effects, and fish would be able to fall back upon leaving these sites. This approach ignores any actual differences between base-of-dam sites and top-of-dam sites. Given the complexity of the model, this simpler approach seems preferable to trying to estimate transitions to sites for which we have no detections, and is effectively the result of the more complex approach taken above.

The necessary composite transition parameters are:

$$\begin{aligned}
 \phi_{D_{1T}, D_{2T}} &= \phi_{D_{1T}, D_{2B}} \phi_{D_{2B}, D_{2T}}; & \phi_{T_1, D_{2T}} &= \phi_{T_1, D_{2B}} \phi_{D_{2B}, D_{2T}}^T; \\
 \phi_{D_{1T}, D_{2T}}^T &= \phi_{D_{1T}, D_{2B}}^T \phi_{D_{2B}, D_{2T}}^T; & \phi_{T_1, D_{2T}}^T &= \phi_{T_1, D_{2B}}^T \phi_{D_{2B}, D_{2T}}^T; \\
 \phi_{D_{1T}, D_{2T}}^{FT} &= \phi_{D_{1T}, D_{2B}}^{FT} \phi_{D_{2B}, D_{2T}}^F; & \phi_{T_1, D_{2T}}^{FT} &= \phi_{T_1, D_{2B}}^{FT} \phi_{D_{2B}, D_{2T}}^F; \\
 \phi_{D_{2T}, D_{3T}} &= \phi_{D_{2T}, D_{3B}} \phi_{D_{3B}, D_{3T}}; & \phi_{T_2, D_{3T}} &= \phi_{T_2, D_{3B}} \phi_{D_{3B}, D_{3T}}^T; \\
 \phi_{D_{2T}, D_{3T}}^T &= \phi_{D_{2T}, D_{3B}}^T \phi_{D_{3B}, D_{3T}}^T; & \phi_{T_2, D_{3T}}^T &= \phi_{T_2, D_{3B}}^T \phi_{D_{3B}, D_{3T}}^T;
 \end{aligned} \tag{3.80}$$

$$\begin{aligned}
\phi_{D_{2T}, D_{3T}}^{FT} &= \phi_{D_{2T}, D_{3B}}^{FT} \phi_{D_{3B}, D_{3T}}^F; & \phi_{T_2, D_{3T}}^{FT} &= \phi_{T_2, D_{3B}}^{FT} \phi_{D_{3B}, D_{3T}}^F; \\
\phi_{D_{6B}, D_{7B}} &= \phi_{D_{6B}, D_{6T}} \phi_{D_{6T}, D_{7B}}; & \phi_{D_{6B}, D_{7B}}^T &= \phi_{D_{6B}, D_{6T}}^T \phi_{D_{6T}, D_{7B}};
\end{aligned}$$

and

$$\begin{aligned}
\phi_{D_{1T}, D_{2T}}^F &= \phi_{D_{1T}, D_{2B}}^F \phi_{D_{2B}, D_{2T}}; & \phi_{T_1, D_{2T}}^F &= \phi_{T_1, D_{2B}}^F \phi_{D_{2B}, D_{2T}}^T; \\
\phi_{D_{2T}, D_{3T}}^F &= \phi_{D_{2T}, D_{3B}}^F \phi_{D_{3B}, D_{3T}}; & \phi_{T_2, D_{3T}}^F &= \phi_{T_2, D_{3B}}^F \phi_{D_{3B}, D_{3T}}^T; \\
\phi_{D_{6B}, D_{7B}}^F &= \phi_{D_{6B}, D_{6T}}^F \phi_{D_{6T}, D_{7B}}; & \phi_{D_{6B}, D_{7B}}^{FT} &= \phi_{D_{6B}, D_{6T}}^{FT} \phi_{D_{6T}, D_{7B}}^{FT}.
\end{aligned} \tag{3.81}$$

In addition to the missing detection sites, Table 3.46 indicates that no fish detected at site T_4 was detected again upstream (i.e., $b_{T_4} + b_{T_4}^T + b_{T_4}^f + b_{T_4}^{fT} + b_{T_4}^{FNT} + b_{T_4}^{F(D_{4T})} + b_{T_4}^{F(D_{4T})T} + h_{T_4} + h_{T_4}^T = 0$), so all types of $\phi_{T_4, D_{5B}}$ parameters must be fixed to 0, and the corresponding χ_{T_4} parameters fixed to 1. Also, all transition parameters ϕ_{ij}^T where $i = D_{5B}, D_{5T}$, or T_5 must be removed from the likelihood. On the other hand, all fish detected at site T_5 were detected again ($a_{T_5} = b_{T_5} = 22$ and $a_{T_5}^f = b_{T_5}^f = 18$), indicating that $\phi_{T_5, D_{6B}}$ should be fixed to 1 and both χ_{T_5} and $\chi_{T_5}^f$ modified accordingly.

A number of parameters displaying tributary effects are unnecessary. With no detections at site T_6 , all parameters ϕ_{ij}^T , with i upstream of T_6 , must be removed. Every fish that visited site T_0 and then was detected at site D_{1B} was also detected at site D_{1T} , indicating that $\phi_{D_{1B}, D_{1T}}^T$ should be fixed to 1. Similarly, $\phi_{T_3, D_{4B}}^T$ and $\phi_{D_{4B}, D_{4T}}^T$ should be fixed to 1. All fish detected at D_{3T} that had previously visited T_2 were detected again upstream, also. Because D_{3T} is a top-of-dam site with two possible subsequent detection sites (i.e., T_3 and D_{4B}), it is necessary to use the relation $\phi_{D_{3T}, T_3}^T + \phi_{D_{3T}, D_{4B}}^T = 1$, so that only one of these transitions must be estimated. On the other hand, neither fish detected at site T_1 that had previously visited T_0 was detected upstream of T_1 , so $\phi_{T_1, D_{2T}}^T$ must be fixed to 0. For each of these cases, the corresponding χ_i^T and χ_i^{fT} parameters must be modified accordingly.

The d_i and d_i^T statistics in Table 3.46 indicate that many sites were not the origin of fallback transitions. In particular, no fish fell back upon leaving any tributary other than site T_3 , so the parameters $f_{T_0}, f_{T_1}, f_{T_1}^T, f_{T_2}, f_{T_2}^T, f_{T_4}, f_{T_4}^T, f_{T_5}$, and $f_{T_5}^T$ must be fixed to

0. The parameter ϕ_{ij}^F includes a fallback effect that may be either a memory effect or representative of fallback during the transition from i to j , so it does not follow that all ϕ_{ij}^F parameters with $i = T_k$ ($k \neq 3$) must be removed. However, the parameters ϕ_{ij}^{FT} are used only during the fallback transition, so these parameters must be removed from the likelihood for $i = T_k$ and $k \neq 3$. No fish fell back at any site other than D_{4T} after visiting the previous tributary, so the parameters $f_{D_{kT}}^T$ ($k \neq 4$) and $f_{T_3}^T$ must be fixed to 0, and the parameters ϕ_{ij}^{FT} where $i = D_{kT}$ or $i = T_3$ must be removed. Likewise, $d_{D_{6B}} = 0$, so $f_{D_{6B}}$ must be fixed to 0.

Not all transitions with fallback effects are needed. Because no fish that fell back between the release site and T_0 was detected again upriver (i.e., $b_{T_0}^{F(R)} = 0$), the transition parameter $\phi_{T_0, D_{1B}}^F$ must be fixed to 0. No fish detected at tributary T_2 that had fallen back within the previous reach (i.e., the fallback memory effect was still operable) was detected again upstream (i.e., $a_{T_2}^{FNT} = 7$ but $b_{T_2}^{FNT} = 0$), so the parameter $\phi_{T_2, D_{3T}}^F$ must be fixed to 0. At some sites, all fallback fish detected there were detected again upstream, requiring the following relations: $\phi_{D_{2T}, T_2}^F + \phi_{D_{2T}, D_{3T}}^F = 1$, $\phi_{D_{5B}, D_{5T}}^F = 1$, and $\phi_{D_{5T}, T_5}^F + \phi_{D_{5T}, D_{6B}}^F = 1$. Also, because no fish fell back from upstream of site D_{4T} , there is no need for any ϕ_{ij}^F parameters where $i = D_{6B}$ or a site farther upstream.

Removing or fixing the values of the parameters listed above leaves 65 parameters to estimate, with 79 non-zero minimal sufficient statistics. Several of these non-zero minimal sufficient statistics are nevertheless very close to 0, and certain memory effects cannot be estimated for this data set. In particular, only two fish were detected at D_{4T} after visiting T_3 without having previously fallen back (i.e., $a_{D_{4T}}^T = 2$). One of these fell back during its next transition ($d_{D_{4T}}^T = 1$) and the other did not. With only a single fish experiencing both fallback and tributary effects during the transition from D_{4T} , it is impossible to estimate the parameter $\phi_{D_{4T}, D_{5B}}^{FT}$. Thus, the tributary effect on fallback was ignored for D_{4T} , giving $f_{D_{4T}}^T = f_{D_{4T}}$ and $\phi_{D_{4T}, D_{5B}}^{FT} = \phi_{D_{4T}, D_{5B}}^F$. Additionally, very few fish that visited tributary T_3 went on to D_{4T} ($g_{D_{4B}}^T + g_{D_{4B}}^{fT} = 7$), so it is difficult to estimate a tributary effect at D_{4T} in general. Thus, the tributary memory effect was ignored at site D_{4T} , giving $\phi_{D_{4T}, T_4}^T = \phi_{D_{4T}, T_4}$ and $\phi_{D_{4T}, D_{5B}}^T = \phi_{D_{4T}, D_{5B}}$, as well as the relations expressed above. With these simplifications, there are 61 parameters to estimate with 78 non-zero minimal sufficient

statistics. The likelihood used to fit Model 5b to the full ($K = 7$) 1996 Chinook data set is given in Equation (3.82), with zero-valued terms omitted, and with $\phi_{D_{2T}, T_2}^F = 1 - \phi_{D_{2T}, D_{3T}}^F$, $\phi_{D_{3T}, T_3}^T = 1 - \phi_{D_{3T}, D_{4B}}^T$, and $\phi_{D_{5T}, T_5}^F = 1 - \phi_{D_{5T}, D_{6B}}^F$:

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \Phi_{R, T_0}^{a_{T_0}} \Phi_{R, D_{1B}}^{g_{T_0}-b_{T_0}} (\Phi_{R, T_0}^F)^{a_{T_0}^{F(R)}} (\Phi_{R, D_{1B}}^F)^{d_R-a_{T_0}^{F(R)}} \chi_{T_0}^{a_{T_0}-b_{T_0}} \phi_{T_0, D_{1B}}^{b_{T_0}} p_{D_{1B}}^{A_{D_{1B}}} q_{D_{1B}}^{G_{T_0}-A_{D_{1B}}} \\
& \times \chi_{D_{1B}}^{a_{D_{1B}}-b_{D_{1B}}-h_{D_{1B}}} (\chi_{D_{1B}}^F)^{a_{D_{1B}}^F-b_{D_{1B}}^F} \phi_{D_{1B}, D_{1T}}^{g_{D_{1B}}} (\phi_{D_{1B}, D_{1T}}^F)^{g_{D_{1B}}^F} \\
& \times p_{D_{1T}}^{A_{D_{1T}}} q_{D_{1T}}^{G_{D_{1B}}-A_{D_{1T}}} \chi_{D_{1T}}^{a_{D_{1T}}-b_{D_{1T}}-h_{D_{1T}}} (\chi_{D_{1T}}^T)^{a_{D_{1T}}^T-b_{D_{1T}}^T} (\chi_{D_{1T}}^F)^{a_{D_{1T}}^F-b_{D_{1T}}^F} f_{D_{1T}}^{d_{D_{1T}}} \\
& \times (1-f_{D_{1T}})^{g_{D_{1T}}-d_{D_{1T}}} \phi_{D_{1T}, T_1}^{a_{T_1}} (\phi_{D_{1T}, T_1}^T)^{a_{T_1}^T} (\phi_{D_{1T}, T_1}^F)^{a_{T_1}^{FNT}} \phi_{D_{1T}, D_{2T}}^{g_{T_1}-b_{T_1}} (\phi_{D_{1T}, D_{2T}}^T)^{g_{T_1}^T+g_{T_1}^{fT}} \\
& \times (\phi_{D_{1T}, D_{2T}}^F)^{g_{D_{1T}}^F+d_{D_{1T}}-a_{T_1}^{FNT}} \chi_{T_1}^{a_{T_1}-b_{T_1}} (\chi_{T_1}^F)^{a_{T_1}^{FNT}+a_{T_1}^{F(D_{1T})T}} -b_{T_1}^{FNT} \phi_{T_1, D_{2T}}^{b_{T_1}} (\phi_{T_1, D_{2T}}^F)^{b_{T_1}^{FNT}} \\
& \times p_{D_{2T}}^{A_{D_{2T}}} q_{D_{2T}}^{G_{T_1}-A_{D_{2T}}} \chi_{D_{2T}}^{a_{D_{2T}}-b_{D_{2T}}-h_{D_{2T}}} (\chi_{D_{2T}}^T)^{a_{D_{2T}}^T-b_{D_{2T}}^T} (\chi_{D_{2T}}^f)^{a_{D_{2T}}^f-b_{D_{2T}}^f} f_{D_{2T}}^{d_{D_{2T}}} \\
& \times (1-f_{D_{2T}})^{g_{D_{2T}}-d_{D_{2T}}} \phi_{D_{2T}, T_2}^{a_{T_2}+a_{T_2}^f} (\phi_{D_{2T}, T_2}^T)^{a_{T_2}^T+a_{T_2}^{fT}} (\phi_{D_{2T}, T_2}^F)^{a_{T_2}^{FNT}} \phi_{D_{2T}, D_{3T}}^{g_{T_2}+g_{T_2}^f-b_{T_2}} \\
& \times (\phi_{D_{2T}, D_{3T}}^T)^{g_{T_2}^T+g_{T_2}^{fT}-(b_{T_2}^T+b_{T_2}^{fT})} (\phi_{D_{2T}, D_{3T}}^F)^{g_{D_{2T}}^F+d_{D_{2T}}-a_{T_2}^{FNT}} \\
& \times \chi_{T_2}^{a_{T_2}-b_{T_2}} (\chi_{T_2}^T)^{a_{T_2}^T-b_{T_2}^T} (\chi_{T_2}^f)^{a_{T_2}^f-b_{T_2}^f} (\chi_{T_2}^{fT})^{a_{T_2}^{fT}-b_{T_2}^{fT}} \phi_{T_2, D_{3T}}^{b_{T_2}} (\phi_{T_2, D_{3T}}^T)^{b_{T_2}^T+b_{T_2}^{fT}} p_{D_{3T}}^{A_{D_{3T}}} q_{D_{3T}}^{G_{T_2}-A_{D_{3T}}} \\
& \times \chi_{D_{3T}}^{a_{D_{3T}}-b_{D_{3T}}-h_{D_{3T}}} (\chi_{D_{3T}}^f)^{a_{D_{3T}}^f-b_{D_{3T}}^f} (\chi_{D_{3T}}^F)^{a_{D_{3T}}^F-b_{D_{3T}}^F} f_{D_{3T}}^{d_{D_{3T}}} (1-f_{D_{3T}})^{g_{D_{3T}}-d_{D_{3T}}} \\
& \times \phi_{D_{3T}, T_3}^{a_{T_3}+a_{T_3}^f} (\phi_{D_{3T}, T_3}^T)^{a_{T_3}^T+a_{T_3}^{fT}} (\phi_{D_{3T}, T_3}^F)^{a_{T_3}^{FNT}} \phi_{D_{3T}, D_{4B}}^{g_{T_3}+g_{T_3}^f-(b_{T_3}+h_{T_3}+b_{T_3}^f)} (\phi_{D_{3T}, D_{4B}}^T)^{g_{T_3}^T+g_{T_3}^{fT}-b_{T_3}^{fT}} \\
& \times (\phi_{D_{3T}, D_{4B}}^F)^{g_{D_{3T}}^F+d_{D_{3T}}-a_{T_3}^{FNT}} \chi_{T_3}^{a_{T_3}-b_{T_3}-h_{T_3}} (\chi_{T_3}^f)^{a_{T_3}^f-b_{T_3}^f} (\chi_{T_3}^F)^{a_{T_3}^{FNT}+a_{T_3}^{F(D_{3T})T}} -b_{T_3}^{FNT}-b_{T_3}^{F(D_{3T})T} \\
& \times f_{T_3}^{d_{T_3}} (1-f_{T_3})^{b_{T_3}+h_{T_3}-d_{T_3}} \phi_{T_3, D_{4B}}^{b_{T_3}+h_{T_3}-d_{T_3}+b_{T_3}^f} (\phi_{T_3, D_{4B}}^F)^{d_{T_3}+b_{T_3}^{FNT}+b_{T_3}^{F(D_{3T})T}} p_{D_{4B}}^{A_{D_{4B}}} q_{D_{4B}}^{G_{T_3}-A_{D_{4B}}} \\
& \times \chi_{D_{4B}}^{a_{D_{4B}}-b_{D_{4B}}} (\chi_{D_{4B}}^f)^{a_{D_{4B}}^f-b_{D_{4B}}^f} (\chi_{D_{4B}}^F)^{a_{D_{4B}}^F-b_{D_{4B}}^F} \phi_{D_{4B}, D_{4T}}^{g_{D_{4B}}+g_{D_{4B}}^f} (\phi_{D_{4B}, D_{4T}}^F)^{g_{D_{4B}}^F} p_{D_{4T}}^{A_{D_{4T}}} \\
& \times q_{D_{4T}}^{G_{D_{4B}}-A_{D_{4T}}} \chi_{D_{4T}}^{a_{D_{4T}}-b_{D_{4T}}-h_{D_{4T}}} (\chi_{D_{4T}}^T)^{a_{D_{4T}}^T-b_{D_{4T}}^T} (\chi_{D_{4T}}^f)^{a_{D_{4T}}^f-b_{D_{4T}}^f} (\chi_{D_{4T}}^F)^{a_{D_{4T}}^F-b_{D_{4T}}^F} \\
& \times f_{D_{4T}}^{d_{D_{4T}}+d_{D_{4T}}^T} (1-f_{D_{4T}})^{g_{D_{4T}}+g_{D_{4T}}^T-d_{D_{4T}}-d_{D_{4T}}^T} \phi_{D_{4T}, T_4}^{a_{T_4}+a_{T_4}^f+a_{T_4}^{fT}} (\phi_{D_{4T}, T_4}^F)^{a_{T_4}^{FNT}} \\
& \times \phi_{D_{4T}, D_{5B}}^{g_{T_4}+g_{T_4}^T+g_{T_4}^f+g_{T_4}^{fT}} (\phi_{D_{4T}, D_{5B}}^F)^{g_{D_{4T}}^F+d_{D_{4T}}+d_{D_{4T}}^T-a_{T_4}^{FNT}} p_{D_{5B}}^{A_{D_{5B}}} q_{D_{5B}}^{G_{T_4}-A_{D_{5B}}} \chi_{D_{5B}}^{a_{D_{5B}}-b_{D_{5B}}-h_{D_{5B}}}
\end{aligned}$$

$$\begin{aligned}
& \times (\chi_{D_{5B}}^f)^{a_{D_{5B}}^f - b_{D_{5B}}^f} \phi_{D_{5B}, D_{5T}}^{g_{D_{5B}} + g_{D_{5B}}^f} p_{D_{5T}}^{A_{D_{5T}}} q_{D_{5T}}^{G_{D_{5B}} - A_{D_{5T}}} \chi_{D_{5T}}^{a_{D_{5T}} - b_{D_{5T}}} (\chi_{D_{5T}}^f)^{a_{D_{5T}}^f - b_{D_{5T}}^f} f_{D_{5T}}^{d_{D_{5T}}} \\
& \times (1 - f_{D_{5T}})^{g_{D_{5T}} - d_{D_{5T}}} \phi_{D_{5T}, T_5}^{a_{T_5}} (\phi_{D_{5T}, T_5}^F)^{a_{T_5}^{FNT}} \phi_{D_{5T}, D_{6B}}^{g_{T_5} + g_{T_5}^f - (b_{T_5} + b_{T_5}^f)} (\phi_{D_{5T}, D_{6B}}^F)^{g_{D_{5T}} + d_{D_{5T}} - a_{T_5}^{FNT}} \\
& \times (\chi_{T_5}^F)^{a_{T_5}^{FNT} + a_{T_5}^{F(D_{5T})T} - b_{T_5}^{FNT} - b_{T_5}^{F(D_{5T})T}} (\phi_{T_5, D_{6B}}^F)^{b_{T_5}^{FNT} + b_{T_5}^{F(D_{5T})T}} p_{D_{6B}}^{A_{D_{6B}}} q_{D_{6B}}^{G_{T_5} - A_{D_{6B}}} \chi_{D_{6B}}^{a_{D_{6B}} - b_{D_{6B}}} \\
& \times (\chi_{D_{6B}}^f)^{a_{D_{6B}}^f - b_{D_{6B}}^f} (\chi_{D_{6B}}^{fT})^{a_{D_{6B}}^{fT} - b_{D_{6B}}^{fT}} \phi_{D_{6B}, D_{7B}}^{g_{D_{6B}} + g_{D_{6B}}^f} (\phi_{D_{6B}, D_{7T}}^T)^{g_{D_{6B}} + g_{D_{6B}}^{fT}} p_{D_{7B}}^{A_{D_{7B}}} q_{D_{7B}}^{G_{D_{6B}} - A_{D_{7B}}} \\
& \times \chi_{D_{7B}}^{a_{D_{7B}} - b_{D_{7B}}} (\chi_{D_{7B}}^f)^{a_{D_{7B}}^f - b_{D_{7B}}^f} \phi_{D_{7B}, D_{7T}}^{g_{D_{7B}} + g_{D_{7B}}^f} p_{D_{7T}}^{A_{D_{7T}}} q_{D_{7T}}^{G_{D_{7B}} - A_{D_{7T}}} \chi_{D_{7T}}^{a_{D_{7T}} - b_{D_{7T}}} \\
& \times (\chi_{D_{7T}}^f)^{a_{D_{7T}}^f - b_{D_{7T}}^f} \phi_{D_{7T}, T_7}^{a_{T_7} + a_{T_7}^f}. \tag{3.82}
\end{aligned}$$

The summary statistics for the reduced 1996 Chinook salmon data set ($K = 4$ [BON, TDA, JD, MCN]) are given in Table 3.47. The restrictions and modifications made to the parameters pertaining to the first 4 dams in the 7-dam model are used here, with the exception that it is possible to distinguish between ϕ_{D_{4T}, T_4}^T and ϕ_{D_{4T}, T_4} in the 4-dam model. This leaves 44 parameters and 55 minimal sufficient statistics.

The 4-dam likelihood tailored to the 1996 Chinook data set is given in Equation (3.83):

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \Phi_{R,T_0}^{a_{T_0}} \Phi_{R,D_{1B}}^{g_{T_0}-b_{T_0}} (\Phi_{R,T_0}^F)^{a_{T_0}^{F(R)}} (\Phi_{R,D_{1B}}^F)^{d_R-a_{T_0}^{F(R)}} \chi_{T_0}^{a_{T_0}-b_{T_0}} \phi_{T_0,D_{1B}}^{b_{T_0}} p_{D_{1B}}^{A_{D_{1B}}} q_{D_{1B}}^{G_{T_0}-A_{D_{1B}}} \\
& \times \chi_{D_{1B}}^{a_{D_{1B}}-b_{D_{1B}}-h_{D_{1B}}} (\chi_{D_{1B}}^F)^{a_{D_{1B}}^F} \phi_{D_{1B},D_{1T}}^{g_{D_{1B}}} (\phi_{D_{1B},D_{1T}}^F)^{g_{D_{1B}}^F} \\
& \times p_{D_{1T}}^{A_{D_{1T}}} q_{D_{1T}}^{G_{D_{1B}}-A_{D_{1T}}} \chi_{D_{1T}}^{a_{D_{1T}}-b_{D_{1T}}-h_{D_{1T}}} (\chi_{D_{1T}}^T)^{a_{D_{1T}}^T} \phi_{D_{1T},D_{2T}}^{g_{D_{1T}}} (\phi_{D_{1T},D_{2T}}^F)^{a_{D_{1T}}^F} \phi_{D_{1T},D_{2T}}^{b_{D_{1T}}^F} f_{D_{1T}}^{d_{D_{1T}}} \\
& \times (1-f_{D_{1T}})^{g_{D_{1T}}-d_{D_{1T}}} \phi_{D_{1T},T_1}^{a_{T_1}} (\phi_{D_{1T},T_1}^T)^{a_{T_1}^T} (\phi_{D_{1T},T_1}^F)^{a_{T_1}^{FNT}} \phi_{D_{1T},D_{2T}}^{g_{T_1}-b_{T_1}} (\phi_{D_{1T},D_{2T}}^T)^{g_{T_1}^T} \phi_{D_{1T},D_{2T}}^{g_{T_1}^{fT}} \\
& \times (\phi_{D_{1T},D_{2T}}^F)^{g_{D_{1T}}^F+d_{D_{1T}}-a_{T_1}^{FNT}} \chi_{T_1}^{a_{T_1}-b_{T_1}} (\chi_{T_1}^F)^{a_{T_1}^{FNT}+a_{T_1}^{F(D_{1T})^T}} \phi_{T_1,D_{2T}}^{b_{T_1}^{FNT}} (\phi_{T_1,D_{2T}}^F)^{b_{T_1}^{FNT}} \\
& \times p_{D_{2T}}^{A_{D_{2T}}} q_{D_{2T}}^{G_{T_1}-A_{D_{2T}}} \chi_{D_{2T}}^{a_{D_{2T}}-b_{D_{2T}}-h_{D_{2T}}} (\chi_{D_{2T}}^T)^{a_{D_{2T}}^T} \phi_{D_{2T},D_{3T}}^{g_{D_{2T}}} (\phi_{D_{2T},D_{3T}}^f)^{a_{D_{2T}}^f} \phi_{D_{2T},D_{3T}}^{b_{D_{2T}}^f} f_{D_{2T}}^{d_{D_{2T}}} \\
& \times (1-f_{D_{2T}})^{g_{D_{2T}}-d_{D_{2T}}} \phi_{D_{2T},T_2}^{a_{T_2}+a_{T_2}^f} (\phi_{D_{2T},T_2}^T)^{a_{T_2}^T} \phi_{D_{2T},T_2}^{a_{T_2}^{fT}} (\phi_{D_{2T},T_2}^F)^{a_{T_2}^{FNT}} \phi_{D_{2T},D_{3T}}^{g_{T_2}+g_{T_2}^f-b_{T_2}} \\
& \times (\phi_{D_{2T},D_{3T}}^T)^{g_{T_2}^T+g_{T_2}^{fT}-(b_{T_2}^T+b_{T_2}^{fT})} (\phi_{D_{2T},D_{3T}}^F)^{g_{D_{2T}}^F+d_{D_{2T}}-a_{T_2}^{FNT}} \\
& \times \chi_{T_2}^{a_{T_2}-b_{T_2}} (\chi_{T_2}^T)^{a_{T_2}^T} \phi_{T_2,D_{3T}}^{b_{T_2}^T} (\phi_{T_2,D_{3T}}^T)^{b_{T_2}^T+b_{T_2}^{fT}} p_{D_{3T}}^{A_{D_{3T}}} q_{D_{3T}}^{G_{T_2}-A_{D_{3T}}} \\
& \times \chi_{D_{3T}}^{a_{D_{3T}}-b_{D_{3T}}-h_{D_{3T}}} (\chi_{D_{3T}}^f)^{a_{D_{3T}}^f} \phi_{D_{3T},D_{4B}}^{g_{D_{3T}}} (\phi_{D_{3T},D_{4B}}^F)^{a_{D_{3T}}^{FNT}} \phi_{D_{3T},D_{4B}}^{g_{T_3}+g_{T_3}^f-(b_{T_3}+h_{T_3}+b_{T_3}^f)} (\phi_{D_{3T},D_{4B}}^T)^{g_{T_3}^T} \phi_{D_{3T},D_{4B}}^{g_{T_3}^{fT}-b_{T_3}^{fT}} \\
& \times (\phi_{D_{3T},D_{4B}}^F)^{g_{D_{3T}}^F+d_{D_{3T}}-a_{T_3}^{FNT}} \chi_{T_3}^{a_{T_3}-b_{T_3}-h_{T_3}} (\chi_{T_3}^f)^{a_{T_3}^f} \phi_{T_3,D_{4B}}^{b_{T_3}^f} (\chi_{T_3}^F)^{a_{T_3}^{FNT}+a_{T_3}^{F(D_{3T})^T}} \phi_{T_3,D_{4B}}^{b_{T_3}^{FNT}-b_{T_3}^{F(D_{3T})^T}} \\
& \times f_{T_3}^{d_{T_3}} (1-f_{T_3})^{b_{T_3}+h_{T_3}-d_{T_3}} \phi_{T_3,D_{4B}}^{b_{T_3}+h_{T_3}-d_{T_3}+b_{T_3}^f} (\phi_{T_3,D_{4B}}^F)^{d_{T_3}+b_{T_3}^{FNT}+b_{T_3}^{F(D_{3T})^T}} p_{D_{4B}}^{A_{D_{4B}}} q_{D_{4B}}^{G_{T_3}-A_{D_{4B}}} \\
& \times \chi_{D_{4B}}^{a_{D_{4B}}-b_{D_{4B}}} (\chi_{D_{4B}}^f)^{a_{D_{4B}}^f} \phi_{D_{4B},D_{4T}}^{g_{D_{4B}}} (\phi_{D_{4B},D_{4T}}^F)^{a_{D_{4B}}^F} \phi_{D_{4B},D_{4T}}^{b_{D_{4B}}^F} \phi_{D_{4B},D_{4T}}^{g_{D_{4B}}+g_{D_{4B}}^f} (\phi_{D_{4B},D_{4T}}^F)^{g_{D_{4B}}^F} p_{D_{4T}}^{A_{D_{4T}}} \\
& \times q_{D_{4T}}^{G_{D_{4B}}-A_{D_{4T}}} \chi_{D_{4T}}^{a_{D_{4T}}-b_{D_{4T}}} (\chi_{D_{4T}}^T)^{a_{D_{4T}}^T} (\chi_{D_{4T}}^f)^{a_{D_{4T}}^f} \phi_{D_{4T},D_{4B}}^{b_{D_{4T}}^f} (\chi_{D_{4T}}^F)^{a_{D_{4T}}^{fT}} (\chi_{D_{4T}}^F)^{a_{D_{4T}}^F} \phi_{D_{4T},D_{4B}}^{b_{D_{4T}}^F} \\
& \times \phi_{D_{4T},T_4}^{a_{T_4}+a_{T_4}^f} (\phi_{D_{4T},T_4}^T)^{a_{T_4}^T} (\phi_{D_{4T},T_4}^F)^{a_{T_4}^{FNT}}, \tag{3.83}
\end{aligned}$$

where $\phi_{D_{2T},T_2}^F = 1 = \phi_{D_{2T},D_{3T}}^F$ and $\phi_{D_{3T},T_3}^F = 1 - \phi_{D_{3T},D_{4B}}^F$.

3.9.3.5 Results

Program USER¹⁷ was used to fit Model 5b to the data via maximum likelihood. Maximum likelihood estimates from the full data set ($K = 7$ dams) are listed in Table 3.48. The log-likelihood was -3743.8691, with an AIC of 7609.7382. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.1048$ ($\widehat{SE} = 0.0106$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2770$ ($\widehat{SE} = 0.0155$).

Model 5b is most closely related to Models 3b and 5a. Like Model 3b, Model 5b incorporates short-term memory effects of tributary visits. Like Model 5a, Model 5b incorporates fallback effects, although Model 5b uses short-term fallback effects whereas Model 5a uses long-term effects. If both tributary effects and fallback effects are significant, then the estimates of perceived system survival and the unaccountable loss rate should be more accurate, but possibly less precise, for Model 5b than for either Model 3b or Model 5a. Comparison of the estimates among the three models shows that for the full, 7-dam analysis, the estimate of \hat{S}_{sys} is smallest for Model 5b but equally precise among the three models ($\hat{S}_{sys} = 0.1048$, $\widehat{SE} = 0.0106$ for Model 5b versus $\hat{S}_{sys} = 0.1057$, $\widehat{SE} = 0.0106$ for Model 3b and $\hat{S}_{sys} = 0.1073$, $\widehat{SE} = 0.0108$ for Model 5a), while the estimate of $\hat{\mu}_R$ is intermediate for Model 5b but equally precise for all three models ($\hat{\mu}_R = 0.2770$, $\widehat{SE} = 0.0155$ for Model 5b versus $\hat{\mu}_R = 0.2800$, $\widehat{SE} = 0.0156$ for Model 3b and $\hat{\mu}_R = 0.2763$, $\widehat{SE} = 0.0156$ for Model 5a).

Table 3.48: Maximum likelihood estimates of parameters from Model 5b, the Short-term Fallback and Tributary Memory model, with $K = 7$ dams. The estimates of ϕ_{D_{2T}, T_2}^F , ϕ_{D_{3T}, T_3}^T , and ϕ_{D_{5T}, T_5}^F come from the relations $\phi_{D_{2T}, T_2}^F + \phi_{D_{2T}, D_{3T}}^F = 1$, $\phi_{D_{3T}, T_3}^T + \phi_{D_{3T}, D_{4B}}^T = 1$, and $\phi_{D_{5T}, T_5}^F + \phi_{D_{5T}, D_{6B}}^F = 1$, respectively.

Category	Parameter	Estimate	S.E.
Transition	Φ_{R, T_0}	0.0083	0.0031
	Φ_{R, T_0}^F	0.0047	0.0024
	$\Phi_{R, D_{1B}}$	0.8448	0.0126
	$\Phi_{R, D_{1B}}^F$	0.1205	0.0113
	$\phi_{T_0, D_{1B}}$	0.5726	0.1873

¹⁷<http://www.cbr.washington.edu/paramEst/USER/>

Table 3.48 continued

Category	Parameter	Estimate	S.E.
Transition	$\phi_{D_{1B}, D_{1T}}$	0.9728	0.0080
	$\phi_{D_{1B}, D_{1T}}^F$	0.9734	0.0213
	ϕ_{D_{1T}, T_1}	0.3614	0.0189
	ϕ_{D_{1T}, T_1}^F	0.3996	0.0435
	ϕ_{D_{1T}, T_1}^T	0.4990	0.2500
	$\phi_{D_{1T}, D_{2T}}$	0.5509	0.0201
	$\phi_{D_{1T}, D_{2T}}^F$	0.4907	0.0454
	$\phi_{D_{1T}, D_{2T}}^T$	0.2529	0.2192
	$\phi_{T_1, D_{2T}}$	0.1224	0.0213
	$\phi_{T_1, D_{2T}}^F$	0.2046	0.0551
	ϕ_{D_{2T}, T_2}	0.1467	0.0177
	ϕ_{D_{2T}, T_2}^F	0.2756	0.0889
	ϕ_{D_{2T}, T_2}^T	0.2240	0.0658
	$\phi_{D_{2T}, D_{3T}}$	0.7631	0.0220
	$\phi_{D_{2T}, D_{3T}}^F$	0.7244	0.0889
	$\phi_{D_{2T}, D_{3T}}^T$	0.7488	0.0693
	$\phi_{T_2, D_{3T}}$	0.0170	0.0167
	$\phi_{T_2, D_{3T}}^T$	0.2222	0.1386
	ϕ_{D_{3T}, T_3}	0.1192	0.0177
	ϕ_{D_{3T}, T_3}^F	0.2072	0.0941
	ϕ_{D_{3T}, T_3}^T	0.3333	0.2723
	$\phi_{D_{3T}, D_{4B}}$	0.8214	0.0216
	$\phi_{D_{3T}, D_{4B}}^F$	0.6801	0.1226
	$\phi_{D_{3T}, D_{4B}}^T$	0.6667	0.2723
	$\phi_{T_3, D_{4B}}$	0.2812	0.1513
	$\phi_{T_3, D_{4B}}^F$	0.0774	0.0561
	$\phi_{D_{4B}, D_{4T}}$	0.9766	0.0102
	$\phi_{D_{4B}, D_{4T}}^F$	0.8712	0.1489
	ϕ_{D_{4T}, T_4}	0.5394	0.0313
	ϕ_{D_{4T}, T_4}^F	0.0692	0.0703
	$\phi_{D_{4T}, D_{5B}}$	0.4141	0.0305
	$\phi_{D_{4T}, D_{5B}}^F$	0.4028	0.1755
	$\phi_{D_{5B}, D_{5T}}$	0.9601	0.0206
	ϕ_{D_{5T}, T_5}	0.3674	0.0465
	ϕ_{D_{5T}, T_5}^F	0.2917	0.1800
	$\phi_{D_{5T}, D_{6B}}$	0.6022	0.0498
	$\phi_{D_{5T}, D_{6B}}^F$	0.7083	0.1800
	$\phi_{T_5, D_{6B}}^F$	0.5091	0.3604
	$\phi_{D_{6B}, D_{7B}}$	0.9376	0.0366
	$\phi_{D_{6B}, D_{7B}}^T$	0.9540	0.0341

Table 3.48 continued

Category	Parameter	Estimate	S.E.
Transition	$\phi_{D_{7B}, D_{7T}}$	0.8573	0.0354
	ϕ_{D_{7T}, T_7}	0.8161	0.0415
Detection	$p_{D_{1B}}$	0.9407	0.0085
	$p_{D_{1T}}$	0.8667	0.0127
	$p_{D_{2T}}$	0.8526	0.0174
	$p_{D_{3T}}$	0.9573	0.0112
	$p_{D_{4B}}$	0.9102	0.0168
	$p_{D_{4T}}$	0.9373	0.0147
	$p_{D_{5B}}$	0.9302	0.0238
	$p_{D_{5T}}$	0.8725	0.0318
	$p_{D_{6B}}$	0.6372	0.0469
	$p_{D_{7B}}$	0.9775	0.0157
	$p_{D_{7T}}$	0.9726	0.0191
Fallback	$f_{D_{1T}}$	0.0527	0.0097
	$f_{D_{2T}}$	0.0341	0.0097
	$f_{D_{3T}}$	0.0357	0.0125
	f_{T_3}	0.7405	0.2408
	$f_{D_{4T}}$	0.0380	0.0230
	$f_{D_{5T}}$	0.0383	0.0268

Maximum likelihood parameter estimates from the reduced data set ($K = 4$ dams) are listed in Table 3.49. The log-likelihood was -3265.9726, with an AIC of 6619.9451. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.3394$ ($\widehat{SE} = 0.0169$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2212$ ($\widehat{SE} = 0.0150$). Just as in the 7-dam analysis, there is little difference between Models 5a and 5b in estimating S_{sys} and μ_R in the 4-dam analysis. The estimate of perceived system survival is slightly smaller for Model 5b ($\hat{S}_{sys} = 0.3394$, $\widehat{SE} = 0.0169$ for Model 5b versus $\hat{S}_{sys} = 0.3408$, $\widehat{SE} = 0.0169$ for Model 5a), while the estimates of the unaccountable loss rate are the same for the two models ($\hat{\mu}_R = 0.2212$, $\widehat{SE} = 0.0150$ for Model 5b versus $\hat{\mu}_R = 0.2211$, $\widehat{SE} = 0.0151$ for Model 5a).

Table 3.49: Maximum likelihood estimates of parameters from Model 5b, the Short-term Fallback and Tributary Memory model, with $K = 4$ dams. The estimates of ϕ_{D_{2T},T_2}^F and ϕ_{D_{3T},T_3}^T come from the relations $\phi_{D_{2T},T_2}^F + \phi_{D_{2T},D_{3T}}^F = 1$ and $\phi_{D_{3T},T_3}^T + \phi_{D_{3T},D_{4B}}^T = 1$, respectively.

Category	Parameter	Estimate	S.E.
Transition	Φ_{R,T_0}	0.0083	0.0031
	Φ_{R,T_0}^F	0.0047	0.0024
	$\Phi_{R,D_{1B}}$	0.8448	0.0126
	$\Phi_{R,D_{1B}}^F$	0.1205	0.0113
	$\phi_{T_0,D_{1B}}$	0.5726	0.1874
	$\phi_{D_{1B},D_{1T}}$	0.9728	0.0080
	$\phi_{D_{1B},D_{1T}}^F$	0.9734	0.0213
	ϕ_{D_{1T},T_1}	0.3614	0.0189
	ϕ_{D_{1T},T_1}^F	0.3996	0.0435
	ϕ_{D_{1T},T_1}^T	0.4990	0.2497
	$\phi_{D_{1T},D_{2T}}$	0.5509	0.0201
	$\phi_{D_{1T},D_{2T}}^F$	0.4907	0.0454
	$\phi_{D_{1T},D_{2T}}^T$	0.2529	0.2188
	$\phi_{T_1,D_{2T}}$	0.1224	0.0213
	$\phi_{T_1,D_{2T}}^F$	0.2046	0.0551
	ϕ_{D_{2T},T_2}	0.1467	0.0177
	ϕ_{D_{2T},T_2}^F	0.2756	0.0889
	ϕ_{D_{2T},T_2}^T	0.2240	0.0658
	$\phi_{D_{2T},D_{3T}}$	0.7632	0.0220
	$\phi_{D_{2T},D_{3T}}^F$	0.7244	0.0889
	$\phi_{D_{2T},D_{3T}}^T$	0.7489	0.0693
	$\phi_{T_2,D_{3T}}$	0.0189	0.0186
	$\phi_{T_2,D_{3T}}^T$	0.2223	0.1388
	ϕ_{D_{3T},T_3}	0.1191	0.0177
	ϕ_{D_{3T},T_3}^F	0.2078	0.0942
	ϕ_{D_{3T},T_3}^T	0.3333	0.2722
	$\phi_{D_{3T},D_{4B}}$	0.8204	0.0218
	$\phi_{D_{3T},D_{4B}}^F$	0.6873	0.1206
	$\phi_{D_{3T},D_{4B}}^T$	0.6667	0.2722
	$\phi_{T_3,D_{4B}}$	0.2822	0.1519
	$\phi_{T_3,D_{4B}}^F$	0.0782	0.0569
	$\phi_{D_{4B},D_{4T}}$	0.9620	0.0167
	$\phi_{D_{4B},D_{4T}}^F$	0.7168	0.1858
	ϕ_{D_{4T},T_4}	0.5408	0.0308
	ϕ_{D_{4T},T_4}^F	0.1935	0.1741
	ϕ_{D_{4T},T_4}^T	0.1425	0.1310

Table 3.49 continued

Category	Parameter	Estimate	S.E.
Detection	$p_{D_{1B}}$	0.9407	0.0085
	$p_{D_{1T}}$	0.8667	0.0127
	$p_{D_{2T}}$	0.8526	0.0174
	$p_{D_{3T}}$	0.9571	0.0112
	$p_{D_{4B}}$	0.9105	0.0171
	$p_{D_{4T}}$	0.9550	0.0166
Fallback	$f_{D_{1T}}$	0.0527	0.0097
	$f_{D_{2T}}$	0.0341	0.0097
	$f_{D_{3T}}$	0.0355	0.0123
	f_{T_3}	0.7407	0.2409

3.9.4 Model 5c: Long-term Fallback Memory and Short-term Tributary Memory Model

Unlike the Fallback model (Model 4) and the Fallback and Memory-Free Tributary model (Model 5a), Model 5b uses short-term fallback effects, rather than long-term fallback effects. The effects of fallback on survival and transitions are simplified in Model 5b to make the model more tractable and easier to fit for the 1996 Chinook data set. It is possible, however, to develop a model that includes both the long-term fallback effects of Models 4 and 5a, and the short-term tributary effects of Model 3a. Such a model, Model 5c, is described briefly here. Due to large number of parameters, it is not possible to fit Model 5c to the 1996 Chinook data set, even for the reduced, 4-dam data set.

As with Model 5b, Model 5c allows entering and exiting a tributary to affect survival, transitions, and fallback parameters in the following reach. Also like Model 5b, Model 5c assumes that tributary effects are dominated by fallback effects if the fallback event occurs after a tributary entry and exit, and either that each fish falls back at most once or else that only the first fallback event affects subsequent transitions. Unlike Model 5b, Model 5c assumes that any fallback effects are permanent, and that tributary effects never override fallback effects. As usual, detection rates at the dams are unaffected by either tributary visits or fallback, and detection rates in the tributaries are assumed to be 100%.

3.9.4.1 Notation

Notation for Model 5c follows the pattern of Models 3b, 4, 5a, and 5b. One difference in definition from Model 5b is that in Model 5c, “fallback fish” refers to any fish that has previously fallen back, regardless of where the fallback event occurred, and “non-fallback fish” refers only to those fish that have not fallen back at all up to the current time.

The transition parameters ϕ_{ij} and ϕ_{ij}^F are defined as for Models 5a and 5b for the cases where $i = R$ and $i = T_0$. For other values of i , define the transition parameters ϕ_{ij} , ϕ_{ij}^F , ϕ_{ij}^T , and ϕ_{ij}^{FT} as follows:

$\phi_{ij} = Pr[\text{Survive and move directly from site } i \text{ to site } j, \text{ as a non-fallback fish that did not enter the tributary in the reach immediately preceding site } i];$

$\phi_{ij}^T = Pr[\text{Survive and move directly from site } i \text{ to site } j \text{ as a non-fallback fish that entered the tributary in the reach immediately preceding site } i];$

$\phi_{ij}^F = Pr[\text{Survive and move directly from site } i \text{ to site } j \text{ as a fallback fish that did not enter the tributary in the reach immediately preceding site } i];$

$\phi_{ij}^{FT} = Pr[\text{Survive and move directly from site } i \text{ to site } j \text{ as a fallback fish that entered the tributary in the reach immediately preceding site } i];$

where $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$, and where

$$j = \begin{cases} D_{kT} & \text{for } i = D_{kB}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = D_{kT}, k = 1, \dots, K-1; \\ T_k & \text{for } i = D_{kT}, k = 1, \dots, K; \\ D_{k+1,B} & \text{for } i = T_k, k = 0, \dots, K-1. \end{cases} \quad (3.84)$$

The parameters p_i , q_i , f_i , and f_i^T are defined as for Model 5b.

Two types of memory effects are used in Model 5c: the permanent memory effect of fallback, and the temporary memory effect of tributary entry and exit. It is assumed that

fallback may affect upstream transition probabilities, regardless of the time or distance between the fallback and the transition, as in Models 4 and 5a. On the other hand, it is assumed that tributary entry and exit (i.e., a tributary visit) affects transition and fallback probabilities only through the following reach, as in Models 3b and 5b. Unlike Model 5b, both fallback and tributary memory effects may be present for the same transition. Thus, a transition between sites i and j , where j is described as in Equation (3.84), is represented by either ϕ_{ij} , ϕ_{ij}^F , ϕ_{ij}^T , or ϕ_{ij}^{FT} . Because the memory effect of tributary visits is assumed to be short-term, it is not assumed to extend past a transition to the post-fallback state, even if the post-fallback transition occurs in the reach following the tributary.

Consider again Figure 3.13(a), with simplified detection history

$$R \ T_1 \ FB \ D_{2B} \ D_{2T} \ D_{3T} \ \dots$$

The portion of the history's probability relating to detections after T_1 is

$$\dots f_{T_1} \phi_{T_1, D_{2B}}^F p_{D_{2B}} \phi_{D_{2B}, D_{2T}}^F p_{D_{2T}} \phi_{D_{2T}, D_{3B}}^F q_{D_{3B}} \phi_{D_{3B}, D_{3T}}^F p_{D_{3T}} \dots \quad (3.85)$$

Equation (3.85) differs from Equation (3.65) (Model 5b) in that the fallback effect does not end at dam 3 in Equation (3.85); parameter $\phi_{D_{3B}, D_{3T}}^F$ is used instead of $\phi_{D_{3B}, D_{3T}}$. For both models, however, any tributary effect is overridden by the fallback effect, because the fallback occurs after the tributary entry.

The path shown in Figure 3.13(b), with simplified detection history

$$R \ D_{1T} \ FB \ T_1 \ D_{2T} \ D_{3T} \ \dots,$$

has probability

$$\dots f_{D_{1T}} \phi_{D_{1T}, T_1}^F \phi_{T_1, D_{2B}}^F q_{D_{2B}} \phi_{D_{2B}, D_{2T}}^{FT} p_{D_{2T}} \phi_{D_{2T}, D_{3B}}^{FT} q_{D_{3B}} \phi_{D_{3B}, D_{3T}}^F p_{D_{3T}} \dots \quad (3.86)$$

Unlike Equation (3.66) (Model 5b), Equation (3.86) uses transitions with both types of memory effect: $\phi_{D_{2B}, D_{2T}}^{FT}$ and $\phi_{D_{2T}, D_{3B}}^{FT}$ include both fallback and tributary memory effects,

because the tributary entry follows the fallback event. At dam 3, the tributary effect ends but the fallback effect continues, with the parameter $\phi_{D_{3B}, D_{3T}}^F$ used instead of $\phi_{D_{3B}, D_{3T}}$ as in Equation (3.66). Had the fish with the migration path shown in Figure 3.13(b) visited tributary T_0 before D_{1T} , then $f_{T_1}^T \phi_{D_{1T}, T_1}^{FT}$ would replace $f_{T_1} \phi_{D_{1T}, T_1}^F$ in Equation (3.86), but because the visit to tributary T_0 occurred before the fallback, the parameter $\phi_{T_1, D_{2B}}^{FT}$ would not replace the parameter $\phi_{T_1, D_{2B}}^F$ in Equation (3.86).

Four types of χ_i parameters are needed in Model 5c, each representing the probability of not being detected after site i , conditional on reaching site i , and each for a particular group of fish. The parameters χ_i and χ_i^F are appropriate for fish who did not enter the tributary in the reach immediately preceding site i , if it exists. The parameter χ_i^F is also appropriate for fish who entered the previous tributary but then fell back between entering that tributary and being last detected at site i . Otherwise, fish that entered the tributary immediately below site i receive either χ_i^T (for non-fallback fish) or χ_i^{FT} (for fallback fish). The probability of not being detected after site i , given having reached that site as a non-fallback fish and not having entered the tributary preceding site i , is χ_i :

$$\begin{aligned}
\chi_R &= 1 - \Phi_{R, T_0} - \Phi_{R, T_0}^F - \Phi_{R, D_{1B}}(1 - q_{D_{1B}} \chi_{D_{1B}}) \\
&\quad - \Phi_{R, D_{1B}}^F(p_{D_{1B}} + q_{D_{1B}} \phi_{D_{1B}, D_{1T}}^F p_{D_{1T}}); \\
\chi_{D_{kB}} &= 1 - \phi_{D_{kB}, D_{kT}}(1 - q_{D_{kT}} \chi_{D_{kT}}), \quad k = 1, \dots, K; \\
\chi_{D_{kT}} &= 1 - (1 - f_{D_{kT}}) \{ \phi_{D_{kT}, T_k} + \phi_{D_{kT}, D_{k+1, B}}(1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}) \} \\
&\quad - f_{D_{kT}} \phi_{D_{kT}, T_k}^F \\
&\quad - f_{D_{kT}} \phi_{D_{kT}, D_{k+1, B}}^F(p_{D_{k+1, B}} + q_{D_{k+1, B}} \phi_{D_{k+1, B}, D_{k+1, T}}^F p_{D_{k+1, T}}), \quad k = 1, \dots, K-1; \\
\chi_{D_{KT}} &= 1 - \phi_{D_{KT}, T_K}; \\
\chi_{T_k} &= 1 - (1 - f_{T_k}) \phi_{T_k, D_{k+1, B}}(1 - q_{D_{k+1, B}} \chi_{D_{k+1, B}}^T) \\
&\quad - f_{T_k} \phi_{T_k, D_{k+1, B}}^F(p_{D_{k+1, B}} + q_{D_{k+1, B}} \phi_{D_{k+1, B}, D_{k+1, T}}^F p_{D_{k+1, T}}), \quad k = 0, \dots, K-1.
\end{aligned} \tag{3.87}$$

The probability of not being detected after site i , given having reached that site as a fallback

fish and not having entered the tributary preceding site i , is χ_i^F :

$$\begin{aligned}
 \chi_{D_{kB}}^F &= 1 - \phi_{D_{kB}, D_{kT}}^F (1 - q_{D_{kT}} \chi_{D_{kT}}^F), & k = 1, \dots, K; \\
 \chi_{D_{kT}}^F &= 1 - \phi_{D_{kT}, T_k}^F - \phi_{D_{kT}, D_{k+1}, B}^F (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^F), & k = 1, \dots, K-1; \\
 \chi_{D_{KT}}^F &= 1 - \phi_{D_{KT}, T_K}^F; \\
 \chi_{T_k}^F &= 1 - \phi_{T_k, D_{k+1}, B}^F (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^{FT}), & k = 0, \dots, K-1.
 \end{aligned} \tag{3.88}$$

The parameters χ_i^T and χ_i^{TF} are appropriate for fish who entered and then exited the tributary in the reach preceding site i . The parameter χ_i^T is the probability of not being detected after site i , conditional on reaching site i , for fish who entered the tributary immediately below site i and who are not fallback fish, where:

$$\begin{aligned}
 \chi_{D_{kB}}^T &= 1 - \phi_{D_{kB}, D_{kT}}^T (1 - q_{D_{kT}} \chi_{D_{kT}}^T), & k = 1, \dots, K; \\
 \chi_{D_{kT}}^T &= 1 - (1 - f_{D_{kT}}^T) \left\{ \phi_{D_{kT}, T_k}^T + \phi_{D_{kT}, D_{k+1}, B}^T (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^T) \right\} \\
 &\quad - f_{D_{kT}}^T \phi_{D_{kT}, T_k}^{FT} \\
 &\quad - f_{D_{kT}}^T \phi_{D_{kT}, D_{k+1}, B}^{FT} (p_{D_{k+1}, B} + q_{D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^F p_{D_{k+1}, T}), & k = 1, \dots, K-1; \\
 \chi_{D_{KT}}^T &= 1 - \phi_{D_{KT}, T_K}^T; \\
 \chi_{T_k}^T &= 1 - (1 - f_{T_k}^T) \phi_{T_k, D_{k+1}, B}^T (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^T) \\
 &\quad - f_{T_k}^T \phi_{T_k, D_{k+1}, B}^{FT} (p_{D_{k+1}, B} + q_{D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^F p_{D_{k+1}, T}), & k = 1, \dots, K-1.
 \end{aligned} \tag{3.89}$$

The parameter χ_i^{FT} is the probability of not being detected after site i , conditional on reaching site i , for fallback fish who entered the tributary immediately below site i , where:

$$\begin{aligned}
 \chi_{D_{kB}}^{FT} &= 1 - \phi_{D_{kB}, D_{kT}}^{FT} (1 - q_{D_{kT}} \chi_{D_{kT}}^{FT}), & k = 1, \dots, K; \\
 \chi_{D_{kT}}^{FT} &= 1 - \phi_{D_{kT}, T_k}^{FT} - \phi_{D_{kT}, D_{k+1}, B}^{FT} (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^F), & k = 1, \dots, K-1; \\
 \chi_{D_{KT}}^{FT} &= 1 - \phi_{D_{KT}, T_K}^{FT}; \\
 \chi_{T_k}^{FT} &= 1 - \phi_{T_k, D_{k+1}, B}^{FT} (1 - q_{D_{k+1}, B} \chi_{D_{k+1}, B}^{FT}), & k = 1, \dots, K-1.
 \end{aligned} \tag{3.90}$$

The parameters used in Model 5c are listed in Table 3.50.

Table 3.50: Parameters used in Model 5c, the Long-term Fallback Memory and Short-term Tributary Memory Model. The number of dams is K .

Parameter	Definition
Φ_{R,T_0}	Probability of surviving and moving from the release point directly to site T_0 without becoming a fallback fish;
$\Phi_{R,D_{1B}}$	Probability of surviving and moving from the release point directly to site D_{1B} without becoming a fallback fish;
Φ_{R,T_0}^F	Probability of surviving, becoming a fallback fish, and then moving from the release point directly to site T_0 ;
$\Phi_{R,D_{1B}}^F$	Probability of surviving, becoming a fallback fish, and then moving from the release point directly to site D_{1B} ;
ϕ_{ij}	Probability of surviving and moving from site i to site j as a non-fallback fish, given reaching site i without entering the tributary (if any) in the reach immediately preceding site i , for $i = T_0, D_{1B}, D_{1T}, T_1, \dots, D_{KT}$ and j as in Equation (3.84);
ϕ_{ij}^T	Probability of surviving and moving from site i to site j as a non-fallback fish, given reaching site i after entering the tributary in the reach immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, T_K$ and j as in Equation (3.84);
ϕ_{ij}^F	Probability of surviving and moving from site i to site j as a fallback fish, given reaching site i without entering the tributary in the reach immediately preceding site i , for $i = T_0, D_{1B}, D_{1T}, T_1, \dots, D_{KT}$ and j as in Equation (3.84);
ϕ_{ij}^{FT}	Probability of surviving and moving from site i to site j as a fallback fish, given reaching site i after entering the tributary in the reach immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$ and j as in Equation (3.84);
p_i	Probability of being detected at site j , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$;
q_i	Probability of avoiding detection at site i , given having reached site i , for $i = D_{1B}, D_{1T}, D_{2B}, \dots, D_{KT}$; $= 1 - p_i$;
f_i	Probability of becoming a post-fallback fish between site i and the next detection site, given having reached site i as a non-fallback fish without entering the tributary in the reach immediately preceding site i , for $i = T_0, D_{1T}, T_1, D_{2T}, \dots, T_{K-1}$;
f_i^T	Probability of becoming a post-fallback fish between site i and the next detection site, given having reached site i as a non-fallback fish after entering the tributary in the reach immediately preceding site i , for $i = D_{1T}, T_1, D_{2T}, T_2, \dots, T_{K-1}$;

Table 3.50 continued

Parameter	Definition
χ_i	Probability of not being detected after site i , given having reached site i as a non-fallback fish without having entered the tributary (if any) in the reach immediately preceding site i , for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$;
χ_i^T	Probability of not being detected after site i , given having reached site i as a non-fallback fish after entering the tributary in the reach immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$;
χ_i^F	Probability of not being detected after site i , given having reached site i as a fallback fish without having entered the tributary (if any) in the reach immediately preceding site i , for $i = T_0, D_{1B}, D_{1T}, \dots, D_{KT}$;
χ_i^{TF}	Probability of not being detected after site i , given having reached site i as a fallback fish after entering the tributary in the reach immediately preceding site i , for $i = D_{1B}, D_{1T}, T_1, \dots, D_{KT}$.

The parameters in Table 3.50 can be used to express the probabilities of the possible detection histories. For example, consider the probabilities of the detection histories examined in Model 5b:

$$\begin{aligned}
 Pr[R \text{ FB } T_0 \text{ } D_{1B} \text{ } D_{2T} \text{ } T_2 \text{ } D_{3T}] &= \Phi_{R,T_0}^F \phi_{T_0,D_{1B}}^F p_{D_{1B}} \phi_{D_{1B},D_{1T}}^{FT} q_{D_{1T}} \phi_{D_{1T},D_{2B}}^{FT} q_{D_{2B}} \\
 &\times \phi_{D_{2B},D_{2T}}^F p_{D_{2T}} \phi_{D_{2T},T_2}^F \phi_{T_2,D_{3B}}^F q_{D_{3B}} \phi_{D_{3B},D_{3T}}^{FT} \\
 &\times p_{D_{3T}} \chi_{D_{3T}}^{FT}; \quad (3.91)
 \end{aligned}$$

$$\begin{aligned}
 Pr[R \text{ } D_{1B} \text{ } T_1 \text{ FB } D_{2B} \text{ } T_2 \text{ } T_3] &= \Phi_{R,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}} q_{D_{1T}} (1 - f_{D_{1T}}) \phi_{D_{1T},T_1} f_{T_1} \\
 &\times \phi_{T_1,D_{2B}}^F p_{D_{2B}} \phi_{D_{2B},D_{2T}}^F q_{D_{2T}} \phi_{D_{2T},T_2}^F \phi_{T_2,D_{3B}}^F q_{D_{3B}} \\
 &\times \phi_{D_{3B},D_{3T}}^{FT} q_{D_{3T}} \phi_{D_{3T},T_3}^{FT} \chi_{T_3}^{FT}; \quad (3.92)
 \end{aligned}$$

$$\begin{aligned}
 Pr[R \text{ } T_0 \text{ } D_{1B} \text{ } T_1 \text{ FB } D_{2B} \text{ } T_2 \text{ } T_3] &= \Phi_{R,T_0} \phi_{T_0,D_{1B}} p_{D_{1B}} \phi_{D_{1B},D_{1T}}^T q_{D_{1T}} (1 - f_{D_{1T}}^T) \phi_{D_{1T},T_1}^T f_{T_1}^T \\
 &\times \phi_{T_1,D_{2B}}^{FT} p_{D_{2B}} \phi_{D_{2B},D_{2T}}^F q_{D_{2T}} \phi_{D_{2T},T_2}^F \phi_{T_2,D_{3B}}^F q_{D_{3B}} \\
 &\times \phi_{D_{3B},D_{3T}}^{FT} q_{D_{3T}} \phi_{D_{3T},T_3}^{FT} \chi_{T_3}^{FT}. \quad (3.93)
 \end{aligned}$$

The detection history in Equation (3.91) shows the fallback occurring on the way to site T_0 . Unlike Equation (3.72) (Model 5b), the fallback effect carries through the detection at site T_0 , and lasts throughout the detection history. The effect of visiting site T_0 ends after

reaching dam 2, and the effect of visiting site T_2 occurs at dam 3. The detection histories in Equations (3.92) and (3.93) are identical except for the visit to site T_0 in the latter. In both cases, the fallback occurs upon leaving site T_1 , so the effect of visiting T_1 is overridden by the fallback effect, which lasts throughout the detection histories. Equation (3.93) shows the effect of visiting site T_0 before falling back at T_1 , using the parameters $f_{D_{1T}}^T$, $f_{T_1}^T$, and $\phi_{T_1, D_{2B}}^{FT}$ instead of $f_{D_{1T}}$, f_{T_1} , and $\phi_{T_1, D_{2B}}^F$, as in Equation (3.92).

3.9.4.2 Likelihood

The likelihood can be expressed as

$$L \propto \prod_i \pi_{CH_i}^{P[CH_i]}, \quad (3.94)$$

where CH_i is observed detection history i , $P[CH_i]$ is the probability of detection history i , and i ranges over all observed detection histories.

For the 1996 Chinook data set, it is impossible to get useful parameter estimates even for the reduced, 4-dam data set. Thus, while Model 5c is a logical continuation of the sequence of models presented in this chapter, it may demand more structure than exists in the data set, and so be too complex to be useful as an analysis tool.

3.10 Model 6: Fallback and Memory Tributary Model with Trap Data

Models 0 through 5b and 5c use only records of type “A1,” “LT,” “F,” and “L” from the radiotelemetry data (see Section 3.2.2). Other types of records are available, such as “MBT” (mobile tracking), “RCP” (tag recovery), and “GRT” (recapture or recovery at Lower Granite adult trap). Mobile tracking records are difficult to include in release-recapture models due to variable sampling effort. The “RCP” records came from multiple sites in the Columbia and Snake river watersheds, including hatcheries, traps, weirs, and spawning sites. Their inclusion requires independent estimates of tag-reporting rates, which are generally less than 100%. The “GRT” records are specific types of recapture or recovery records, occurring at the adult trap off the fish ladder at Lower Granite Dam. There it is reasonable to assume 100% detection. Fish that enter the adult trap at LGR are examined

and may undergo some degree of handling. Most are released back into the ladder and continue to ascend LGR. Some fish from particular hatcheries are not released back into the river, but are trucked from the adult trap to the hatchery; others are released to the river with their radio transmitters removed. It is possible to include the detections at the adult trap in the models developed in this chapter by treating trap detections as detections at LGR, and right-censoring either all the fish detected in the trap, or only those that were not released back into the river with intact radio tags. Because fish in the trap have reached LGR but have not completely ascended it yet, it is reasonable to use trap detections as base-of-dam detections. The model developed here (Model 6) uses the trap detections in this way: both "A1" and "GRT" codes become base-of-dam (D_{KB}) detections, and censoring is possible after detection at D_{KB} . Otherwise, Model 6 is identical to Model 5b (Short-term Fallback and Tributary Memory Model). Although such trap detections occurred only at LGR for the 1996 data set, it is conceivable that they may occur at other dams in the future. Thus, Model 6 allows for censoring at all base-of-dam sites (D_{kB} , for $k = 1, \dots, K$).

3.10.1 Data and Assumptions

Additional steps are needed to prepare radiotelemetry data for Model 6. As alluded to above, any records indicating recapture at an adult trap at a dam should be included as base-of-dam detections (D_{kB}). If any or all trap detections are to be censored, then the detection histories should reflect this (i.e., $\dots D_{kB} C$). Any trap detection that is not censored is represented as D_{kB} , unless detection at D_{kB} occurred immediately before the trap detection in the non-simplified detection history; a trap detection should not become a repeated D_{kB} detection, which would imply fallback at dam k . After the trap detections are converted to base-of-dam detections, any detection histories including censoring should be right-censored, and finally the detection histories should be reduced to the post-fallback paths, if necessary.

The 1996 data set included several questionable records at the Lower Granite adult trap, as well as records indicating release back into the river or transportation to a hatchery. All non-questionable records at the LGR adult trap that indicated release back into the river

were treated as base-of-dam detections (not following by censoring) at LGR. All questionable records at the adult trap, including those indicating transportation to a hatchery or release after removal of the radio tag, were treated as base-of-dam detections followed by right-censoring at LGR.

In addition to the assumptions described in Section 3.3.3, Model 6 assumes that all fish that reach site D_{kB} ascend the ladder at dam k at least as far as the trap, if a trap exists. If there is no adult trap, then no assumption is made that fish that reach the base of dam k ascend any part of the ladder. For existing traps, it is assumed that the detection rate in the trap is 100%, i.e., that all radio-tagged fish that enter the trap are correctly identified. If the former of these two assumptions is incorrect, then the estimated censoring rate at D_{kB} (i.e., $\hat{\delta}_{D_{kB}}$) will be biased. If the latter of these assumptions is incorrect, then the undetected fish will either contribute to the unaccountable loss estimate (if they are removed from the migrating population without detection), or else bias transition estimates upriver (if they are returned to the river but have decreased survival due to handling). If only some detection histories including trap detections are right-censored, then only the first of these two possibilities will occur. In general, the estimated detection rate $\hat{p}_{D_{kB}}$ will be positively biased for the actual detection rate at D_{kB} if fish enter the trap after evading detection at the base of the ladder. If dam k has multiple fish ladders, then the estimated censoring rate will be a weighted average of the trap entry and censoring rates at each ladder, some of which may be zero.

If only certain trap detections lead to right-censoring of the detection histories, then it is assumed that the correct detection histories are labeled for censoring, and that detection at the trap does not affect subsequent survival, movement, and fallback behavior for those fish released back into the river with intact radio tags. This assumption is reasonable if handling at the trap is minimized. At the Lower Granite trap, fish may be weighed or photographed. This degree of handling is less than that experienced by all fish in the radio-tagged releases at the Bonneville adult trap, where the fish are originally collected for tagging. If it is assumed that the handling and tagging at Bonneville is insufficient to prevent application of estimates from tagged fish to run-of-river fish, then it may be reasonable to assume that the lesser degree of handling at the Lower Granite trap is also insufficient to require

censoring of all tagged fish that entered the trap. Whether or not this assumption is justified is left to the researcher; by treating trap detections as base-of-dam detections, Model 6 can accommodate both the policy of right-censoring all detection histories with trap detections, and the policy of right-censoring only selected trap detection histories.

3.10.2 Notation

The notation used in Model 5b may be used in Model 6, with several modifications. First, the transition parameters $\phi_{D_{kB}, D_{kT}}$, $\phi_{D_{kB}, D_{kT}}^T$, and $\phi_{D_{kB}, D_{kT}}^F$ and the “last detection” parameters $\chi_{D_{kB}}$, $\chi_{D_{kB}}^T$, $\chi_{D_{kB}}^F$, $\chi_{D_{kB}}^f$, and $\chi_{D_{kB}}^{fT}$ must be redefined as follows:

For $k = 1, \dots, K$ unless otherwise specified:

$\phi_{D_{kB}, D_{kT}} = Pr[\text{Survive and move directly from site } D_{kB} \text{ to site } D_{kT} \mid \text{Neither fell back during the transition to site } D_{kB}, \text{ nor visited site } T_{k-1}, \text{ nor was censored at } D_{kB}];$

$\phi_{D_{kB}, D_{kT}}^T = Pr[\text{Survive and move directly from site } D_{kB} \text{ to site } D_{kT} \mid \text{Visited site } T_{k-1}, \text{ did not fall back between sites } T_{k-1} \text{ and } D_{kB}, \text{ and was not censored at site } D_{kB}];$

$\phi_{D_{kB}, D_{kT}}^F = Pr[\text{Survive and move directly from site } D_{kB} \text{ to site } D_{kT} \mid \text{Fell back during the transition to site } D_{kB} \text{ without visiting site } T_{k-1} \text{ after fallback, and was not censored at site } D_{kB}];$

$\chi_{D_{kB}} = Pr[\text{Not detected again after reaching site } D_{kB} \mid \text{Neither visited site } T_{k-1}, \text{ nor fell back before reaching site } D_{kB}, \text{ nor was censored at } D_{kB}];$

$\chi_{D_{kB}}^T = Pr[\text{Not detected again after reaching site } D_{kB} \mid \text{Visited site } T_{k-1} \text{ but neither fell back before reaching site } D_{kB} \text{ nor was censored at } D_{kB}];$

$\chi_{D_{kB}}^F = Pr[\text{Not detected again after reaching site } D_{kB} \mid \text{Fell back during the transition to site } D_{kB} \text{ and was not censored at } D_{kB}];$

$\chi_{D_{kB}}^f = Pr[\text{Not detected again after reaching site } D_{kB} \mid \text{Fell back before the transition to site } D_{kB}, \text{ and neither visited site } T_{k-1} \text{ nor was censored at } D_{kB}],$
for $k = 2, \dots, K$;

$\chi_{D_{kB}}^{fT} = Pr[\text{Not detected again after reaching site } D_{kB} \mid \text{Visited site } T_{k-1} \text{ after falling back, and was not censored at } D_{kB}].$

The mathematical definitions of $\chi_{D_{kB}}$, $\chi_{D_{kB}}^T$, $\chi_{D_{kB}}^F$, $\chi_{D_{kB}}^f$, and $\chi_{D_{kB}}^{fT}$ are unchanged from Equations (3.67), (3.68), (3.69), (3.70), and (3.71), respectively.

New parameters are necessary to handle censoring at the base-of-dam sites. Define $\delta_{D_{kB}}$ as follows:

$$\delta_{D_{kB}} = Pr[\text{Censored at site } D_{kB} \mid \text{Detected at site } D_{kB}].$$

3.10.3 Likelihood

The summary statistics and minimal sufficient statistics used with Model 5b are also used here, with no change in interpretation or definition. In addition to those statistics, the following censoring statistics are needed for Model 6 ($k = 1, \dots, K$):

$c_{D_{kB}} = \text{Number censored at } D_{kB} \text{ that neither fell back during the transition to } D_{kB} \text{ nor visited } T_{k-1};$

$c_{D_{kB}}^T = \text{Number censored at } D_{kB} \text{ that visited site } T_{k-1} \text{ and did not fall back during the transition from } T_{k-1} \text{ to } D_{kB};$

$c_{D_{kB}}^F = \text{Number censored at } D_{kB} \text{ that fell back during the transition to } D_{kB}; \quad (3.95)$

$c_{D_{kB}}^f = \text{Number censored at } D_{kB} \text{ that fell back before the transition to } D_{kB}, \text{ and did not visit } T_{k-1};$

$c_{D_{kB}}^{fT} = \text{Number censored at } D_{kB} \text{ that visited site } T_{k-1} \text{ and fell back before reaching } T_{k-1}.$

The statistics $c_{D_{kB}}$, $c_{D_{kB}}^T$, $c_{D_{kB}}^F$, $c_{D_{kB}}^f$, and $c_{D_{kB}}^{fT}$ are part of the minimal sufficient statistic for Model 6. Also useful is their sum, $C_{D_{kB}}$:

$$C_{D_{kB}} = c_{D_{kB}} + c_{D_{kB}}^T + c_{D_{kB}}^F + c_{D_{kB}}^f + c_{D_{kB}}^{fT}.$$

The likelihood for Model 6 can be expressed as follows:

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \Phi_{R,T_0}^{a_{T_0}} \Phi_{R,D_{1B}}^{g_{T_0}-b_{T_0}-h_{T_0}} (\Phi_{R,T_0}^F)^{a_{T_0}^{F(R)}} (\Phi_{R,D_{1B}}^F)^{d_R-a_{T_0}^{F(R)}} \\
& \times (\chi_{T_0}^F)^{a_{T_0}^{F(R)}-b_{T_0}^{F(R)}} (\phi_{T_0,D_{1B}}^F)^{d_{T_0}+b_{T_0}^{F(R)}} \\
& \times \prod_{k=0}^{K-1} \left\{ \chi_{T_k}^{a_{T_k}-b_{T_k}-h_{T_k}} f_{T_k}^{d_{T_k}} (1-f_{T_k})^{b_{T_k}+h_{T_k}-d_{T_k}} \phi_{T_k,D_{k+1,B}}^{b_{T_k}+h_{T_k}-d_{T_k}+b_{T_k}^f} \right\} \\
& \times \prod_{k=1}^K \left\{ \phi_{D_{kB},D_{kT}}^{g_{D_{kB}}+g_{D_{kT}}^f} (\phi_{D_{kB},D_{kT}}^T)^{g_{D_{kB}}+g_{D_{kT}}^{fT}} (\phi_{D_{kB},D_{kT}}^F)^{g_{D_{kB}}^F} \phi_{D_{kT},T_k}^{a_{T_k}+a_{T_k}^f} (\phi_{D_{kT},T_k}^T)^{a_{T_k}^T+a_{T_k}^{fT}} \right. \\
& \quad \times (\phi_{D_{kT},T_k}^F)^{a_{T_k}^{FNT}} p_{D_{kB}}^{A_{D_{kB}}} q_{D_{kB}}^{G_{T_k-1}-A_{D_{kB}}} \delta_{D_{kB}}^{C_{D_{kB}}} (1-\delta_{D_{kB}})^{A_{D_{kB}}-C_{D_{kB}}} \\
& \quad \times p_{D_{kT}}^{A_{D_{kT}}} q_{D_{kT}}^{G_{D_{kB}}-A_{D_{kT}}} \chi_{D_{kB}}^{a_{D_{kB}}-c_{D_{kB}}-b_{D_{kB}}-h_{D_{kB}}} (\chi_{D_{kB}}^T)^{a_{D_{kB}}^T-c_{D_{kB}}^T-b_{D_{kB}}^T-h_{D_{kB}}^T} \\
& \quad \times (\chi_{D_{kB}}^{fT})^{a_{D_{kB}}^{fT}-c_{D_{kB}}^{fT}-b_{D_{kB}}^{fT}} (\chi_{D_{kB}}^F)^{a_{D_{kB}}^F-c_{D_{kB}}^F-b_{D_{kB}}^F} \chi_{D_{kT}}^{a_{D_{kT}}-b_{D_{kT}}-h_{D_{kT}}} \\
& \quad \times (\chi_{D_{kT}}^T)^{a_{D_{kT}}^T-b_{D_{kT}}^T-h_{D_{kT}}^T} (\chi_{D_{kT}}^{fT})^{a_{D_{kT}}^{fT}-b_{D_{kT}}^{fT}} (\chi_{D_{kT}}^F)^{a_{D_{kT}}^F-b_{D_{kT}}^F} \left. \right\} \\
& \times \prod_{k=1}^{K-1} \left\{ f_{D_{kT}}^{d_{D_{kT}}} (1-f_{D_{kT}})^{g_{D_{kT}}-d_{D_{kT}}} (f_{D_{kT}}^T)^{d_{D_{kT}}^T} (1-f_{D_{kT}}^T)^{g_{D_{kT}}^T-d_{D_{kT}}^T} (\phi_{D_{kT},T_k}^{FT})^{a_{T_k}^{FT}} \right. \\
& \quad \times \phi_{D_{kT},D_{k+1,B}}^{g_{T_k}+g_{T_k}^f-(b_{T_k}+h_{T_k}+b_{T_k}^f)} \left(\phi_{D_{kT},D_{k+1,B}}^T \right)^{g_{T_k}^T+g_{T_k}^{fT}-(b_{T_k}^T+h_{T_k}^T+b_{T_k}^{fT})} \\
& \quad \times \left(\phi_{D_{kT},D_{k+1,B}}^F \right)^{g_{D_{kT}}^F+d_{D_{kT}}-a_{T_k}^{FNT}} \left(\phi_{D_{kT},D_{k+1,B}}^{FT} \right)^{d_{D_{kT}}^T-a_{T_k}^{F(D_{kT})T}} (f_{T_k}^T)^{d_{T_k}^T} \\
& \quad \times (1-f_{T_k}^T)^{b_{T_k}^T+h_{T_k}^T-d_{T_k}^T} \left(\phi_{T_k,D_{k+1,B}}^T \right)^{b_{T_k}^T+h_{T_k}^T-d_{T_k}^T+b_{T_k}^{fT}} \\
& \quad \times \left(\phi_{T_k,D_{k+1,B}}^F \right)^{d_{T_k}+b_{T_k}^{FNT}+b_{T_k}^{F(D_{kT})T}} \left(\phi_{T_k,D_{k+1,B}}^{FT} \right)^{d_{T_k}^T} (\chi_{T_k}^T)^{a_{T_k}^T-b_{T_k}^T-h_{T_k}^T} \\
& \quad \times \left(\chi_{T_k}^{fT} \right)^{a_{T_k}^{fT}-b_{T_k}^{fT}} (\chi_{T_k}^F)^{a_{T_k}^{FNT}+a_{T_k}^{F(D_{kT})T}-b_{T_k}^{FNT}-b_{T_k}^{F(D_{kT})T}} \left. \right\} \\
& \times \prod_{k=2}^K \left\{ \left(\chi_{D_{kB}}^f \right)^{a_{D_{kB}}^f-c_{D_{kB}}^f-b_{D_{kB}}^f} \left(\chi_{D_{kT}}^f \right)^{a_{D_{kT}}^f-b_{D_{kT}}^f} \right\} \prod_{k=2}^{K-1} \left(\chi_{T_k}^f \right)^{a_{T_k}^f-b_{T_k}^f}, \quad (3.96)
\end{aligned}$$

where N is the size of the initial release and K is the number of dams. The only differences between Equation (3.96) and Equation (3.77) are the additional censoring parameters, and the exponents of the $\chi_{D_{kB}}$ parameters are adjusted for censoring. As with Equation (3.77), Equation (3.96) may be tailored to a particular data set by specifying K , removing any extraneous parameters, and renaming parameters according to observed detections, if necessary. This is done for the 1996 Chinook salmon data set in the next section.

The initial values used for Model 5b may be used for Model 6, with the following ratios used as initial values for $\delta_{D_{kB}}$, $\delta_{D_{kB}}^T$, and $\delta_{D_{kB}}^F$, respectively:

$$\frac{c_{D_{kB}} + c_{D_{kB}}^f}{a_{D_{kB}} + a_{D_{kB}}^f}, \quad \frac{c_{D_{kB}}^T + c_{D_{kB}}^{fT}}{a_{D_{kB}}^T + a_{D_{kB}}^{fT}}, \quad \frac{c_{D_{kB}}^F}{a_{D_{kB}}^F}.$$

The initial values from Model 5b may need to be modified to ensure that all derived parameters (e.g., χ_i , χ_i^T , and χ_i^F) are between 0 and 1.

3.10.4 Performance Measures

The perceived probability of surviving from the release to the top of dam K , or perceived system survival (S_{sys}), and the unaccountable loss rate (μ_R) are defined as for Model 5b; see Section 3.9.3.3.

3.10.5 1996 Chinook Data Set

The summary statistics for the 1996 Chinook salmon data set for Model 6 are given in Table 3.51. Most values are identical to those for Model 5b, although the a_i and b_i values change for a few sites. The alterations of the model parameters necessary to fit Model 5b to the 1996 data set are also necessary for Model 6. The censoring parameters $\delta_{D_{kB}}$ must be fixed to 0 for $k = 1, \dots, 6$. Also, all of the fish detected at site D_{7B} that were not censored there survived to reach D_{7T} or T_7 (i.e., $a_{D_{7B}} - b_{D_{7B}} - c_{D_{7B}} = 0$ and $a_{D_{7B}}^f - b_{D_{7B}}^f - c_{D_{7B}}^f = 0$); thus, $\phi_{D_{7B}, D_{7T}}$ must be fixed to 1, giving $\chi_{D_{7B}} = q_{D_{7T}} \chi_{D_{7T}}$ and $\chi_{D_{7B}}^f = q_{D_{7T}} \chi_{D_{7T}}^f$. Finally, all fish seen after site D_{6B} were seen at D_{7B} (i.e., $G_{D_{6B}} - A_{D_{7B}} = 0$), so $p_{D_{7B}}$ must be fixed to 1.

The likelihood for Model 6, tailored to the 1996 data set is as follows:

$$\begin{aligned}
L \propto & \chi_R^{N-g_R} \Phi_{R,T_0}^{a_{T_0}} \Phi_{R,D_{1B}}^{g_{T_0}-b_{T_0}} (\Phi_{R,T_0}^F)^{a_{T_0}^{F(R)}} (\Phi_{R,D_{1B}}^F)^{d_R-a_{T_0}^{F(R)}} \chi_{T_0}^{a_{T_0}-b_{T_0}} \phi_{T_0,D_{1B}}^{b_{T_0}} p_{D_{1B}}^{A_{D_{1B}}} q_{D_{1B}}^{G_{T_0}-A_{D_{1B}}} \\
& \times \chi_{D_{1B}}^{a_{D_{1B}}-b_{D_{1B}}-h_{D_{1B}}} (\chi_{D_{1B}}^F)^{a_{D_{1B}}^F-b_{D_{1B}}^F} \phi_{D_{1B},D_{1T}}^{g_{D_{1B}}} (\phi_{D_{1B},D_{1T}}^F)^{g_{D_{1B}}^F} \\
& \times p_{D_{1T}}^{A_{D_{1T}}} q_{D_{1T}}^{G_{D_{1B}}-A_{D_{1T}}} \chi_{D_{1T}}^{a_{D_{1T}}-b_{D_{1T}}-h_{D_{1T}}} (\chi_{D_{1T}}^T)^{a_{D_{1T}}^T-b_{D_{1T}}^T} (\chi_{D_{1T}}^F)^{a_{D_{1T}}^F-b_{D_{1T}}^F} f_{D_{1T}}^{d_{D_{1T}}} \\
& \times (1-f_{D_{1T}})^{g_{D_{1T}}-d_{D_{1T}}} \phi_{D_{1T},T_1}^{a_{T_1}} (\phi_{D_{1T},T_1}^T)^{a_{T_1}^T} (\phi_{D_{1T},T_1}^F)^{a_{T_1}^{FNT}} \phi_{D_{1T},D_{2T}}^{g_{T_1}-b_{T_1}} (\phi_{D_{1T},D_{2T}}^T)^{g_{T_1}^T+g_{T_1}^{fT}} \\
& \times (\phi_{D_{1T},D_{2T}}^F)^{g_{D_{1T}}^F+d_{D_{1T}}-a_{T_1}^{FNT}} \chi_{T_1}^{a_{T_1}-b_{T_1}} (\chi_{T_1}^F)^{a_{T_1}^{FNT}+a_{T_1}^{F(D_{1T})T}} -b_{T_1}^{FNT} \phi_{T_1,D_{2T}}^{b_{T_1}} (\phi_{T_1,D_{2T}}^F)^{b_{T_1}^{FNT}} \\
& \times p_{D_{2T}}^{A_{D_{2T}}} q_{D_{2T}}^{G_{T_1}-A_{D_{2T}}} \chi_{D_{2T}}^{a_{D_{2T}}-b_{D_{2T}}-h_{D_{2T}}} (\chi_{D_{2T}}^T)^{a_{D_{2T}}^T-b_{D_{2T}}^T} (\chi_{D_{2T}}^f)^{a_{D_{2T}}^f-b_{D_{2T}}^f} f_{D_{2T}}^{d_{D_{2T}}} \\
& \times (1-f_{D_{2T}})^{g_{D_{2T}}-d_{D_{2T}}} \phi_{D_{2T},T_2}^{a_{T_2}+a_{T_2}^f} (\phi_{D_{2T},T_2}^T)^{a_{T_2}^T+a_{T_2}^{fT}} (\phi_{D_{2T},T_2}^F)^{a_{T_2}^{FNT}} \phi_{D_{2T},D_{3T}}^{g_{T_2}+g_{T_2}^f-b_{T_2}} \\
& \times (\phi_{D_{2T},D_{3T}}^T)^{g_{T_2}^T+g_{T_2}^{fT}-(b_{T_2}^T+b_{T_2}^{fT})} (\phi_{D_{2T},D_{3T}}^F)^{g_{D_{2T}}^F+d_{D_{2T}}-a_{T_2}^{FNT}} \\
& \times \chi_{T_2}^{a_{T_2}-b_{T_2}} (\chi_{T_2}^T)^{a_{T_2}^T-b_{T_2}^T} (\chi_{T_2}^f)^{a_{T_2}^f} (\chi_{T_2}^{fT})^{a_{T_2}^{fT}-b_{T_2}^{fT}} \phi_{T_2,D_{3T}}^{b_{T_2}} (\phi_{T_2,D_{3T}}^T)^{b_{T_2}^T+b_{T_2}^{fT}} p_{D_{3T}}^{A_{D_{3T}}} q_{D_{3T}}^{G_{T_2}-A_{D_{3T}}} \\
& \times \chi_{D_{3T}}^{a_{D_{3T}}-b_{D_{3T}}-h_{D_{3T}}} (\chi_{D_{3T}}^f)^{a_{D_{3T}}^f-b_{D_{3T}}^f} (\chi_{D_{3T}}^F)^{a_{D_{3T}}^F-b_{D_{3T}}^F} f_{D_{3T}}^{d_{D_{3T}}} (1-f_{D_{3T}})^{g_{D_{3T}}-d_{D_{3T}}} \\
& \times \phi_{D_{3T},T_3}^{a_{T_3}+a_{T_3}^f} (\phi_{D_{3T},T_3}^T)^{a_{T_3}^T} (\phi_{D_{3T},T_3}^F)^{a_{T_3}^{FNT}} \phi_{D_{3T},D_{4B}}^{g_{T_3}+g_{T_3}^f-(b_{T_3}+h_{T_3}+b_{T_3}^f)} (\phi_{D_{3T},D_{4B}}^T)^{g_{T_3}^T+g_{T_3}^{fT}-b_{T_3}^{fT}} \\
& \times (\phi_{D_{3T},D_{4B}}^F)^{g_{D_{3T}}^F+d_{D_{3T}}-a_{T_3}^{FNT}} \chi_{T_3}^{a_{T_3}-b_{T_3}-h_{T_3}} (\chi_{T_3}^f)^{a_{T_3}^f-b_{T_3}^f} (\chi_{T_3}^F)^{a_{T_3}^{FNT}+a_{T_3}^{F(D_{3T})T}} -b_{T_3}^{FNT}-b_{T_3}^{F(D_{3T})T} \\
& \times f_{T_3}^{d_{T_3}} (1-f_{T_3})^{b_{T_3}+h_{T_3}-d_{T_3}} \phi_{T_3,D_{4B}}^{b_{T_3}+h_{T_3}-d_{T_3}+b_{T_3}^f} (\phi_{T_3,D_{4B}}^F)^{d_{T_3}+b_{T_3}^{FNT}+b_{T_3}^{F(D_{3T})T}} p_{D_{4B}}^{A_{D_{4B}}} q_{D_{4B}}^{G_{T_3}-A_{D_{4B}}} \\
& \times \chi_{D_{4B}}^{a_{D_{4B}}-b_{D_{4B}}} (\chi_{D_{4B}}^f)^{a_{D_{4B}}^f-b_{D_{4B}}^f} (\chi_{D_{4B}}^F)^{a_{D_{4B}}^F-b_{D_{4B}}^F} \phi_{D_{4B},D_{4T}}^{g_{D_{4B}}+g_{D_{4B}}^f} (\phi_{D_{4B},D_{4T}}^F)^{g_{D_{4B}}^F} p_{D_{4T}}^{A_{D_{4T}}} \\
& \times q_{D_{4T}}^{G_{D_{4B}}-A_{D_{4T}}} \chi_{D_{4T}}^{a_{D_{4T}}-b_{D_{4T}}-h_{D_{4T}}} (\chi_{D_{4T}}^T)^{a_{D_{4T}}^T-h_{D_{4T}}^T} (\chi_{D_{4T}}^f)^{a_{D_{4T}}^f-b_{D_{4T}}^f} (\chi_{D_{4T}}^F)^{a_{D_{4T}}^F-b_{D_{4T}}^F} \\
& \times f_{D_{4T}}^{d_{D_{4T}}+d_{D_{4T}}^T} (1-f_{D_{4T}})^{g_{D_{4T}}+g_{D_{4T}}^T-d_{D_{4T}}-d_{D_{4T}}^T} \phi_{D_{4T},T_4}^{a_{T_4}+a_{T_4}^f+a_{T_4}^{fT}} (\phi_{D_{4T},T_4}^F)^{a_{T_4}^{FNT}} \\
& \times \phi_{D_{4T},D_{5B}}^{g_{T_4}+g_{T_4}^T+g_{T_4}^f+g_{T_4}^{fT}} (\phi_{D_{4T},D_{5B}}^F)^{g_{D_{4T}}^F+d_{D_{4T}}+d_{D_{4T}}^T-a_{T_4}^{FNT}} p_{D_{5B}}^{A_{D_{5B}}} q_{D_{5B}}^{G_{T_4}-A_{D_{5B}}} \chi_{D_{5B}}^{a_{D_{5B}}-b_{D_{5B}}-h_{D_{5B}}} \\
& \times (\chi_{D_{5B}}^f)^{a_{D_{5B}}^f-b_{D_{5B}}^f} \phi_{D_{5B},D_{5T}}^{g_{D_{5B}}+g_{D_{5B}}^f} p_{D_{5T}}^{A_{D_{5T}}} q_{D_{5T}}^{G_{D_{5B}}-A_{D_{5T}}} \chi_{D_{5T}}^{a_{D_{5T}}-b_{D_{5T}}} (\chi_{D_{5T}}^f)^{a_{D_{5T}}^f-b_{D_{5T}}^f} f_{D_{5T}}^{d_{D_{5T}}} \\
& \times (1-f_{D_{5T}})^{g_{D_{5T}}-d_{D_{5T}}} \phi_{D_{5T},T_5}^{a_{T_5}} (\phi_{D_{5T},T_5}^F)^{a_{T_5}^{FNT}} \phi_{D_{5T},D_{6B}}^{g_{T_5}+g_{T_5}^f-(b_{T_5}+b_{T_5}^f)} (\phi_{D_{5T},D_{6B}}^F)^{g_{D_{5T}}^F+d_{D_{5T}}-a_{T_5}^{FNT}}
\end{aligned}$$

$$\begin{aligned}
& \times (\chi_{T_5}^F)^{a_{T_5}^{FNT} + a_{T_5}^{F(D_5T)^T} - b_{T_5}^{FNT} - b_{T_5}^{F(D_5T)^T}} (\phi_{T_5, D_6B}^F)^{b_{T_5}^{FNT} + b_{T_5}^{F(D_5T)^T}} p_{D_6B}^{A_{D_6B}} q_{D_6B}^{G_{T_5} - A_{D_6B}} \chi_{D_6B}^{a_{D_6B} - b_{D_6B}} \\
& \times (\chi_{D_6B}^f)^{a_{D_6B}^f - b_{D_6B}^f} (\chi_{D_6B}^{fT})^{a_{D_6B}^{fT} - b_{D_6B}^{fT}} \phi_{D_6B, D_7B}^{g_{D_6B} + g_{D_6B}^f} (\phi_{D_6B, D_7T}^T)^{g_{D_6B}^T + g_{D_6B}^{fT}} \\
& \times \delta_{D_7B}^{C_{D_7B}} (1 - \delta_{D_7B})^{A_{D_7B} - C_{D_7B}} \chi_{D_7B}^{a_{D_7B} - b_{D_7B} - c_{D_7B}} (\chi_{D_7B}^f)^{a_{D_7B}^f - b_{D_7B}^f - c_{D_7B}^f} p_{D_7T}^{A_{D_7T}} \\
& \times q_{D_7T}^{G_{D_7B} - A_{D_7T}} \chi_{D_7T}^{a_{D_7T} - b_{D_7T}} (\chi_{D_7T}^f)^{a_{D_7T}^f - b_{D_7T}^f} \phi_{D_7T, T_7}^{a_{T_7} + a_{T_7}^f}. \tag{3.97}
\end{aligned}$$

3.10.6 Results

Program USER¹⁸ was used to fit Model 6 to the data via maximum likelihood. Maximum likelihood estimates from the full data set ($K = 7$ dams) are listed in Table 3.52. The log-likelihood was -3838.7199, with an AIC of 7797.4398. The perceived system survival rate is estimated at $\hat{S}_{sys} = 0.1349$ ($\widehat{SE} = 0.0119$), and the unaccountable loss rate from the release is estimated at $\hat{\mu}_R = 0.2468$ ($\widehat{SE} = 0.0151$). Model 6 incorporates censoring of sampled individuals, in this case only at LGR and only if the sampled fish was not returned to the adult fish ladder with an intact tag; otherwise, Model 6 is identical to Model 5b. It is reasonable to expect that censoring of sampled fish would increase the estimate of perceived survival and decrease the estimate of unaccountable loss, because some fish that were previously viewed as mortalities are now accounted for via censoring. This was observed for this data set: $\hat{S}_{sys} = 0.1349$ ($\widehat{SE} = 0.0119$) for Model 6 versus $\hat{S}_{sys} = 0.1048$ ($\widehat{SE} = 0.0106$) for Model 5b, and $\hat{\mu}_R = 0.2468$ ($\widehat{SE} = 0.0151$) for Model 6 versus $\hat{\mu}_R = 0.2770$ ($\widehat{SE} = 0.0155$) for Model 5b.

Table 3.52: Maximum likelihood estimates of parameters from Model 6, the Short-term Fallback and Tributary Memory model with censoring, with $K = 7$ dams. The estimates of ϕ_{D_{2T}, T_2}^F , ϕ_{D_{3T}, T_3}^T , and ϕ_{D_{5T}, T_5}^F come from the relations $\phi_{D_{2T}, T_2}^F + \phi_{D_{2T}, D_{3T}}^F = 1$, $\phi_{D_{3T}, T_3}^T + \phi_{D_{3T}, D_{4B}}^T = 1$, and $\phi_{D_{5T}, T_5}^F + \phi_{D_{5T}, D_{6B}}^F = 1$, respectively.

Category	Parameter	Estimate	S.E.
Transition	Φ_{R, T_0}	0.0083	0.0031
	Φ_{R, T_0}^F	0.0047	0.0024
	$\Phi_{R, D_{1B}}$	0.8448	0.0126

¹⁸<http://www.cbr.washington.edu/paramEst/USER/>

Table 3.52 continued

Category	Parameter	Estimate	S.E.
Transition	$\Phi_{R,D_{1B}}^F$	0.1205	0.0113
	$\phi_{T_0,D_{1B}}$	0.5726	0.1874
	$\phi_{D_{1B},D_{1T}}$	0.9758	0.0077
	$\phi_{D_{1B},D_{1T}}^F$	0.9737	0.0213
	ϕ_{D_{1T},T_1}	0.3604	0.0186
	ϕ_{D_{1T},T_1}^F	0.3991	0.0435
	ϕ_{D_{1T},T_1}^T	0.4990	0.2504
	$\phi_{D_{1T},D_{2T}}$	0.5535	0.0201
	$\phi_{D_{1T},D_{2T}}^F$	0.4905	0.0454
	$\phi_{D_{1T},D_{2T}}^T$	0.2526	0.2198
	$\phi_{T_1,D_{2T}}$	0.1224	0.0213
	$\phi_{T_1,D_{2T}}^F$	0.2046	0.0551
	ϕ_{D_{2T},T_2}	0.1458	0.0176
	ϕ_{D_{2T},T_2}^F	0.2739	0.0886
	ϕ_{D_{2T},T_2}^T	0.2240	0.0659
	$\phi_{D_{2T},D_{3T}}$	0.7740	0.0216
	$\phi_{D_{2T},D_{3T}}^F$	0.7261	0.0886
	$\phi_{D_{2T},D_{3T}}^T$	0.7495	0.0695
	$\phi_{T_2,D_{3T}}$	0.0170	0.0168
	$\phi_{T_2,D_{3T}}^T$	0.2222	0.1385
	ϕ_{D_{3T},T_3}	0.1170	0.0174
	ϕ_{D_{3T},T_3}^F	0.2069	0.0941
	ϕ_{D_{3T},T_3}^T	0.3333	0.2719
	$\phi_{D_{3T},D_{4B}}$	0.8242	0.0214
	$\phi_{D_{3T},D_{4B}}^F$	0.6812	0.1226
	$\phi_{D_{3T},D_{4B}}^T$	0.6667	0.2719
	$\phi_{T_3,D_{4B}}$	0.2813	0.1518
	$\phi_{T_3,D_{4B}}^F$	0.0777	0.0567
	$\phi_{D_{4B},D_{4T}}$	0.9778	0.0102
	$\phi_{D_{4B},D_{4T}}^F$	0.8775	0.1533
	ϕ_{D_{4T},T_4}	0.5272	0.0309
	ϕ_{D_{4T},T_4}^F	0.0692	0.0692
	$\phi_{D_{4T},D_{5B}}$	0.4259	0.0303
	$\phi_{D_{4T},D_{5B}}^F$	0.4059	0.1747
	$\phi_{D_{5B},D_{5T}}$	0.9821	0.0166
	ϕ_{D_{5T},T_5}	0.3415	0.0441
	ϕ_{D_{5T},T_5}^F	0.2837	0.1775
	$\phi_{D_{5T},D_{6B}}$	0.6623	0.0473
	$\phi_{D_{5T},D_{6B}}^F$	0.7163	0.1775
	$\phi_{T_5,D_{6B}}^F$	0.5050	0.3567

Table 3.52 continued

Category	Parameter	Estimate	S.E.
Transition	$\phi_{D_{6B}, D_{7B}}$	0.9651	0.0297
	$\phi_{D_{6B}, D_{7B}}^T$	0.9826	0.0251
	ϕ_{D_{7T}, T_7}	0.7991	0.0465
Detection	$p_{D_{1B}}$	0.9409	0.0085
	$p_{D_{1T}}$	0.8644	0.0128
	$p_{D_{2T}}$	0.8476	0.0175
	$p_{D_{3T}}$	0.9401	0.0130
	$p_{D_{4B}}$	0.8917	0.0181
	$p_{D_{4T}}$	0.9170	0.0166
	$p_{D_{5B}}$	0.8856	0.0288
	$p_{D_{5T}}$	0.8128	0.0360
	$p_{D_{6B}}$	0.5951	0.0460
	$p_{D_{7T}}$	0.9635	0.0254
Fallback	$f_{D_{1T}}$	0.0528	0.0097
	$f_{D_{2T}}$	0.0343	0.0097
	$f_{D_{3T}}$	0.0350	0.0123
	f_{T_3}	0.7405	0.2414
	$f_{D_{4T}}$	0.0368	0.0220
	$f_{D_{5T}}$	0.0371	0.0261
	$\delta_{D_{7B}}$	0.3158	0.0435

3.11 Discussion

One of the objectives of this chapter was to develop a statistical model that can be used with adult radiotelemetry data to estimate large-scale quantities such as perceived system survival (i.e., probability of surviving and remaining in the migrating population through the top of the final dam) and unaccountable loss. A sequence of release-recapture models was developed, ranging from simple models using only dam detections to more complex ones using both dam and tributary detections, fallback information, and censoring (i.e., adult trap or sampling room) information. Each model was fit to radiotelemetry data from a 1996 release of spring and summer Chinook salmon, and used to estimate both perceived system survival and the unaccountable loss rate; results from the models are summarized in Table 3.53.

Of these models, Model 6 seems the most appropriate for general use, incorporating tributary detections, fallback information, and censoring information. However, the appro-

priate model may depend on the data set and the release year. It is obvious from Table 3.53 that tributary detections should be used in estimating unaccountable loss rates. Censoring also appears important in estimating both perceived system survival and unaccountable loss rates. It is less obvious whether fallback data are necessary, or whether non-terminal tributary detections are necessary as well as terminal tributary detections. Model 6 is general enough that it can be reduced to a simpler model if it is decided that either or both of fallback effects and tributary effects are unnecessary. If there is little or no censoring of a particular release group, then it may be possible to use a relatively simple model such as Model 3a, which includes all tributary detections, or Model 4, which includes terminal tributary detections and adjusts for fallback effects.

The second objective of this chapter was to compare the use of PIT tags to the use of radio tags for estimating system survival and unaccountable loss. In general, the main benefit of radio tags over PIT tags in estimating these large-scale quantities appears to be the tributary data available from radio tags; the adult trap (i.e., censoring) data available from radio tags is a secondary benefit. Although all models developed here were fit to a subset of radiotelemetry data, Model 0 is also appropriate for PIT-tag data, with single detections at each dam. If PIT-tag data were available with two detections at each dam, then Model 1 could also be used with PIT-tag data. It is obvious from Table 3.53 that PIT-tag data and radio-tag data can produce comparable estimates of (perceived) system survival if censoring is not accounted for. Including information on censoring (due to known removals at adult traps) can increase the estimate of perceived survival, however; if trap information were available for PIT-tags, then PIT tags would yield the same information on perceived system survival as radio tags.

Table 3.53 shows a large decrease in estimates of unaccountable loss between Models 0 and 1 (PIT-tag models) and the remaining models (radio-tag models). The difference between these models is the use of tributary data, which are currently unavailable for PIT tags. Thus, radiotelemetry data currently offer considerably more information than PIT-tag data on unaccountable loss rates. Among the radio-tag models, the estimate of unaccountable loss is approximately $\hat{\mu}_R = 28\%$, except when censoring is accounted for, when $\hat{\mu}_R$ is approximately 25%. This implies that if both known removal and tributary

data were available from PIT-tags, then the cheaper PIT-tags would provide comparable information on both unaccountable loss and perceived system survival as the more expensive radio tags.

Table 3.53: Results from the radio-tag models for the 1996 Chinook salmon data set. The parameter \hat{S}_{sys} is the perceived system survival rate, i.e., the probability of remaining in the migrating population in the river to the top of dam K (i.e., LGR for the 7-dam analyses and MCN for the 4-dam analyses). The parameter μ_R is the unaccounted loss rate, i.e., the probability of *not* ending either at a tributary or at the top of LGR. Results are not available for Model 5c.

Model	No. Dams	Log-Likelihood	No. Parameters	\hat{S}_{sys}	\widehat{SE}	$\hat{\mu}_R$	\widehat{SE}
0	7	-1903.4948	11	0.1028	0.0104	0.8972	0.0104
1	7	-2457.4142	21	0.1028	0.0104	0.8972	0.0104
2	7	-2926.7083	29	0.0863	0.0097	0.2784	0.0154
3a	7	-3219.6910	34	0.1057	0.0106	0.2803	0.0156
3b ¹⁹	7	-3209.1992	43	0.1057	0.0106	0.2800	0.0156
4	7	-3452.7375	51	0.1075	0.0108	0.2743	0.0155
4	4	-3267.0957	31	0.3412	0.0170	0.2199	0.0151
5a	7	-3744.8799	61	0.1073	0.0108	0.2763	0.0156
5a	4	-3267.0957	37	0.3408	0.0169	0.2211	0.0151
5b	7	-3743.8691	61	0.1048	0.0106	0.2770	0.0155
5b	4	-3264.9726	44	0.3394	0.0169	0.2212	0.0150
6	7	-3838.7199	60	0.1349	0.0119	0.2468	0.0151

Below is a summary of the models developed in this chapter, followed by a discussion of the results of these models in relation to other analyses of these data. Model limitations and concerns about the data are discussed next, followed by a short conclusion to this chapter.

3.11.1 Summary of Models

In general, the models presented in this chapter are not nested because they each use different types of data. For example, Model 0 uses only top-of-dam detections, while Model 1 uses both top-of-dam and base-of-dam detections, and Model 2 uses both those and

¹⁹Models 3a and 3b are nested, and a likelihood ratio test comparing the two models for the 1996 data set fails to reject the null hypothesis that the two models are equivalent at the 95% level ($\chi^2 = 20.9836$, $df = 9$, $P = 0.0127$).

terminal tributary detections. As another example, consider Models 2, 3a, and 3b. The only tributary detections used by Model 2 are terminal detections, while Models 3a and 3b use both terminal and non-terminal tributary detections. Because the data for Model 2 were simplified by first removing all non-terminal tributary detections, Model 2 uses different data than do Models 3a and 3b. Thus, Model 2 is not nested in Models 3a and 3b. The only nested models are Models 3a and 3b, and Models 5a and 5c. Models 3a and 3b use the same data set, with the only difference the assumption in Model 3a that tributary visits have no effect on subsequent transition probabilities. The same is true for Models 5a and 5c. Models 5a and 5b use the same data, but are not nested because of Model 5a's use of permanent fallback effects, and Model 5b's use of short-term fallback effects and tributary effects. Model 6 includes censoring, unlike any of the previous models; the model structure but not the data used for Model 5b is nested in that for Model 6. Non-nested models may be compared via goodness-of-fit statistics, or via the values of the performance measures. It should be noted if different models use data that have been prepared in different ways, however. Comparing performance measures from both different models and different data sets is equivalent to comparing both the models and the data simplification processes, or the types of data available; such comparisons do not compare the models alone.

Model 0 is the simplest model presented here, and is the model most like existing PIT-tag models (e.g., the adult portion of the model presented in Chapter 2). It uses single detections at each dam, and no tributary detections. The difference between it and a PIT-tag model is that adult PIT-tag detections occur in the interior of adult fish ladders, while the detections used in Model 0 occurred at the top of the adult fish ladders. If it is assumed that fish that pass the PIT-tag detectors in the interior of the ladders continue to ascend the dam, then Model 0 is identical to the typical PIT-tag model used to estimate adult survival.

Model 1 adds detections at the base of dams to the detections used in Model 0; tributary detections are not used. Model 1 is equivalent to a PIT-tag model that uses two detections, one at or near the base of the adult ladder, and one at or near the top of the ladder. Currently, PIT-tag detections occur in the interior of the ladder. The added benefit of Model 1 relative to Model 0 is that dam ascension rates and the transition rate from the penultimate

dam (dam $K - 1$) to the base of the final dam (dam K) can both be estimated. Models 0 and 1 are not nested due to the additional types of data used in Model 1. Despite the additional data in Model 1, Models 0 and 1 produce identical values of the performance measures S_{sys} and μ_R (Table 3.53), indicating that the additional detection sites are unnecessary for estimating these large-scale quantities.

The remaining models all use both base-of-dam detections and top-of-dam detections, and vary only on how they use tributary detections, fallback information, and adult trap data (i.e., censoring). Model 2 uses only terminal tributary detections; tributary detections of fish that entered tributaries and then returned to the river are ignored. Model 2 and the remaining models all assume 100% detection in the tributaries, so all fish passing through a tributary mouth are detected there. Because Model 2 includes detections in the tributaries above the final dam (dam K), it allows for estimation of the ascension of the final dam, which is not possible in Model 1. Model 2 also estimates the rates at which fish permanently exit the river for the tributaries below the final dam (parameters $\phi_{D_k T, T_k}$). For the 1996 data set, estimated system survival is smaller for Model 2 than for Model 1 for the 1996 data set ($\hat{S}_{sys} = 0.0863$, $\widehat{SE} = 0.0097$ for Model 2, versus $\hat{S}_{sys} = 0.1028$, $\widehat{SE} = 0.0104$ for Model 1), due to the turn-offs into the tributaries. However, the estimate for unaccountable loss for Model 2 is considerably smaller than the unaccountable loss estimate for Model 1: $\hat{\mu}_R = 0.2784$ ($\widehat{SE} = 0.0154$) for Model 2 versus $\hat{\mu}_R = 0.8972$ ($\widehat{SE} = 0.0104$) for Model 1. This suggests that much of the unaccountable loss in Model 1 is due to fish turning off to tributaries. Because the 1996 release was composed of non-known-source fish, it is likely that most, if not all, of these turn-offs were fish heading toward their spawning grounds, rather than instances of straying.

Model 3a is similar to Model 2, but incorporates non-terminal as well as terminal tributary detections. Model 3a allows fish to temporarily visit tributaries, and then return to the river to continue migrating. Fish may visit tributaries downstream of their natal tributary either to rest during their migration, or to explore the tributary in an effort to locate their spawning grounds. For the 1996 data set, Model 3a estimates perceived system survival to be somewhat higher than that estimated by Model 2 ($\hat{S}_{sys} = 0.1057$, $\widehat{SE} = 0.0106$ for Model 3a versus $\hat{S}_{sys} = 0.0863$, $\widehat{SE} = 0.0154$ for Model 2), and very close to that estimated

for Models 0 and 1 ($\hat{S}_{sys} = 0.1028$, $\widehat{SE} = 0.0104$ for Models 0 and 1), because Model 3a allows fish to return from the tributaries. However, the estimate of unaccountable loss for Model 3a is similar to the estimate for Model 2: $\hat{\mu}_R = 0.2803$ ($\widehat{SE} = 0.0156$) for Model 3a versus $\hat{\mu}_R = 0.2784$ ($\widehat{SE} = 0.0154$) for Model 2.

Model 3b differs from Model 3a in that it allows tributary visits to affect transition rates through the next reach (i.e., up to two dams upstream of the tributary). A memory effect of tributary visits is reasonable if fish use tributaries as resting places or as temperature refugia during hot weather (Bjornn and Peery, 1992; Keefer et al., 2002). Such a memory effect may be more prominent in hotter years, if fish use tributaries primarily as temperature refugia. It is also possible that fish that enter a tributary in one reach to determine if it leads to their spawning grounds, and then return to the river, may be more likely to enter tributaries in the following reach. Model 3a is nested in Model 3b, and a likelihood ratio test comparing the two models for the 1996 data set fails to reject the null hypothesis that the two models are equivalent at the 95% level ($\chi^2 = 20.9836$, $df = 9$, $P = 0.0127$). Thus, the estimated tributary memory effects are insignificant for this data set. Also for the 1996 data set, there is no difference between estimates of system survival between the two models, and very little difference in estimates of unaccountable loss between the two models (Table 3.53).

Model 4 is similar to Model 2 in that it uses only terminal tributary detections (i.e., no tributary visits are allowed), but Model 4 incorporates a memory effect of a fish's first fallback on subsequent transitions. Model 4 is useful if fallback affects subsequent survival. Examination of the ϕ_{ij}^F and ϕ_{ij} parameter estimates in Table 3.34 shows that in some cases, there is considerable difference between these two types of parameters, but that the type of difference is inconsistent from site to site. In some cases, $\hat{\phi}_{ij}^F > \hat{\phi}_{ij}$, while in other cases $\hat{\phi}_{ij}^F < \hat{\phi}_{ij}$. It should be remembered that ϕ_{ij}^F represents both the memory effect of previous fallback and the actual transition during which the fallback occurs if i is a top-of-dam site. Comparing estimates of only the post-fallback parameters $\phi_{D_{kB}, D_{k+1}, T}^F$ and their non-fallback analogues $\phi_{D_{kB}, D_{k+1}, T}$, there appears to be little effect of fallback until the higher reaches, when the post-fallback transition parameter estimates tend to be lower than the analogous non-fallback estimates. Relative to Model 2, the estimate of system survival for the 1996 data set is higher for Model 4 ($\hat{S}_{sys} = 0.1075$, $\widehat{SE} = 0.0108$ for Model

4 versus $\hat{S}_{sys} = 0.0863$, $\widehat{SE} = 0.0154$ for Model 2), and the estimate of unaccountable loss is approximately the same for the two models ($\hat{\mu}_R = 0.2743$, $\widehat{SE} = 0.0155$ for Model 4 versus $\hat{\mu}_R = 0.2784$, $\widehat{SE} = 0.0154$ for Model 2).

Model 5a incorporates the fallback effect of Model 4 and the tributary visits of Model 3a, without allowing tributary visits to affect subsequent transition parameters. Comparing estimates of post-fallback transition parameters (i.e., $\hat{\phi}_{D_{kB}, D_{kT}}^F$ for $k = 1, \dots, 7$ and $\hat{\phi}_{T_k, D_{k+1}, B}^F$ for $k = 1, 2, 4$, and 5) to estimates of the analogous non-fallback transition parameters shows that in the lower reaches, the post-fallback parameter estimates tend to be greater than the non-fallback estimates, with the reverse true in the upper reaches. The fallback parameters f_i , representing the probability of becoming a post-fallback fish (for the first time) and then continuing to migrate upstream, have very low estimates in general (Table 3.41). The estimate of system survival for the 1996 data set is approximately the same for Model 5a as for Models 3a and 4 ($\hat{S}_{sys} = 0.1073$, $\widehat{SE} = 0.0108$ for Model 5a, versus $\hat{S}_{sys} = 0.1057$, $\widehat{SE} = 0.0106$ for Model 3a and $\hat{S}_{sys} = 0.1075$, $\widehat{SE} = 0.0108$ for Model 4). Estimates of unaccountable loss are approximately the same among the three models ($\hat{\mu}_R = 0.2763$, $\widehat{SE} = 0.0156$ for Model 5a, versus $\hat{\mu}_R = 0.2803$ ($\widehat{SE} = 0.0156$) for Model 3a and $\hat{\mu}_R = 0.2743$, $\widehat{SE} = 0.0155$ for Model 4).

Model 5b includes the tributary memory effects used in Model 3b, as well as fallback effects. Unlike Models 4 and 5a, however, Model 5b uses short-term fallback effects that extend only to the second dam after the transition during which the fallback occurred. Additionally, both types of memory effects are simplified in that only one applies at a time, with the effect of the most recent event dominating. The estimates of both perceived system survival and unaccountable loss are similar for Models 5b and 3b for the 1996 data set (7 dams): $\hat{S}_{sys} = 0.1048$ ($\widehat{SE} = 0.0106$) for Model 5b versus $\hat{S}_{sys} = 0.1057$ ($\widehat{SE} = 0.0106$) for Model 3b, and $\hat{\mu}_R = 0.2770$ ($\widehat{SE} = 0.0155$) for Model 5b versus $\hat{\mu}_R = 0.2800$ ($\widehat{SE} = 0.0156$) for Model 3b.

Because of the modification of the fallback effect used in Model 5b, Model 5a is not nested in Model 5b. However, the likelihood structures are similar, and so AIC (Burnham and Anderson, 2002) may be a reasonable tool with which to compare these models. For the full 1996 data set (7 dams), the AIC values for Models 5a and 5b are similar, with Model 5b

slightly favored (AIC = 7611.780 for Model 5a vs. AIC = 7609.738 for Model 5b). For the reduced data set with only the first 4 dams included, however, the AIC values favor Model 5a: AIC = 6612.191 for Model 5a vs. AIC = 6619.945 for Model 5b. The difference in model selection between the full data set and the reduced data set may be due to reduced importance of tributary effects in the lower reaches; however, most tributary effects are estimated in the lower reaches. Alternatively, it is possible that the actual duration of fallback effects is neither as short as that assumed in Model 5b nor as long as that assumed in Model 5a, but rather somewhere in between, so that Model 5a captures the fallback effects among the lower reaches when data from only 4 dams are used, but not as well as Model 5b when data from all 7 dams are used. Model 5b is considerably more complex than Model 5a, and in general, Model 5a requires fewer assumptions about particular parameters. The estimate of system survival is slightly smaller for Model 5b than for Model 5a for the full (i.e., 7-dam) 1996 data set ($\hat{S}_{sys} = 0.1048$, $\widehat{SE} = 0.0106$ for Model 5b versus $\hat{S}_{sys} = 0.1073$, $\widehat{SE} = 0.0108$ for Model 5a), while the estimate of unaccountable loss is very slightly larger for Model 5b ($\hat{\mu}_R = 0.2770$, $\widehat{SE} = 0.0155$ for Model 5b versus $\hat{\mu}_R = 0.2763$, $\widehat{SE} = 0.0156$ for Model 5a).

Model 5c includes the tributary memory effects of Model 3b and the long-term fallback effects of Model 4, and allows both effects to occur at the same time. However, Model 5c is unstable, and cannot be fit to the 1996 data set. It may be possible to fit Model 5c to a larger data set, but the number of parameters and degree of complexity in Model 5c suggest that it is not a practical model to use in general.

Model 6 has the same structure as Model 5b, but allows for censoring after base-of-dam detections to accommodate adult trap data. Only fish with questionable trap detections and those not returned to the river after trap detection with intact radio tags were censored for analysis of the 1996 data set. The estimate of perceived system survival rate ($\hat{S}_{sys} = 0.1349$, $\widehat{SE} = 0.0119$) is larger than the estimates from the previous models (7 dams), while the estimate of the unaccountable loss rate ($\hat{\mu}_R = 0.2468$, $\widehat{SE} = 0.0151$) is smaller than those from Models 2-5b (7 dams). Because Model 6 accounts for the known removal of tagged fish from the migrating population, it is reasonable that unaccountable loss should decrease and perceived survival increase. Depending on the number of known removals, accounting

for removals via censoring may be an important part of a suitable model.

3.11.2 Model Results

Some estimates of transition parameters involving fallback from Model 5b are considerably different from those in Model 5a. For example, for Model 5a, $\hat{\phi}_{T_3, D_{4B}}^F = 0.3354$ ($\widehat{SE} = 0.1225$), while for Model 5b, $\hat{\phi}_{T_3, D_{4B}}^F = 0.0774$ ($\widehat{SE} = 0.0561$). A similar pattern is seen with estimates of $\phi_{T_5, D_{6B}}^T$: the MLE from Model 5a is $\hat{\phi}_{T_5, D_{6B}}^T = 0.9895$ ($\widehat{SE} = 0.0559$), while the MLE from Model 5b is $\hat{\phi}_{T_5, D_{6B}}^T = 0.5091$ ($\widehat{SE} = 0.3604$). The different estimates arise from the different groups of fish (equivalently, detection histories) parameterized with the fallback transition in the two models. Model 5a parameterizes all fish who have fallen back before reaching site T_3 with $\phi_{T_3, D_{4B}}^F$, as well as fish that fall back during the transition from T_3 to D_{4B} . Model 5b, on the other hand, parameterizes only those that fall back during the T_3 - D_{4B} transition and those that have recently fallen back before reaching T_3 with $\phi_{T_3, D_{4B}}^F$. If the effect of fallback on subsequent transitions is both short-term rather than long-term and detrimental rather than beneficial, then it makes sense that the estimate from the long-term fallback-effect model (Model 5a) is larger than the estimate from the short-term fallback-effect model (Model 5b).

Several parameters were fixed to either 0 or 1 in fitting some of the models. For example, $\phi_{T_4, D_{5B}}$ was fixed to 0 in Models 3a, 3b, 5a, 5b, and 6 because no fish detected at site T_4 was detected upstream of T_4 . Site T_4 included the Mid-Columbia River, upstream of McNary Reservoir, with its tributaries and Priest Rapids Dam. It is reasonable that most fish detected in these locations are directed to spawning areas, rather than exploring or using them as resting areas. Thus, it makes biological sense that $\phi_{T_4, D_{5B}}$ is either zero or very small. Another example is $\phi_{T_5, D_{6B}}$, which was fixed to 1 in Models 4, 5a, and 5b. Site T_5 is actually Charbonneau Park, upstream of Ice Harbor Dam on the Snake River. Charbonneau Park is a river-side park, not a tributary, and it makes sense that all fish detected at T_5 continued upriver.

Other work done on these data (e.g., Bjornn et al., 2000; Reischel and Bjornn, 2003; Boggs et al., 2004) have focused on migration rates, fallback rates at individual dams, and

the final distribution of tagged individuals. Bjornn et al. (2000) found that approximately 14% of the tagged Chinook salmon (that retained their transmitters) passed Lower Granite Dam; this number is similar to the estimated perceived system survival rate of approximately $\hat{S}_{sys} = 10\%$ ($\widehat{SE} = 0.01$) estimated from the models in this chapter. Bjornn et al. (2000) also found that approximately 76% of the release group survived to enter tributaries or pass either LGR or Priest Rapids (PR). Survival either to tributaries or LGR is the complement of the unaccountable loss performance measure, μ_R . Estimates of μ_R from Models 2 through 5b are approximately $\hat{\mu}_R = 0.28$ ($\widehat{SE} = 0.02$), with survival to tributaries or LGR estimated at approximately 0.72 ($\widehat{SE} = 0.02$). The radiotelemetry data used in Bjornn et al. (2000) was augmented with tag recoveries from fisheries, hatcheries, weirs, traps, and spawning grounds, so it is reasonable that their estimate of survival is somewhat higher than that found from release-recapture data alone. For the same reason, the unaccountable loss measure defined in this chapter is not directly comparable to the unaccountable loss rate reported in Bjornn et al. (2000), which uses the extra tag-recovery data. It is worth noting, however, that the estimated unaccountable loss rate from Model 6 ($\hat{\mu}_R = 0.25$, $\widehat{SE} = 0.02$) and the resulting estimate of survival to tributaries or the top of LGR (0.75, $\widehat{SE} = 0.02$) are comparable to that reported in Bjornn et al. (2000). This is expected because Model 6 accounts for fish removed from the adult trap at LGR, who do not then reach the top of that dam.

The fallback rates reported in Bjornn et al. (2000) and in Boggs et al. (2004) are not comparable to the fallback parameters estimated by the models in this chapter. The fallback parameters f_i represent the probability of becoming a post-fallback fish between site i and the next detection site; such a fish does not fall back at site i , but rather upstream of site i . The fallback rates reported in Bjornn et al. (2000) and in Boggs et al. (2004) represent the proportion of tagged fish that fell back at a particular dam. The models in this chapter were not designed to estimate dam-specific fallback rates. On the other hand, the models presented here are able to estimate an effect of fallback on subsequent survival and movement (i.e., transition) probabilities via the ϕ_{ij}^F parameters. The ratio ϕ_{ij}^F/ϕ_{ij} measures the effect of previous fallback on the transition rate between sites i and j . For example, for $i = T_1$ and $j = D_{2T}$, Model 5a estimates a fallback effect of $\hat{\phi}_{ij}^F/\hat{\phi}_{ij} = 1.6749$ ($\widehat{SE} = 0.5369$), indicating that fish entering tributaries between BON and TDA that had previously fallen

back were approximately 67% more likely to continue migrating upstream to TDA than fish that had not previously fallen back. Models 5b and 6 give similar estimates.

3.11.3 *Model Limitations*

There are several limitations to the models presented in this chapter. First, only upstream travel is modeled. Travel and survival during fallback and other retracing of previously traveled paths is not explicitly modeled here, although the fallback transitions incorporated in Models 4, 5a, 5b, and 6 implicitly include such travel. If the goal is to estimate survival to an upstream site, however, it is not necessary to explicitly model travel directed away from that site, as long as any subsequent effects of such travel are included. Modeling downriver travel may be useful for pinpointing the locations in the river where unaccountable loss is significant. However, it should not improve estimates of overall unaccountable loss (μ_R).

A related limitation of these models is that the probability of fallback is not estimated, but rather the probability (f_i) of swimming upriver from site i , falling back, and then continuing to migrate upriver. The f_i parameters should not be construed as fallback rates or fallback percentages. First, fish parameterized with f_i did not turn around to swim downriver at site i , but rather at a point upriver from site i yet in the same reach as site i . Second, any fish that fall back from site i may or may not turn around again to swim on upriver; those that do not swim back upriver after falling back are not detectable as fallback fish from these data and would not be parameterized as such in any model, including those presented here. This second point is a problem more with the data than with the modeling approach; the model is only as good as the data, and without detection of fallback fish during fallback or during downstream travel, the model cannot easily represent downstream travel. However, it should be possible to estimate both fallback rates and survival during fallback (conditional on subsequent detections during upriver travel) with a smaller-scale model that focuses on only a single dam. That problem was not addressed by these models.

A third limitation is the assumption of 100% detection rates in the tributaries. This assumption was necessary to distinguish transitions from dam k to dam $k+1$ from transitions from dam k to tributary k and then on to dam $k+1$, and subsequently, to estimate tributary

memory effects. It is unlikely that such an extreme assumption is true for all tributaries, all of the time. However, it is likely to be true or approximately true for some tributaries at least most of the time. The effect of $< 100\%$ tributary detection rates on parameter estimates would be negatively biased dam-tributary transition probabilities, and possibly positively biased dam-dam transition probabilities. Perceived system survival (to the final dam, typically LGR) may be negatively biased if more fish are entering tributaries than are detected. If these fish do not then return to the river, unaccountable loss would be positively biased, because it would appear that these fish are "disappearing" (i.e., dying) in the river rather than permanently remaining in the tributaries. Had multiple antenna arrays been used in the tributaries, it would be possible to estimate detection rates there, and this assumption could be dropped.

Another limiting assumption of these models is that fish fall back at most once during their upstream migration. This is certainly a faulty assumption; the 1996 data set considered here contained several fish that fell back more than once. This assumption was necessary to keep the models relatively simple. It could be relaxed and subsequent fallbacks could be modeled; however, with the existing level of complexity in the single-fallback models, multiple-fallback models may be prohibitively complex. Additionally, it may be that the first fallback has a larger effect on subsequent survival than later fallbacks, in which case the assumption of at most one fallback per fish is reasonable.

Finally, the multinomial models considered here each assume that all tagged individuals have common transition, fallback, and detection probabilities, with a possible differential effect of previous tributary detections or fallback. The primary result of violations of this assumption is variance estimates that are too small. Ideally, this problem would be avoided by applying these models only to release groups of known-source fish. In the absence of this option, it may be possible to correct for this assumption by modeling the variance structure and using estimating equations, or by adjusting standard errors by an overdispersion coefficient.

3.11.4 Data Issues

One benefit of radiotelemetry is the many types of data available: fixed-site receiver detections from dams and tributaries, mobile tracking detections, and tag-recoveries from hatcheries, fisheries, traps, and spawning grounds. Although these data are all useful in determining the fate of individual fish, only some are suitable for release-recapture models. The mobile tracking data and tag-recovery data are not useful for modeling without independent estimates of overall mobile tracking detection efficiencies and tag-recovery and reporting rates, respectively. With additional assumptions about tag-detection rates, the detections from the adult trap at LGR were used in Model 6. The other tag-recovery or recapture detections could be used together with estimates of recovery rates from the various recovery sites. Without these estimates, using these data in a model would require the assumption of 100% recovery and reporting rates, which is certainly incorrect. Unlike any missed detections at the tributary mouths, where the detection rates are also assumed to be 100%, the missed tags at the hatcheries and traps are unlikely to occur at random. Also, there is likely to be a higher percentage of tags missed at these sites than at the tributary mouths because of sampling methods. Typically, hatcheries keep and examine for tags only the early-arriving fish, so all late-arriving fish are undetected at the hatcheries. Because of these issues, only the data from the fixed-site receivers are used in the models here, with additional data from the adult trap at LGR used in Model 6.

Of the fixed-site dam detections, only those at the base ("A1") and top ("LT") of the ladders are used, to limit the modeling of small-scale movements. A drawback of this policy is that some fallback events may be missed by the data simplification protocol described in Section 3.2. Using only the "A1" and "LT" codes, the only fallback events detectable are those followed by reascension or tributary entry, whereas the other tailrace receivers may provide evidence of fallback as the fish swim downriver past the dams. The database containing these data (<http://rtagweb.nwfsc.noaa.gov/home/index.cfm>) includes fallback codes ("FB") based on all dam detections, not limited to the "A1" and "LT" codes used here. The "FB" codes in the database imply fallback over a particular dam. They do not have the same meaning as the "FB" codes used in these models, which imply fallback

and reascension between detection at the previous site and detection at the following site. The reason for not using the fallback codes from the database is that their use would require modeling downstream travel during fallback, which was found to be mathematically intractable in a large-scale survival model with imperfect dam detection rates. However, it should be possible to develop a single-dam model using the tailrace detection sites and the *FB* codes from the database to estimate fallback rates at a particular dam.

3.11.5 Conclusion

The large-scale collection of radiotelemetry data is costly and labor intensive. Both the radio tags and the radio receivers are expensive, while the receiver data must be downloaded on-site on a regular basis. Extensive pre-processing of the data is necessary before analysis can begin. In addition, radio-tagging adults requires considerable handling and resultant stress to the fish, and typically produces mixed-stock, unknown-source release groups. PIT tags are considerably cheaper than radio tags, the data may be downloaded automatically to the PTAGIS database, and there is less pre-processing of the data necessary. Additionally, fish may be tagged as juveniles, producing release groups with known sources and, presumably, no residual tagging stress by the time of the adult migration. Using PIT-tagged juveniles requires considerably larger sample sizes (e.g., 51,318 for the PIT-tag data in Chapter 2 versus 846 for the radio-tag data in Chapter 3), but provides comparable precision on estimates of adult system (or “inriver”) survival: the CV (coefficient of variation) of \hat{S}_A was 0.269 in Chapter 2, while the CV of \hat{S}_{sys} was 0.148 from Model 6 in this chapter. Additionally, data from fish PIT-tagged as smolts provide information about the juvenile migration, ocean survival, and transportation as well as the adult migration.

Both radio tags and PIT tags are detected at dams, although radio tags typically have higher detection rates (i.e., 80%-100%) and provide more complete information about fallback and known removals (i.e., adult trap detections). More importantly, radio tags provide detections in tributaries, while PIT tags currently do not. Adjusting for loss to tributaries is important in reducing estimates of unaccountable loss. New PIT-tag technology is being developed that will allow for tributary detection of PIT-tagged fish, and ideally, estimates

of tributary detection rates. With this new technology, the tributary (radio-tag) models presented in this chapter could be used with PIT-tag data, with the following modifications: (1) the double detections at the dams must be reduced to a single detection, and (2) the assumption of 100% detection in the tributaries can be relaxed. If adult PIT-tag dam detection rates were improved to mimic radio-tag detection rates, and if the tributary PIT-tag detector technology were successfully installed, then PIT tags may provide comparable information to radio tags about large-scale upstream survival and unaccountable loss, but at a lower cost and in a more systematic, less labor intensive manner.

Chapter 4

CONCLUSION

4.1 Summary of Work and Ramifications

A considerable amount of money is spent on tagging studies of Columbia and Snake river salmonids; in 2002, 100 million fish were tagged with coded wire tags, 10 million were tagged with PIT tags, and 10,000 were tagged with radio tags. There are a variety of methods available to analyze tagging and release-recapture data, including the relative recovery methods of Ricker (1975), the treatment-effect models of Burnham et al. (1987), and the juvenile survival models of Skalski et al. (1998). The models presented in this dissertation contribute to the analysis tools available to researchers on the Columbia and Snake rivers, providing new tools for use with new types of data.

4.1.1 Juvenile-Adult PIT-tag model

Until recently, PIT-tag detections were available only for juvenile salmonids. Inriver survival of juveniles (smolts) could be estimated, but only to John Day or The Dalles dams. The records of transported smolts were censored at transportation, and neither ocean survival, nor adult inriver survival, nor transportation effects could be estimated from PIT-tag data alone. Measuring transportation effects required paired releases, and estimating adult inriver survival required capturing and tagging adults as they migrated upriver. The PIT-tag model developed in Chapter 2 takes advantage of the newly available adult PIT-tag detections, and jointly analyzes the juvenile, adult, and transportation data from any juvenile release group. This joint analysis provides model-based estimates of juvenile survival to Bonneville Dam, ocean survival, and adult inriver survival. Each of these quantities is important in measuring the recovery of endangered populations, and in determining the life stages at which future recovery operations should be directed. With this new PIT-tag model, these survival rates can be estimated from any PIT-tagged juvenile release group

using currently available detection sites. It is no longer necessary to capture and tag migrating adults in order to estimate adult inriver survival, and ocean survival can now be easily separated from upstream adult survival.

Smolt transportation is a major mitigation strategy used on the Snake and Columbia rivers. Precise, well-understood measures of the effects of transportation are an important part of evaluating the success of management and recovery efforts on the river. In the past, measuring the effects of smolt transportation on adult return rates has required paired juvenile releases, with one release group transported and the other left to migrate inriver. The "inriver" fish may have been transported from a downriver site, so the transportation effect historically measured by the relative recovery rates of the two groups was confounded by the effect of transportation at downriver sites. Additionally, adjusting the relative recovery rates to apply to untagged fish is difficult. These difficulties, among others, have resulted in miscommunication and disagreement among various river and fisheries management groups on the effect of smolt transportation on adult return rates, and on whether smolt transportation is a reasonable dam mitigation option.

The PIT-tag model developed here uses the combined adult data of transported and non-transported fish and thus directly provides a measure of transportation effects. The estimated model parameters are then used to define other measures of transportation effects, each appropriate for management from a different perspective. The contextual site-specific measure assesses the effect of transportation at a particular dam but in the context of the rest of the transportation system; this is analogous to the traditional relative recovery ratio used historically, and is useful for dam or transportation managers interested in whether or not fish should be transported from their dam. The isolated site-specific measure assesses the effect of transportation at a particular dam as if it were the only transportation site in the river. Thus, this measure evaluates transportation at a site unconfounded by the rest of the transportation system. The isolated measure is useful for managers of transportation operations at a particular site. The system-wide transportation effect measure compares the return rate of the entire release group under the existing transportation system to the hypothetical return rate if there had been no transportation. Thus, the system-wide measure evaluates the effect of the entire transportation system, including the proportion of fish

transported, but without requiring smolts to migrate in a river in which no transportation is available. All of these measures are available for either the tagged fish in the release group, or for untagged fish of the same species and stock that migrate at the same time as the tagged fish. Thus, results may be extrapolated to the untagged migrating population. Each of these different transportation effect measures may be estimated for any single PIT-tagged juvenile release group for which both transportation and inriver migration strategies are available; it is no longer necessary to use paired releases to evaluate the transportation system for spring and summer Chinook salmon, Sockeye salmon, and Steelhead trout.

The transportation effect measures developed here are useful in their own right as quantifications of transportation effects from a variety of management perspectives. Managers may use the appropriate measure based on their needs. Both the various measures themselves and the fact that there are several different yet valid perspectives from which to measure transportation effects helps to resolve some of the conflict in resource management surrounding transportation.

In addition to the transportation effect measures, several other performance measures from the PIT-tag model were presented, including the smolt-to-adult return rate (SAR), adult age composition, inriver adult survival, and differential mortality (D), together with their estimated precision. Each is available for either tagged or untagged fish. The smolt-to-adult return rate and D are important for assessing recovery efforts, while SAR , adult age composition, and inriver adult survival are useful for monitoring salmonid migrations. Because these measures are defined using the model parameters, they are each estimable for any PIT-tagged release group.

4.1.2 Adult Radio-tag model

The adult radio-tag models developed in Chapter 3 break new ground in the analysis of radiotelemetry data from adult migrating salmon to estimate large-scale performance measures such as unaccountable loss and system survival. No formal, modeling approach had previously been used to analyze these data. Just as juvenile inriver survival, ocean survival, and transportation effects can be estimated for any PIT-tagged juvenile release group with

the PIT-tag model developed here, so can system survival and unaccountable loss be estimated for any radio-tagged adult release group included in the Adult Anadromous Fish Radiotelemetry Project at NOAA Fisheries and the University of Idaho.

System survival, or the probability of surviving and remaining in the migrating population, is a useful performance measure if the release group is composed of a single stock, or of fish that are all directed to the same region of the river basin. Unaccountable loss is an important performance measure named by the 2000 and 2004 biological opinions on the Columbia River Power System (NOAA Fisheries, 2000a, 2004). Unaccountable loss is a useful evaluation tool even for mixed-stock release groups, and can help identify regions of high loss. The models developed here estimate both system survival and unaccountable loss together with measures of uncertainty. Estimates of uncertainty can help river and fishery managers interpret the reported values of system survival and unaccountable loss, yet are unavailable from previous analysis methods for these data.

The radio-tag models developed here also provide a method of analyzing the effects of fallback on subsequent survival rates. This can help managers focus attention and funds appropriately, by identifying dams where fallback rates should be reduced.

The comparison of PIT tags and radio tags in Chapter 3 demonstrates that PIT tags and radio tags provide nearly comparable estimates of system survival, with the main difference due to the additional adult trap data at Lower Granite Dam available from the radio tags. Additionally, because radio tags are detected at more sites and at higher rates than PIT tags, the estimates from radio-tag data may be more precise than estimates from PIT-tag data. Thus, if the treatment of PIT-tagged fish at the adult traps at Bonneville and Lower Granite were apparent from the PTAGIS database, and if detection rates of PIT tags in the adult fish ladders at dams were improved, then it would be unnecessary to spend additional funds on collecting and processing the more expensive radiotelemetry data if the goal is to estimate system survival.

The main disadvantage to using fish that were PIT-tagged as smolts to estimate adult system survival is the large sample sizes necessary with PIT tags. For example, the PIT-tag data used in Chapter 2 came from 51,318 fish tagged as smolts, while the radio-tag data used in Chapter 3 came from only 846 fish tagged as adults. The larger sample size for the

PIT-tag data was needed to offset low ocean survival rates. Despite adult returns spread over multiple years and low ocean return rates, the coefficient of variation (CV) of adult system (i.e., inriver) survival from the juvenile-adult PIT-tag data was comparable to that from the adult radio-tag data: $CV=0.269$ from the PIT-tag data, versus $CV=0.148$ from the radio-tag data. Also, the PIT-tag data provided estimates of juvenile inriver survival, ocean survival, SAR, and transportation effects in addition to adult inriver survival. Thus, depending on the research goals, PIT-tag detections from fish tagged as juveniles may reasonably replace adult radio-tag studies to estimate adult system survival.

Although comparable information is provided by PIT tags and radio tags about adult system survival, radiotelemetry data currently provide considerably more information than PIT-tag data about unaccountable loss. This is primarily due to the detection of radio tags in tributary mouths, which allows for identification of loss due to tributary exit. If proposed PIT-tag tributary detectors are successfully developed and installed in tributary mouths, then PIT tags and radio tags should provide comparable estimates of unaccountable loss. Thus, it will be possible to reduce the costs of monitoring the adult migration by switching from large-scale radiotelemetry studies to large-scale PIT-tag studies. Radiotelemetry may remain the preferred tool for studying small-scale salmon movements and passage patterns at individual dams, but it will be unnecessary for studying large-scale issues such as unaccountable loss and system survival.

4.2 *Benefits of Modeling Approach*

It is possible to analyze the data used here without statistical models, and non-model-based analyses of both the PIT-tag data (e.g., Sandford and Smith, 2002) and the radio-tag data (e.g., Bjornn et al., 2000) have been performed, necessitated by the types of data and analysis tools available, respectively. The model-based approach presented in this dissertation offers several advantages to these alternative approaches. First, parameter estimation is performed via a statistically rigorous method (i.e., maximum likelihood) with well-understood properties of the resulting estimators. Expected values of the estimators may be easily computed, thus reducing the amount of uncertainty involved in management. Also, the modeling approach provides researchers and decision-makers with easily computed

measures of uncertainty on their analysis results (e.g., parameter estimates), which are necessary for informed decisions with respect to both policy and future research.

A second benefit of the model-based approach is that hypotheses may be tested via well-understood likelihood ratio tests. For example, the PIT-tag model may be used to test for the effect of juvenile transportation or the age or year of adult return on adult upriver survival rates. The radio-tag model may be used to test for the effect of fallback or temporary tributary visits on adult upriver survival.

An important benefit of the modeling approach is that it offers a framework from which to address research questions. In particular, it directs attention to the definitions of the quantities to be estimated. In this way, it also helps identify what quantities are estimable. Model parameters estimated directly from the data must be clearly defined in development of the model, while derived parameters must be expressible in terms of the model parameters. Focusing on these parameter definitions can reveal ambiguities within the research community, and in turn lead to useful discussions and result in more transparent definitions. For example, the concept of an effect of juvenile transportation on adult returns appears straightforward until an attempt is made to quantify such an effect. There have been several different approaches taken within the research community (e.g., Ricker, 1975; Sanford and Smith, 2002; differential mortality [D]), resulting in considerable disagreement over what a true transportation effect is. The PIT-tag model developed here includes transportation effect parameters which allow for at least 6 different measures of transportation effect to be defined, varying in domain and applicability. Whether or not these measures are adopted by the research community, the fact that so many different definitions are viable sheds light on the various approaches within the community to defining transportation effect, and helps identify what the real differences among the various measures are. Any measure of transportation effect that is used should be expressible in terms of the basic model parameters. In effect, the modeling approach provides the building blocks with which to construct clearly defined quantities to be used in decision-making.

A related benefit of the model-based approach to scientific inquiry and management decisions is that it helps identify the types and quality of information that can be learned from different types of data. As an example, the modeling exercise in Chapter 3 allows for

comparison of PIT-tag and radio-tag data and the information each yields about the upriver adult migration. For such a modeling exercise to be useful, the assumptions underlying the various models involved and the types of data they use must be clearly specified. This offers an opportunity to identify what more is needed to answer certain questions either more fully or at all. For example, in order to use the tag-recovery information from the radio-tag database, tag-reporting and tag-return rates must be known. Additionally, 100% detection rates at the dams would allow for a system-wide fallback or movement model based on the radiotelemetry data, which would in turn facilitate exploration of fallback rates at the different dams.

Because of the advantages of model-based analyses described above, the models presented in this work provide valuable tools to the research community in both a practical sense (e.g., parameter estimation) and an abstract sense (e.g., a definition-based orientation).

4.3 Contribution to the Release-Recapture Field

Generally, the models developed in this work may be considered primarily as migration models. Unlike some other migration models that model overall migration rates to particular sites over a number of generations (e.g., Schwarz et al., 1993), the models developed here model animal movement and survival during migration, and bear a resemblance to the multi-strata model of Brownie et al. (1993). The type of model developed here could be used for any species that migrates along a corridor and whose survival during migration is of interest; the general applicability of these models is not restricted to salmonids.

More specifically, the models in this work are single-release branching models, where the branches may represent either temporary or permanent memory or treatment effects. The PIT-tag model models migration paths that branch in space (e.g., transportation) and in time (e.g., adults may return in any of several years after reaching the ocean). The radio-tag models include migration paths that branch in space: adults headed upriver may enter certain tributaries or avoid them, and they may fall back over dams or not.

Another way of viewing the models developed here are as movement-*cum*-survival models. They use the basic framework of release-recapture models whose focus is survival

through time (e.g., Cormack, 1964; Jolly, 1965; Seber, 1965) and redirect the focus to survival through space. Thus, the usual time-based survival is now space-based. This is a relatively simple exercise for migration paths that are effectively linear, such as that of juvenile salmonids, and models of migrating juveniles already exist (e.g., Burnham et al., 1987; Skalski et al., 1998). However, although time is linear, space is generally not linear, and modeling the migration of animals with non-linear migration paths, such as adult salmonids, is not as straightforward as modeling the juvenile migration. Adult salmonids fall back or otherwise swim downriver, either intentionally or by accident; they may or may not visit certain optional detection sites (e.g., tributaries). These issues require decisions made about the level of data to be used, and about the assumptions made about the optional detection sites (e.g., detection rates in the tributaries are 100%), which may or may not be appropriate. Thus, refocusing a linear, time-based survival model to a bi- or multi-directional, space-based process raises certain issues that must be addressed.

As conservation efforts focus more on migration corridors, and as researchers explore more questions about animal movement, the questions addressed by models such as those developed here will become more important, e.g., where is survival the lowest along a migration route, or what is the effect on survival of certain actions or treatments. As more detailed data on animal movement become available from telemetry and remote sensing techniques, the types of migration models developed in this work will become more prevalent, and the issues encountered here (e.g., non-linearity of space, imperfect detection rates) will need to be addressed further.

REFERENCES

- Anganuzzi, A., Hilborn, H. and Skalski, J. R. (1994). Estimation of size selectivity and movement rates from mark-recovery data. *Canadian Journal of Fisheries and Aquatic Sciences* **51**, 734-42.
- Arnason, A. N. (1972). Parameter estimates from mark-recapture experiments on two populations subject to migration and death. *Researches on Population Ecology* **13**, 97-113.
- Arnason, A. N. (1973). The estimation of population size, migration rates and survival in a stratified population. *Researches on Population Ecology* **15**, 1-8.
- Barrat, R., Barré, H. and Mougin, J. L. (1976). Données écologiques sur les grands albatrox *Diomedea exultans* de L'Ile de la Possession (Archipel Crozet). *L'Oiseau et la Revue Française D'Ornithologie* **46**, 143-155.
- Bjornn, T. C., Keefer, M. L., Peery, C. A., Tolotti, K. R., Ringe, R. R., Keniry, P. J. and Stuehrenberg, L. C. (2000). Migration of adult spring and summer chinook salmon past Columbia and Snake river dams, through reservoirs and distribution into tributaries, 1996. Technical Report 2000-5, Bonneville Power Administration.
- Bjornn, T. C., Keefer, M. L. and Stuehrenburg, L. C. (1999). Behavior and survival of adult chinook salmon that migrate past dams and into tributaries in the Columbia River drainage as assessed with radio telemetry. In Eiler, J. H., Alcorn, D. J. and Neuman, M. R., editors, *Proceedings of the Fifteenth International Symposium on Biotelemetry*, pages 305-312, Juneau, AK.
- Bjornn, T. C. and Peery, C. A. (1992). A review of literature related to movements of adult salmon and Steelhead past dams and through reservoirs in the lower Snake River. Technical Report 92-1, U. S. Army Corps of Engineers, Walla Walla District.
- Boggs, C. T., Keefer, M. L., Peery, C. A. and Bjornn, T. C. (2004). Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook salmon and Steelhead at Columbia and Snake river dams. *Transactions of the American Fisheries Society* **133**, 932-949.
- Boulanger, J., McLellan, B. N., Woods, J. G., Proctor, M. F. and Strobeck, C. (2004). Sampling design and bias in DNA-based capture-mark-recapture population and density estimates of grizzly bears. *Journal of Wildlife Management* **68**, 457-469.
- Bouwes, N., Schaller, H., Budy, P., Petrosky, C., Kiefer, R., Wilson, P., Langness, O., Weber, E. and Tinus, E. (1999). An analysis of differential delayed mortality experienced by stream-type chinook salmon of the Snake River: A response by state, tribal, and USFWS technical staff to the 'D' analysis and discussion in the draft anadromous fish appendix

- to the U.S. Army Corps of Engineers' lower Snake River juvenile salmonid migration feasibility study/environmental impact statement.
- Bradford, M. J. (1995). Comparative review of Pacific salmon survival rates. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1327–1338.
- Brownie, C., Anderson, D. R., Burnham, K. P. and Robson, D. S. (1985). Statistical inference from band recovery data: A handbook. US Fish and Wildlife Resource Publication (156), Washington, DC.
- Brownie, C., Hines, J. E., Nichols, J. D., Pollock, K. H. and Hestbeck, J. B. (1993). Capture-recapture studies for multiple strata including non-Markovian transitions. *Biometrics* **49**, 1173–1187.
- Brownie, C. and Pollock, K. H. (1985). Analysis of multiple capture-recapture data using band-recovery methods. *Biometrics* **41**, 411–420.
- Brownie, C. and Robson, D. S. (1983). Estimation of time-specific survival rates from tag-resighting samples: a Generalization of the Jolly-Seber model. *Biometrics* **39**, 437–453.
- Bunck, C. M. and Pollock, K. H. (1993). Estimating survival of radio-tagged birds. In Lebreton, J.-D. and North, P. M., editors, *Marked Individuals in the Study of Bird Populations*, pages 5–63. Boston: Birhauser Verlag.
- Burnham, K. P. (1993). A theory for combined analysis of ring recovery and recapture data. In Lebreton, J.-D. and North, P. M., editors, *Marked Individuals in the Study of Bird Populations*, pages 199–213. Boston: Birhauser Verlag.
- Burnham, K. P. and Anderson, D. R. (2002). *Model Selection and Multimodel Inference: a practical information-theoretic approach*, 2nd edition. New York: Springer-Verlag.
- Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. and Pollock, K. (1987). Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.
- Cameron, R. A. D. and Williamson, P. (1977). Estimating migration and the effects of disturbance in mark-recapture studies on the snail *Cepaea nemoralis* L. *Journal of Animal Ecology* **46**, 173–179.
- Carothers, A. D. (1973). The effects of unequal catchability on Jolly-Seber estimates. *Biometrics* **29**, 79–100.
- Chapman, D. G. and Junge, C. O. (1956). The estimation of the size of a stratified animal population. *Annals of Mathematical Statistics* **27**, 375–389.
- Cleaver, F. C. (1969). Effects of ocean fishing on the 1961-brood fall chinook salmon from Columbia River hatcheries. *Research Report Fish Commission of Oregon* **1**, 76 p.
- Clobert, J., Lebreton, J. D., Allaine, D. and Gaillard, J. M. (1994). The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. *Biometrics* **50**, 375–387.

- Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* **51**, 429–438.
- Cormack, R. M. (1989). Log-linear models for capture-recapture. *Biometrics* **45**, 395–413.
- Cowen, L. and Schwarz, C. J. (2005). Capture-recapture studies using radio telemetry with premature radio-tag failure. *Biometrics* **61**, 657–664.
- Darroch, J. N. (1958). The multiple-recapture census. I. Estimation of a closed population. *Biometrika* **45**, 343–359.
- Darroch, J. N. (1959). The multiple-recapture census. I. Estimation when there is immigration or death. *Biometrika* **46**, 336–351.
- Darroch, J. N. (1961). The two-sample capture-recapture census when tagging and sampling are stratified. *Biometrika* **48**, 241–260.
- Ebel, W. J. (1980). Transportation of Chinook salmon, *Oncorhynchus tshawytscha*, and Steelhead, *Salmo gairdneri*, smolts in the Columbia River and effects on adult returns. *Fishery Bulletin* **78**, 491–505.
- Flamm, R. O., Weigle, B. L., Wright, E., Ross, M. and Aglietti, S. (2005). Estimation of manatee *trichechus manatus latirostris* places and movement corridors using telemetry data. *Ecological Applications* **15**, 1415–1426.
- Hartt, A. C. and Dell, M. B. (1986). Early oceanic migrations and growth of juvenile Pacific salmon and steelhead trout. *International North Pacific Fisheries Commission Bulletin* **46**, 105 p.
- Hestbeck, J. B., Nichols, J. D. and Malecki, R. A. (1991). Estimates of movement and site fidelity using mark-resight data of winter Canada geese. *Ecology* **72**, 523–533.
- Hilborn, R. (1990). Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 635–643.
- Iwamoto, R. N., Muir, W. D., Sandford, B. P., McIntyre, K. W., Frost, D. A., Williams, J. G., Smith, S. G. and Skalski, J. R. (1994). Survival estimates for the passage of juvenile Chinook salmon through Snake River dams and reservoirs, 1993. Technical report, Bonneville Power Administration, Portland, OR.
- Jackson, C. H. N. (1939). The analysis of an animal population. *Journal of Animal Ecology* **8**, 236–46.
- Joe, M. and Pollock, K. H. (2002). Separation of survival and movement rates in multi-stage tag-return and capture-recapture models. *Journal of Applied Statistics* **29**, 373–384.
- Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration - stochastic model. *Biometrika* **52**, 225–247.
- Kaplan, E. L. and Meier, P. (1958). Nonparametric estimation from incomplete observations. *Journal of the American Statistical Association* **53**, 457–481.

- Keefer, M. L., Bjornn, T. C., Peery, C. A., Tolotti, K. R., Ringe, R. R., Keniry, P. J. and Stuehrenberg, L. C. (2002). Migration of adult steelhead past Columbia and Snake River dams, through reservoirs, and distribution into tributaries, 1996. Technical report, Bonneville Power Administration, Portland, OR.
- Kendall, W. L. and Nichols, J. D. (1995). On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* **22**, 751–762.
- Kendall, W. L., Nichols, J. D. and Hines, J. E. (1997). Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology* **78**, 563–578.
- Kendall, W. L., Pollock, K. H. and Brownie, C. (1995). A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics* **51**, 293–308.
- Lady, J. (1996). Release-recapture models for estimating the stream residence time of spawning salmon. Master's thesis, University of Washington, Seattle, WA.
- Lady, J. and Skalski, J. R. (1998). Estimators of stream residence time of Pacific salmon (*Oncorhynchus* spp.) based on release-recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 2580–2587.
- Lebreton, J.-D. (1978). Un modèle probabiliste de la dynamique des populations de cigogne blanche (*Ciconia ciconia* L.) en Europe Occidentale. In Legay, J. M. and Tomassone, R., editors, *Biométrie et écologie*, pages 277–343. Paris: Société Française de Biométrie.
- Lebreton, J.-D., Burnham, K. P., Clobert, J. and Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals. *Ecological Monographs* **62**, 67–118.
- Lebreton, J.-D., Hemery, F., Clobert, J. and Coquillart, H. (1990). The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations. I. Transversal models. *Biometrics* **46**, 609–622.
- Lebreton, J.-D. and Pradel, R. (2002). Multistate recapture models: Modeling incomplete individual histories. *Journal of Applied Statistics* **29**, 353–369.
- Lowther, A. B. and Skalski, J. R. (1998). A multinomial likelihood model for estimating survival probabilities and overwintering for fall Chinook salmon using release-recapture models. *Journal of Agricultural, Biological, and Environmental Statistics* **3**, 223–236.
- Manly, B. F. J. and Chatterjee, C. (1993). A model for mark-recapture data allowing for animal movement. In Lebreton, J.-D. and North, P. M., editors, *Marked Individuals in the Study of Bird Populations*, pages 309–322. Boston: Birkhäuser Verlag.
- Manske, M. and Schwarz, C. J. (2000). Estimates of stream residence time and escapement based on capture-recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 241–246.

- Mardekian, S. Z. and McDonald, L. (1981). Simultaneous analysis of band-recovery and live-recapture data. *Journal of Wildlife Management* **45**, 789-792.
- McIsaac, D. (1995). *Factors affecting the abundance of 1977-79 brood year wild fall chinook salmon (*Oncorhynchus tshawytscha*) in the Lewis River, Washington*. PhD thesis, University of Washington.
- Miller, D. R., Williams, J. G. and Sims, C. W. (1983). Distribution, abundance, and growth of juvenile salmonids off the coast of Oregon and Washington, summer 1980. *Fisheries Research* **2**, 1-17.
- Muir, W. D., Smith, S. G., Hockersmith, E. E., Achord, S., Absolon, R. F., Ocker, P. A., Eppard, B. M., Ruehle, T. E., Williams, J. G., Iwamoto, R. N. and Skalski, J. R. (1996). Survival estimates for the passage of the yearling chinook salmon and steelhead through Snake River dams and reservoirs, 1995. Technical report, US Army Corps of Engineers and Bonneville Power Administration, Portland, OR.
- Muir, W. D., Smith, S. G., Iwamoto, R. N., Kamikawa, D. J., McIntyre, K. W., Hockersmith, E. E., Sandford, B. P., Ocker, P. A., Ruehle, T. E., Williams, J. G. and Skalski, J. R. (1995). Survival estimates for the passage of juvenile salmonids through Snake River dams and reservoirs, 1994. Technical report, Bonneville Power Administration, Portland, OR.
- Muir, W. D., Smith, S. G., Williams, J. G., Hockersmith, E. E. and Skalski, J. R. (2001). Survival estimates for migrant yearling chinook and steelhead tagged with passive integrated transponders in the lower Snake and lower Columbia rivers, 1993-1998. *North American Journal of Fisheries Management* **21**, 269-282.
- Muir, W. D., Smith, S. G., Williams, J. G. and Sandford, B. P. (2001). Survival of juvenile salmonids passing through bypass systems, turbines, and spillways with and without flow deflectors at Snake River dams. *North American Journal of Fisheries Management* **21**, 135-146.
- Netboy, A. (1980). *The Columbia River Salmon and Steelhead Trout: Their Fight for Survival*. University of Washington Press, Seattle, WA.
- Nichols, J. D., Brownie, C., Hines, H. E., Pollock, K. H. and Hestbeck, J. B. (1993). The estimation of exchanges among populations or subpopulations. In Lebreton, J.-D. and North, P. M., editors, *Marked Individuals in the Study of Bird Populations*, pages 265-279. Boston: Birhauser Verlag.
- Nichols, J. D. and Pollock, K. H. (1990). Estimation of recruitment from immigration versus in situ reproduction using Pollock's robust design. *Ecology* **71**, 21-26.
- NOAA Fisheries (National Oceanic and Atmospheric Administration, National Marine Fisheries Service) (2000a). Biological opinion - reinitiation of consultation on operation of the Federal Columbia River Power System, including the juvenile fish transportation program, and 19 Bureau of Reclamation projects in the Columbia Basin. 180 pp.

- NOAA Fisheries (National Oceanic and Atmospheric Administration, National Marine Fisheries Service) (2000b). Passage of juvenile and adult salmonids past Columbia and Snake river dams. white paper.
- NOAA Fisheries (National Oceanic and Atmospheric Administration, National Marine Fisheries Service) (2000c). Summary of research related to transportation of juvenile anadromous salmonids around Snake and Columbia river dams. white paper.
- NOAA Fisheries (National Oceanic and Atmospheric Administration, National Marine Fisheries Service) (2004). Biological Opinion - Consultation on remand for operation of the Columbia River Power System and 19 Bureau of Reclamation projects in the Columbia Basin.
- Otis, D. L., Burnham, K. P., White, G. C. and Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**, 1-135.
- Pledger, S. and Schwarz, C. J. (2002). Modeling heterogeneity of survival in band-recovery data using mixtures. *Journal of Applied Statistics* **29**, 315-327.
- Pollock, K. H. (1975). A K-sample tag-recapture model allowing for unequal survival and catchability. *Biometrika* **62**, 577-583.
- Pollock, K. H. (1981). Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics* **37**, 521-29.
- Pollock, K. H. (1982). A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management* **46**, 752-757.
- Pollock, K. H., Bunck, C. M., Winterstein, S. R. and Chen, C.-L. (1995). A capture-recapture survival analysis model for radio-tagged animals. *Journal of Applied Statistics* **22**, 661-672.
- Pollock, K. H., Jiang, H. and Hightower, J. E. (2004). Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates. *Transactions of the American Fisheries Society* **133**, 639-648.
- Pollock, K. H., Nichols, J. D., Hines, J. E. and Brownie, C. (1990). Statistical inference for capture-recapture experiments. *Wildlife Monographs* **107**.
- Pollock, K. H., Winterstein, S. R. and Conroy, M. J. (1989). Estimation and analysis of survival distributions for radio-tagged animals. *Biometrics* **45**, 99-109.
- Powell, L. A., Conroy, M. J., Hines, J. E., Nichols, J. D. and Kremenetz, D. G. (2000). Simultaneous use of mark-recapture and radiotelemetry to estimate survival, movement, and capture rates. *Journal of Wildlife Management* **64**, 302-313.
- Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* **52**, 371-377.
- Pradel, R., Clobert, J. and Lebreton, J.-D. (1990). Recent developments for the analysis of multiple capture-recapture data sets. An example concerning two Blue Tit populations. *The Ring* **13**, 193-204.

- Pradel, R., Johnson, A. R., Viallefont, A., Nager, R. G. and Cézilly, F. (1997). Local recruitment in the greater flamingo: A new approach using capture-mark-recapture data. *Ecology* **78**, 1431–1445.
- Prentice, E. F. (1990). A new telemetry tag for fish and crustaceans. Technical Report 85, NOAA Fisheries (National Oceanic and Atmospheric Administration, National Marine Fisheries Service).
- Prentice, E. F., Flagg, T. A. and McCutcheon, C. S. (1987). A study to determine the biological feasibility of a new fish tagging system, 1986–1987. Bonneville Power Administration, Portland, OR.
- Prentice, E. F., Flagg, T. A. and McCutcheon, C. S. (1990). Feasibility of using implantable passive integrated transponder (PIT) tags in salmonids. *American Fisheries Society Symposium* **7**, 317–322.
- Prentice, E. F., Flagg, T. A., McCutcheon, C. S. and Brastow, D. F. (1990). PIT-tag monitoring systems for hydroelectric dams and fish hatcheries. *American Fisheries Society Symposium* **7**, 323–334.
- Raymond, H. (1988). Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook salmon and Steelhead in the Columbia River Basin. *North American Journal of Fisheries Management* **8**, 1–23.
- Reischel, T. S. and Bjornn, T. C. (2003). Influence of fishway placement on fallback of adult salmon at the Bonneville Dam on the Columbia River. *North American Journal of Fisheries Management* **23**, 1215–1224.
- Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191**, 382 p.
- Robson, D. S. (1969). Mark-recapture methods of population estimation. In Johnson, N. L. and Smith, H., editors, *New Developments in Survey Sampling*, pages 120–140. New York: Wiley.
- Ross, C. and Domingue, D. (2004). FCRPS effects on adult survival. Attachment 4 to Appendix D to State/Tribal Review Draft - FCRPS Biological Opinion on Remand.
- Sandercock, F. K. (1991). Life history of coho salmon (*Oncorhynchus kisutch*). In Groot, C. and Margolis, L., editors, *Pacific Salmon Life Histories*, pages 394–445. UBC Press, Vancouver, B.C.
- Sandford, B. P. and Smith, S. G. (2002). Estimation of smolt-to-adult return percentages for Snake River Basin anadromous salmonids, 1990–1997. *Journal of Agricultural, Biological, and Environmental Statistics* **7**, 243–263.
- Schwarz, C. J. (1993). Estimating migration rates using tag-recovery data. In Lebreton, J.-D. and North, P. M., editors, *Marked Individuals in the Study of Bird Populations*, pages 255–264. Boston: Birhauser Verlag.

- Schwarz, C. J. and Arnason, A. N. (1996). A general methodology for the analysis of capture-recapture experiments in open populations. *Biometrics* **52**, 860–873.
- Schwarz, C. J. and Arnason, A. N. (2000). Estimation of age-specific breeding probabilities from capture-recapture data. *Biometrics* **56**, 59–64.
- Schwarz, C. J., Burnham, K. P. and Arnason, A. N. (1988). Post-release stratification in band-recovery models. *Biometrics* **44**, 765–785.
- Schwarz, C. J. and Dempson, J. B. (1994). Mark-recapture estimation of a salmon smolt population. *Biometrics* **50**, 98–108.
- Schwarz, C. J., Schweigert, J. F. and Arnason, A. N. (1993). Estimating migration rates using tag-recovery data. *Biometrics* **49**, 177–193.
- Schwarz, C. J. and Stobo, W. T. (1997). Estimating temporary migration using the robust design. *Biometrics* **53**, 178–194.
- Seber, G. A. F. (1965). A note on the multiple recapture census. *Biometrika* **52**, 249–259.
- Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters*, 2nd edition. Blackburn Press, Caldwell, NJ.
- Skalski, J. R. (1998). Estimating season-wide survival rates of outmigrating salmon smolt in the Snake River, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 761–769.
- Skalski, J. R., Lady, J., Townsend, R., Giorgi, A. E., Stevenson, J. R., Peven, C. M. and McDonald, R. D. (2001). Estimating in-river survival of migrating salmonid smolts using radiotelemetry. *Canadian Journal of Fisheries and Aquatic Sciences* **58**, 1987–1997.
- Skalski, J. R., Smith, S. G., Iwamoto, R. N., Williams, J. G. and Hoffman, A. (1998). Use of passive integrated transponder tags to estimate survival of migrant juvenile salmonids in the Snake and Columbia rivers. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1484–1493.
- Skalski, J. R., Townsend, R., Lady, J., Giorgi, A. E., Stevenson, J. R. and McDonald, R. D. (2002). Estimating route-specific passage and survival probabilities at a hydroelectric project from smolt radiotelemetry studies. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 1385–1393.
- Smith, S. G., Muir, W. D., Hockersmith, E. E., Achord, S., Eppard, M. B., Ruehle, T. E. and Williams, J. G. (1998). Survival estimates for the passage of juvenile salmonids through Snake River dams and reservoirs, 1996. Technical report, Bonneville Power Administration, Seattle, WA.
- Smith, S. G., Skalski, J. R., Schlechte, W., Hoffmann, A. and Cassen, V. (1994). Statistical survival analysis of fish and wildlife tagging studies. Survival with proportional hazards manual 1.

- Stokes, S. L. (1984). The Jolly-Seber method applied to age-stratified populations. *Journal of Wildlife Management* **43**, 1053-1059.
- USACE (U. S. Army Corps of Engineers) (1993). Endangered Species Act section 10 permit application. November 15, 1993, revised December 7, 1993.
- Ward, D. L., Boyce, R. R., Young, F. R. and Olney, F. E. (1997). A review and assessment of transportation studies for juvenile chinook salmon in the Snake River. *North American Journal of Fisheries Management* **17**, 652-662.
- White, G. C. (1983). Numerical estimation of survival rates from band-recovery and biotelemetry data. *Journal of Wildlife Management* **47**, 716-728.
- Williams, J. G. (1989). Snake River spring and summer chinook salmon: Can they be saved? *Regulated Rivers: Research and Management* **4**, 17-26.
- Williams, J. G., Smith, S. G. and Muir, W. D. (2001). Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia Rivers hydropower system, 1966-1980 and 1993-1999. *North American Journal of Fisheries Management* **21**, 310-317.
- Zeng, Z. and Brown, J. H. (1987). A method for distinguishing dispersal from death in mark-recapture studies. *Journal of Mammalogy* **68**, 656-665.

Appendix A

RADIOTELEMETRY DATA FOR SAMPLE ADULT CHINOOK SALMON

Table A.1: Radiotelemetry data from a sample Chinook salmon from 1996 release. The data were downloaded from the Adult Anadromous Fish Radiotelemetry Project website at <http://rtagweb.nwfsc.noaa.gov/home/index.cfm>. The records shown are from the fish with radio-tag ID 2054, species 1 (spring/summer Chinook salmon), released at Dodson's Landing (RKM 225.6) in study year 1996. The column "Corr" indicates the movements or behaviors of the tagged fish summarized by the individual record. Briefly, the code "TAG" indicates the initial tagging and release record. Codes beginning with "A" indicate an approach to a receiver site. Those starting with "E", "I", or "X" indicate records at the entrance, inside, and exit of a site or dam, respectively. In particular, "A1" codes indicate the first approach to a dam. The "LT" code indicates the last record at a top-of-ladder site. The codes "F1" and "L1" indicate the first and last records at the Yagi antennas downstream from the tailrace of the dam. The codes "F" and "L" indicate the first and last records fixed receiver sites in either the tailrace of a dam or a tributary. The codes "MBT" and "RCP" indicate mobile tracking and tag-recovery records, respectively. More information on the Corr codes is available at http://rtagweb.nwfsc.noaa.gov/datades_sed/index.cfm. Only the "TAG", "A1", "LT", "F" (at tributaries), "L" (at tributaries), and "F" (at LMO) are used with the models in this chapter. Records without dam information are from fixed-site tributary receivers.

Corr	Detection		Antenna	Date		RKM	Power
	Dam	Site		Recorded			
TAG		DOD	8	12-May-1996 09:47:00		225.6	
F1	BO	1BO	1	12-May-1996 12:50:54		232.3	132
L1	BO	2BO	1	12-May-1996 13:39:02		232.3	107
F	BO	3BO	1	12-May-1996 13:39:26		235.1	136
L	BO	3BO	1	12-May-1996 14:23:57		235.1	119
A161	BO	6BO	1	12-May-1996 14:29:37		235.1	12
A64	BO	6BO	4	12-May-1996 14:30:37		235.1	220
A81	BO	8BO	1	12-May-1996 14:33:30		235.1	51
A83	BO	8BO	3	12-May-1996 14:33:36		235.1	22
A81	BO	8BO	1	12-May-1996 14:41:05		235.1	27
A83	BO	8BO	3	12-May-1996 14:43:19		235.1	17
A61	BO	6BO	1	12-May-1996 14:49:21		235.1	134

Table A.1 continued

Corr	Detection		Antenna	Date	RKM	Power
	Dam	Site		Recorded		
A64	BO	6BO	4	12-May-1996 14:50:27	235.1	19
A61	BO	6BO	1	12-May-1996 14:52:21	235.1	38
A41	BO	4BO	1	12-May-1996 14:53:40	235.1	28
F	BO	3BO	1	12-May-1996 15:00:14	235.1	146
L	BO	3BO	1	12-May-1996 15:01:03	235.1	142
A41	BO	4BO	1	12-May-1996 15:05:38	235.1	23
A61	BO	6BO	1	12-May-1996 15:07:49	235.1	30
A64	BO	6BO	4	12-May-1996 15:08:49	235.1	231
A71	BO	7BO	1	12-May-1996 15:10:44	235.1	98
A81	BO	8BO	1	12-May-1996 15:11:01	235.1	19
A83	BO	8BO	3	12-May-1996 15:11:32	235.1	122
A41	BO	4BO	1	12-May-1996 15:25:34	235.1	31
A51	BO	5BO	1	12-May-1996 15:29:34	235.1	58
A61	BO	6BO	1	12-May-1996 15:30:27	235.1	36
A64	BO	6BO	4	12-May-1996 15:31:27	235.1	15
A71	BO	7BO	1	12-May-1996 15:33:45	235.1	50
A81	BO	8BO	1	12-May-1996 15:33:52	235.1	59
A83	BO	8BO	3	12-May-1996 15:34:10	235.1	79
A41	BO	4BO	1	12-May-1996 16:13:59	235.1	31
A61	BO	6BO	1	12-May-1996 16:16:15	235.1	59
A64	BO	6BO	4	12-May-1996 16:17:21	235.1	168
A71	BO	7BO	1	12-May-1996 16:19:29	235.1	116
A81	BO	8BO	1	12-May-1996 16:19:40	235.1	51
A83	BO	8BO	3	12-May-1996 16:19:52	235.1	60
AC1	BO	CBO	1	12-May-1996 17:23:34	235.1	10
E1C1	BO	CBO	1	12-May-1996 17:34:54	235.1	999
FP	BO	CBO	2	12-May-1996 17:34:55	235.1	212
IC3	BO	CBO	3	12-May-1996 17:38:01	235.1	37
IC4	BO	CBO	4	12-May-1996 17:38:19	235.1	99
IO1	BO	OBO	1	12-May-1996 20:41:24	235.1	16
IO3	BO	OBO	3	12-May-1996 20:43:32	235.1	101
FT	BO	PBO	1	13-May-1996 06:48:56	235.1	25
LT	BO	PBO	1	13-May-1996 06:51:34	235.1	8
F	BO	SBO	1	13-May-1996 06:51:38	235.3	163
L	BO	SBO	1	13-May-1996 07:02:11	235.3	162
F		LWS	1	14-May-1996 07:23:16	260.7	115
L		LWS	1	14-May-1996 07:23:17	260.7	999
F1	TD	2TD	1	14-May-1996 10:47:54	304.9	148
L1	TD	2TD	1	14-May-1996 10:53:34	304.9	202
FT	TD	5TD	1	15-May-1996 15:59:58	308.1	16

Table A.1 continued

Corr	Detection		Antenna	Date		RKM	Power
	Dam	Site		Recorded			
LT	TD	5TD	1	15-May-1996 16:00:47		308.1	24
FB	TD	3TD	1	17-May-1996 08:15:24		308.1	999
FP	TD	3TD	1	17-May-1996 08:15:25		308.1	9
LP	TD	3TD	1	17-May-1996 08:50:12		308.1	4
I41	TD	4TD	1	17-May-1996 09:14:58		308.1	21
I42	TD	4TD	2	17-May-1996 09:35:22		308.1	112
FT	TD	4TD	3	17-May-1996 09:36:47		308.1	27
LT	TD	4TD	3	17-May-1996 09:38:18		308.1	41
EFB	TD	4TD	3	17-May-1996 09:38:19		308.1	999
F	TD	4TD	4	17-May-1996 09:38:42		308.1	16
L	TD	4TD	4	17-May-1996 09:40:19		308.1	96
F1	JD	1JD	1	18-May-1996 01:04:32		345.0	160
L	JD	1JD	1	18-May-1996 04:33:16		345.0	169
FB	TD	2TD	1	18-May-1996 12:02:25		304.9	999
F	TD	2TD	1	18-May-1996 12:02:26		304.9	135
L	TD	2TD	1	18-May-1996 12:12:51		304.9	165
FB	BO	1BO	1	19-May-1996 01:28:11		232.3	999
F	BO	1BO	1	19-May-1996 01:28:12		232.3	152
L	BO	1BO	1	19-May-1996 01:37:08		232.3	129
F1 2ND	BO	1BO	1	20-May-1996 13:12:59		232.3	115
L1	BO	1BO	1	20-May-1996 13:21:55		232.3	123
A141	BO	4BO	1	20-May-1996 14:11:02		235.1	32
E141	BO	4BO	1	20-May-1996 14:11:19		235.1	999
I42	BO	4BO	2	20-May-1996 14:11:20		235.1	68
I43	BO	4BO	3	20-May-1996 14:11:38		235.1	58
I42	BO	4BO	2	20-May-1996 14:11:50		235.1	54
I43	BO	4BO	3	20-May-1996 14:12:51		235.1	41
I42	BO	4BO	2	20-May-1996 14:13:15		235.1	97
X41	BO	4BO	1	20-May-1996 14:14:40		235.1	46
A81	BO	8BO	1	20-May-1996 14:33:59		235.1	171
A74	BO	7BO	4	20-May-1996 14:34:06		235.1	39
F	BO	3BO	1	20-May-1996 14:42:03		235.1	125
L	BO	3BO	1	20-May-1996 14:42:04		235.1	999
A41	BO	4BO	1	20-May-1996 15:04:22		235.1	27
A61	BO	6BO	1	20-May-1996 15:05:55		235.1	26
A64	BO	6BO	4	20-May-1996 15:06:49		235.1	29
A81	BO	8BO	1	20-May-1996 15:08:33		235.1	17
F	BO	3BO	1	20-May-1996 15:12:45		235.1	131
L	BO	3BO	1	20-May-1996 15:12:46		235.1	999
AB1	BO	BBO	1	20-May-1996 16:01:13		235.1	32

Table A.1 continued

Corr	Detection		Antenna	Date		RKM	Power
	Dam	Site		Recorded			
EB1	BO	BBO	1	20-May-1996 16:02:43		235.1	255
FP	BO	BBO	3	20-May-1996 16:03:18		235.1	17
IB4	BO	BBO	4	20-May-1996 16:04:18		235.1	54
IB3	BO	BBO	3	20-May-1996 16:04:23		235.1	37
IB4	BO	BBO	4	20-May-1996 16:04:28		235.1	58
IB3	BO	BBO	3	20-May-1996 16:07:53		235.1	17
XB1	BO	BBO	1	20-May-1996 16:08:13		235.1	7
UAB	BO	BBO	3	20-May-1996 16:51:21		235.1	999
UEB	BO	BBO	3	20-May-1996 16:51:22		235.1	999
IB3	BO	BBO	3	20-May-1996 16:51:23		235.1	22
IB4	BO	BBO	4	20-May-1996 16:52:38		235.1	35
IB3	BO	BBO	3	20-May-1996 17:22:58		235.1	86
IB4	BO	BBO	4	20-May-1996 17:24:08		235.1	70
XB1	BO	BBO	1	20-May-1996 17:37:08		235.1	178
AB1	BO	BBO	1	20-May-1996 17:39:58		235.1	25
EB1	BO	BBO	1	20-May-1996 17:40:13		235.1	12
IB4	BO	BBO	4	20-May-1996 17:41:08		235.1	24
IB3	BO	BBO	3	20-May-1996 17:48:18		235.1	91
IB4	BO	BBO	4	20-May-1996 17:48:33		235.1	37
IB3	BO	BBO	3	20-May-1996 17:54:38		235.1	23
IB4	BO	BBO	4	20-May-1996 17:54:58		235.1	193
I92	BO	9BO	2	20-May-1996 18:13:16		235.1	25
I93	BO	9BO	3	20-May-1996 18:26:46		235.1	28
FT	BO	ABO	1	20-May-1996 19:05:49		235.1	17
LT	BO	ABO	1	20-May-1996 19:08:14		235.1	7
EFB	BO	ABO	1	20-May-1996 19:08:15		235.1	999
F	BO	SBO	1	20-May-1996 19:20:09		235.3	129
L	BO	SBO	1	20-May-1996 20:17:34		235.3	163
F1 2ND	TD	2TD	1	22-May-1996 02:42:19		304.9	117
L1	TD	2TD	1	22-May-1996 04:00:04		304.9	115
FP	TD	3TD	1	23-May-1996 14:25:58		308.1	6
LP	TD	3TD	1	23-May-1996 14:46:43		308.1	10
I41	TD	4TD	1	23-May-1996 15:05:54		308.1	85
I42	TD	4TD	2	23-May-1996 15:15:56		308.1	31
UFT	TD	4TD	3	23-May-1996 15:16:28		308.1	999
ULT	TD	4TD	3	23-May-1996 15:16:29		308.1	999
EFB	TD	4TD	3	23-May-1996 15:16:30		308.1	999
F	JD	1JD	1	24-May-1996 07:55:53		345.0	999
L1	JD	1JD	1	24-May-1996 08:24:11		345.0	118
FP	JD	3JD	1	24-May-1996 11:58:14		346.9	18

Table A.1 continued

Corr	Detection		Antenna	Date		RKM	Power
	Dam	Site		Recorded			
I32	JD	3JD	2	24-May-1996 12:01:52		346.9	29
I31	JD	3JD	1	24-May-1996 12:05:07		346.9	24
I32	JD	3JD	2	24-May-1996 12:08:03		346.9	47
I31	JD	3JD	1	24-May-1996 12:08:57		346.9	86
I32	JD	3JD	2	24-May-1996 12:15:05		346.9	21
I31	JD	3JD	1	24-May-1996 12:15:29		346.9	60
I32	JD	3JD	2	24-May-1996 12:19:00		346.9	18
I31	JD	3JD	1	24-May-1996 12:19:18		346.9	65
I32	JD	3JD	2	24-May-1996 12:21:25		346.9	95
I31	JD	3JD	1	24-May-1996 12:21:43		346.9	96
I32	JD	3JD	2	24-May-1996 12:22:56		346.9	63
I31	JD	3JD	1	24-May-1996 12:24:45		346.9	62
I31	JD	3JD	1	24-May-1996 14:24:37		346.9	99
I32	JD	3JD	2	24-May-1996 14:25:38		346.9	32
I31	JD	3JD	1	24-May-1996 14:26:08		346.9	65
I32	JD	3JD	2	24-May-1996 14:27:27		346.9	47
I31	JD	3JD	1	24-May-1996 14:28:15		346.9	41
I32	JD	3JD	2	24-May-1996 14:29:10		346.9	18
I31	JD	3JD	1	24-May-1996 14:29:34		346.9	20
I32	JD	3JD	2	24-May-1996 14:30:53		346.9	50
I31	JD	3JD	1	24-May-1996 14:31:17		346.9	48
I32	JD	3JD	2	24-May-1996 14:53:04		346.9	88
I31	JD	3JD	1	24-May-1996 14:53:28		346.9	95
I32	JD	3JD	2	24-May-1996 14:57:17		346.9	22
I31	JD	3JD	1	24-May-1996 14:57:23		346.9	15
I32	JD	3JD	2	24-May-1996 14:58:36		346.9	40
I33	JD	3JD	3	24-May-1996 15:10:28		346.9	26
I34	JD	3JD	4	24-May-1996 15:16:43		346.9	18
I35	JD	3JD	5	24-May-1996 15:17:25		346.9	36
I41	JD	4JD	1	24-May-1996 15:35:43		346.9	12
I42	JD	4JD	2	24-May-1996 15:58:02		346.9	12
I51	JD	5JD	1	24-May-1996 15:59:32		346.9	10
I52	JD	5JD	2	24-May-1996 16:23:25		346.9	9
FT	JD	6JD	1	24-May-1996 16:29:00		346.9	40
LT	JD	6JD	1	24-May-1996 16:29:49		346.9	9
FB	JD	2JD	1	24-May-1996 21:21:59		345.1	999
F	JD	2JD	1	24-May-1996 21:22:00		345.1	162
L	JD	1JD	1	24-May-1996 21:34:53		345.0	134
FB	TD	1TD	1	25-May-1996 05:20:00		304.9	999
F	TD	2TD	1	25-May-1996 05:23:05		304.9	129

Table A.1 continued

Corr	Detection		Antenna	Date	RKM	Power
	Dam	Site		Recorded		
L	TD	1TD	1	25-May-1996 05:38:48	304.9	133
F	BO	SBO	1	25-May-1996 18:07:26	235.3	146
L	BO	SBO	1	25-May-1996 18:24:26	235.3	166
FB	BO	1BO	1	25-May-1996 19:11:39	232.3	999
F	BO	1BO	1	25-May-1996 19:11:40	232.3	160
L	BO	1BO	1	25-May-1996 19:15:43	232.3	148
F1 3RD	BO	1BO	1	29-May-1996 00:41:29	232.3	146
L1	BO	1BO	1	29-May-1996 02:29:27	232.3	125
F	BO	3BO	1	29-May-1996 02:43:51	235.1	138
L	BO	3BO	1	29-May-1996 02:51:57	235.1	119
A171	BO	7BO	1	29-May-1996 02:55:29	235.1	26
A74	BO	7BO	4	29-May-1996 02:55:47	235.1	33
A81	BO	8BO	1	29-May-1996 02:55:56	235.1	111
F	BO	3BO	1	29-May-1996 02:57:36	235.1	148
L	BO	3BO	1	29-May-1996 03:23:30	235.1	129
F	BO	1BO	1	29-May-1996 03:26:03	232.3	121
L	BO	1BO	1	29-May-1996 04:06:28	232.3	116
AL1	BO	LBO	1	29-May-1996 05:44:06	235.1	153
E1L1	BO	LBO	1	29-May-1996 05:44:18	235.1	28
FP	BO	LBO	2	29-May-1996 05:44:24	235.1	54
IL4	BO	LBO	4	29-May-1996 05:48:01	235.1	136
IM2	BO	MBO	2	29-May-1996 05:49:33	235.1	255
IM1	BO	MBO	1	29-May-1996 05:54:45	235.1	14
IM2	BO	MBO	2	29-May-1996 05:59:03	235.1	28
IK2	BO	KBO	2	29-May-1996 06:15:32	235.1	35
IJ3	BO	JBO	3	29-May-1996 06:15:47	235.1	85
IJ2	BO	JBO	2	29-May-1996 06:15:53	235.1	29
IH4	BO	HBO	4	29-May-1996 06:15:59	235.1	42
IH3	BO	HBO	3	29-May-1996 06:16:11	235.1	24
IH2	BO	HBO	2	29-May-1996 06:16:17	235.1	45
IG5	BO	GB0	5	29-May-1996 06:16:35	235.1	48
IG3	BO	GB0	3	29-May-1996 06:16:50	235.1	59
IF4	BO	FBO	4	29-May-1996 06:17:12	235.1	36
IF2	BO	FBO	2	29-May-1996 06:17:24	235.1	41
IE5	BO	EBO	5	29-May-1996 06:17:33	235.1	21
XE4	BO	EBO	4	29-May-1996 06:17:45	235.1	24
AC1	BO	CBO	1	29-May-1996 06:53:22	235.1	137
AB1	BO	BBO	1	29-May-1996 13:46:02	235.1	45
EB1	BO	BBO	1	29-May-1996 13:46:37	235.1	44
IB3	BO	BBO	3	29-May-1996 13:47:22	235.1	18

Table A.1 continued

Corr	Detection		Antenna	Date		RKM	Power
	Dam	Site		Recorded			
IB4	BO	BBO	4	29-May-1996 13:48:02	235.1	94	
IB3	BO	BBO	3	29-May-1996 14:17:07	235.1	138	
IB4	BO	BBO	4	29-May-1996 14:17:17	235.1	95	
IB3	BO	BBO	3	29-May-1996 14:44:57	235.1	39	
XB1	BO	BBO	1	29-May-1996 14:45:12	235.1	25	
AL1	BO	LBO	1	30-May-1996 09:47:30	235.1	144	
EL1	BO	LBO	1	30-May-1996 09:47:54	235.1	44	
IL2	BO	LBO	2	30-May-1996 09:48:42	235.1	49	
IM1	BO	MBO	1	30-May-1996 09:55:47	235.1	30	
IM4	BO	MBO	4	30-May-1996 09:59:53	235.1	50	
IN1	BO	NBO	1	30-May-1996 10:01:20	235.1	49	
IN2	BO	NBO	2	30-May-1996 10:02:09	235.1	49	
IN3	BO	NBO	3	30-May-1996 10:06:35	235.1	18	
IN4	BO	NBO	4	30-May-1996 10:07:30	235.1	14	
IO2	BO	OBO	2	30-May-1996 10:48:28	235.1	15	
IO3	BO	OBO	3	30-May-1996 10:56:13	235.1	65	
FT	BO	PBO	1	30-May-1996 11:32:30	235.1	36	
LT	BO	PBO	1	30-May-1996 11:34:26	235.1	8	
EFB	BO	PBO	1	30-May-1996 11:34:27	235.1	999	
F		LWS	1	30-May-1996 21:33:44	260.7	138	
L		LWS	1	30-May-1996 21:36:11	260.7	112	
F		WHR	1	31-May-1996 01:47:34	270.8	120	
L		WHR	1	31-May-1996 02:06:59	270.8	140	
F1 3RD	TD	2TD	1	31-May-1996 16:40:37	304.9	163	
L1	TD	1TD	1	31-May-1996 17:08:54	304.9	186	
FT	TD	5TD	1	31-May-1996 20:07:29	308.1	15	
LT	TD	5TD	1	31-May-1996 20:09:43	308.1	9	
EFB	TD	5TD	1	31-May-1996 20:09:44	308.1	999	
F		DES	1	1-Jun-1996 06:02:31	328.9	123	
L		DES	1	1-Jun-1996 06:50:59	328.9	151	
F		DES	1	1-Jun-1996 13:59:49	328.9	163	
L		DES	1	1-Jun-1996 14:07:05	328.9	118	
FB	TD	2TD	1	1-Jun-1996 21:25:22	304.9	999	
F	TD	2TD	1	1-Jun-1996 21:25:23	304.9	174	
L	TD	2TD	1	1-Jun-1996 21:29:26	304.9	169	
FB	BO	1BO	1	2-Jun-1996 14:23:41	232.3	999	
F	BO	1BO	1	2-Jun-1996 14:23:42	232.3	142	
L	BO	1BO	1	2-Jun-1996 14:32:36	232.3	136	
F1 4TH	BO	1BO	1	5-Jun-1996 18:39:19	232.3	128	
L1	BO	1BO	1	5-Jun-1996 19:15:43	232.3	103	

Table A.1 continued

Corr	Detection		Antenna	Date		RKM	Power
	Dam	Site		Recorded			
A1L1	BO	LBO	1	5-Jun-1996 20:34:21		235.1	79
E1L1	BO	LBO	1	5-Jun-1996 20:35:08		235.1	999
FP	BO	LBO	2	5-Jun-1996 20:35:09		235.1	55
IM4	BO	MBO	4	5-Jun-1996 20:45:34		235.1	255
IN1	BO	NBO	1	5-Jun-1996 20:47:18		235.1	24
IN2	BO	NBO	2	5-Jun-1996 20:48:48		235.1	29
LP	BO	NBO	3	5-Jun-1996 20:51:00		235.1	13
IN4	BO	NBO	4	5-Jun-1996 20:59:28		235.1	10
IO2	BO	OBO	2	5-Jun-1996 21:25:24		235.1	39
IO3	BO	OBO	3	5-Jun-1996 21:34:58		235.1	23
UFT	BO	PBO	1	6-Jun-1996 02:36:08		235.1	999
ULT	BO	PBO	1	6-Jun-1996 02:36:09		235.1	999
EFB	BO	PBO	1	6-Jun-1996 02:36:10		235.1	999
F1 4TH	TD	2TD	1	7-Jun-1996 08:47:52		304.9	122
L1	TD	2TD	1	7-Jun-1996 09:35:03		304.9	112
FP	TD	3TD	1	7-Jun-1996 12:49:13		308.1	7
LP	TD	3TD	1	7-Jun-1996 12:50:16		308.1	3
I41	TD	4TD	1	7-Jun-1996 13:17:51		308.1	17
I42	TD	4TD	2	7-Jun-1996 13:33:05		308.1	27
FT	TD	4TD	3	7-Jun-1996 13:35:18		308.1	20
LT	TD	4TD	3	7-Jun-1996 13:35:42		308.1	23
EFB	TD	4TD	3	7-Jun-1996 13:35:43		308.1	999
F	TD	4TD	4	7-Jun-1996 13:36:36		308.1	55
L	TD	4TD	4	7-Jun-1996 13:36:37		308.1	999
F1 2ND	JD	2JD	1	8-Jun-1996 00:50:28		345.1	123
L1	JD	2JD	1	8-Jun-1996 01:28:57		345.1	141
FP	JD	3JD	1	8-Jun-1996 02:44:52		346.9	40
I32	JD	3JD	2	8-Jun-1996 02:47:31		346.9	37
I31	JD	3JD	1	8-Jun-1996 02:49:45		346.9	46
I32	JD	3JD	2	8-Jun-1996 02:53:00		346.9	28
I31	JD	3JD	1	8-Jun-1996 02:53:24		346.9	57
I32	JD	3JD	2	8-Jun-1996 02:56:15		346.9	16
I31	JD	3JD	1	8-Jun-1996 02:58:17		346.9	55
I32	JD	3JD	2	8-Jun-1996 03:00:00		346.9	20
I33	JD	3JD	3	8-Jun-1996 03:19:28		346.9	20
I34	JD	3JD	4	8-Jun-1996 03:57:27		346.9	42
I35	JD	3JD	5	8-Jun-1996 03:59:05		346.9	71
I41	JD	4JD	1	8-Jun-1996 04:53:57		346.9	10
I42	JD	4JD	2	8-Jun-1996 05:14:57		346.9	19
I51	JD	5JD	1	8-Jun-1996 05:17:59		346.9	18

Table A.1 continued

Corr	Detection		Antenna	Date		RKM	Power
	Dam	Site		Recorded			
I52	JD	5JD	2	8-Jun-1996 05:44:03		346.9	42
FT	JD	6JD	1	8-Jun-1996 05:48:33		346.9	28
LT	JD	6JD	1	8-Jun-1996 05:49:22		346.9	107
EFB	JD	6JD	1	8-Jun-1996 05:49:23		346.9	999
F1	MN	1MN	1	10-Jun-1996 02:43:23		467.3	119
L1	MN	2MN	1	10-Jun-1996 03:28:16		467.3	124
A164	MN	6MN	4	10-Jun-1996 04:40:27		469.8	17
A71	MN	7MN	1	10-Jun-1996 04:41:59		469.8	25
A81	MN	8MN	1	10-Jun-1996 04:48:23		469.8	29
AC1	MN	CMN	1	10-Jun-1996 05:56:55		469.8	118
E1C1	MN	CMN	1	10-Jun-1996 05:57:20		469.8	10
FP	MN	CMN	3	10-Jun-1996 05:58:13		469.8	12
ID1	MN	DMN	1	10-Jun-1996 06:14:56		469.8	60
ID2	MN	DMN	2	10-Jun-1996 06:16:14		469.8	24
ID3	MN	DMN	3	10-Jun-1996 06:18:20		469.8	24
ID2	MN	DMN	2	10-Jun-1996 06:19:08		469.8	9
ID1	MN	DMN	1	10-Jun-1996 06:19:51		469.8	41
ID2	MN	DMN	2	10-Jun-1996 06:21:09		469.8	35
ID3	MN	DMN	3	10-Jun-1996 06:22:15		469.8	9
ID2	MN	DMN	2	10-Jun-1996 06:23:16		469.8	61
ID1	MN	DMN	1	10-Jun-1996 06:23:46		469.8	31
ID2	MN	DMN	2	10-Jun-1996 06:25:46		469.8	36
ID3	MN	DMN	3	10-Jun-1996 06:26:53		469.8	38
ID2	MN	DMN	2	10-Jun-1996 06:27:41		469.8	49
ID1	MN	DMN	1	10-Jun-1996 06:28:11		469.8	111
ID2	MN	DMN	2	10-Jun-1996 06:30:59		469.8	58
ID3	MN	DMN	3	10-Jun-1996 06:31:59		469.8	30
ID2	MN	DMN	2	10-Jun-1996 06:33:36		469.8	15
ID1	MN	DMN	1	10-Jun-1996 06:34:12		469.8	52
ID2	MN	DMN	2	10-Jun-1996 06:37:12		469.8	18
ID3	MN	DMN	3	10-Jun-1996 06:38:06		469.8	18
ID3	MN	DMN	3	10-Jun-1996 07:19:47		469.8	15
LP	MN	DMN	3	10-Jun-1996 07:22:29		469.8	17
FT	MN	FMN	1	10-Jun-1996 07:49:13		469.8	5
LT	MN	FMN	1	10-Jun-1996 07:59:41		469.8	16
F1	IH	1IH	1	11-Jun-1996 12:33:08		537.2	118
L1	IH	1IH	1	11-Jun-1996 14:34:29		537.2	118
A181	IH	8IH	1	11-Jun-1996 16:14:43		537.7	93
F	IH	1IH	1	11-Jun-1996 18:00:44		537.2	150
L	IH	1IH	1	11-Jun-1996 18:16:15		537.2	183

Table A.1 continued

Corr	Detection		Antenna	Date		RKM	Power
	Dam	Site		Recorded			
F	IH	1IH	1	11-Jun-1996 23:41:00		537.2	118
L	IH	1IH	1	11-Jun-1996 23:41:01		537.2	999
A41	IH	4IH	1	12-Jun-1996 06:34:59		537.7	14
A43	IH	4IH	3	12-Jun-1996 06:35:41		537.7	73
A51	IH	5IH	1	12-Jun-1996 06:36:39		537.7	26
A53	IH	5IH	3	12-Jun-1996 06:38:01		537.7	76
A51	IH	5IH	1	12-Jun-1996 06:42:15		537.7	13
E151	IH	5IH	1	12-Jun-1996 06:43:29		537.7	81
I52	IH	5IH	2	12-Jun-1996 06:43:36		537.7	26
I44	IH	4IH	4	12-Jun-1996 06:45:34		537.7	11
I42	IH	4IH	2	12-Jun-1996 06:46:52		537.7	13
I34	IH	3IH	4	12-Jun-1996 06:47:34		537.7	14
I34	IH	3IH	4	12-Jun-1996 06:47:35		537.7	20
I42	IH	4IH	2	12-Jun-1996 06:47:35		537.7	19
IT2	IH	TIH	2	12-Jun-1996 06:48:55		537.7	12
I34	IH	3IH	4	12-Jun-1996 06:49:35		537.7	22
I42	IH	4IH	2	12-Jun-1996 06:50:10		537.7	26
I34	IH	3IH	4	12-Jun-1996 06:50:12		537.7	19
I42	IH	4IH	2	12-Jun-1996 06:50:17		537.7	116
I44	IH	4IH	4	12-Jun-1996 06:50:41		537.7	25
I42	IH	4IH	2	12-Jun-1996 06:51:35		537.7	17
I34	IH	3IH	4	12-Jun-1996 06:52:05		537.7	22
I42	IH	4IH	2	12-Jun-1996 06:52:05		537.7	17
I34	IH	3IH	4	12-Jun-1996 06:52:12		537.7	27
IT2	IH	TIH	2	12-Jun-1996 06:53:18		537.7	26
FP	IH	TIH	3	12-Jun-1996 06:54:39		537.7	27
IT2	IH	TIH	2	12-Jun-1996 06:55:09		537.7	37
IT3	IH	TIH	3	12-Jun-1996 06:55:16		537.7	33
IT4	IH	TIH	4	12-Jun-1996 06:57:49		537.7	39
IT5	IH	TIH	5	12-Jun-1996 07:02:44		537.7	16
LP	IH	TIH	5	12-Jun-1996 07:29:38		537.7	10
FT	IH	9IH	1	12-Jun-1996 08:25:55		537.7	31
LT	IH	9IH	1	12-Jun-1996 08:31:02		537.7	100
F	IH	9IH	2	12-Jun-1996 08:31:03		537.7	90
L	IH	9IH	2	12-Jun-1996 08:43:37		537.7	155
FB	IH	1IH	1	12-Jun-1996 09:30:50		537.2	999
F1 2ND	IH	1IH	1	12-Jun-1996 09:30:51		537.2	147
L	IH	1IH	1	12-Jun-1996 09:36:41		537.2	120
F	IH	1IH	1	13-Jun-1996 07:54:16		537.2	115
L1	IH	1IH	1	13-Jun-1996 08:08:52		537.2	194

Table A.1 continued

Corr	Detection		Antenna	Date	RKM	Power
	Dam	Site		Recorded		
A141	IH	4IH	1	13-Jun-1996 09:36:04	537.7	22
A43	IH	4IH	3	13-Jun-1996 09:36:22	537.7	46
A31	IH	3IH	1	13-Jun-1996 18:42:19	537.7	11
E131	IH	3IH	1	13-Jun-1996 18:42:49	537.7	25
I32	IH	3IH	2	13-Jun-1996 18:42:55	537.7	21
FP	IH	TIH	1	13-Jun-1996 18:44:29	537.7	12
I32	IH	3IH	2	13-Jun-1996 18:46:13	537.7	16
IT1	IH	TIH	1	13-Jun-1996 18:48:49	537.7	15
I32	IH	3IH	2	13-Jun-1996 18:49:08	537.7	15
IT1	IH	TIH	1	13-Jun-1996 18:51:22	537.7	33
I32	IH	3IH	2	13-Jun-1996 18:52:08	537.7	23
X31	IH	3IH	1	13-Jun-1996 18:55:34	537.7	36
A33	IH	3IH	3	13-Jun-1996 18:55:47	537.7	75
A41	IH	4IH	1	13-Jun-1996 18:56:00	537.7	43
A43	IH	4IH	3	13-Jun-1996 18:56:42	537.7	136
A51	IH	5IH	1	13-Jun-1996 18:57:36	537.7	58
A53	IH	5IH	3	13-Jun-1996 18:58:22	537.7	51
A63	IH	6IH	3	13-Jun-1996 18:58:58	537.7	21
A71	IH	7IH	1	13-Jun-1996 18:59:28	537.7	101
E71	IH	7IH	1	13-Jun-1996 18:59:29	537.7	999
I72	IH	7IH	2	13-Jun-1996 18:59:36	537.7	15
I64	IH	6IH	4	13-Jun-1996 19:04:06	537.7	23
I62	IH	6IH	2	13-Jun-1996 19:05:13	537.7	15
I54	IH	5IH	4	13-Jun-1996 19:06:23	537.7	65
I52	IH	5IH	2	13-Jun-1996 19:07:17	537.7	34
I44	IH	4IH	4	13-Jun-1996 19:08:16	537.7	15
I42	IH	4IH	2	13-Jun-1996 19:09:23	537.7	64
I34	IH	3IH	4	13-Jun-1996 19:09:38	537.7	11
I42	IH	4IH	2	13-Jun-1996 19:09:41	537.7	56
I34	IH	3IH	4	13-Jun-1996 19:11:01	537.7	21
I42	IH	4IH	2	13-Jun-1996 19:11:12	537.7	68
I44	IH	4IH	4	13-Jun-1996 19:11:24	537.7	14
I52	IH	5IH	2	13-Jun-1996 19:11:43	537.7	36
I44	IH	4IH	4	13-Jun-1996 19:13:06	537.7	16
I42	IH	4IH	2	13-Jun-1996 19:14:13	537.7	14
I34	IH	3IH	4	13-Jun-1996 19:14:37	537.7	20
I42	IH	4IH	2	13-Jun-1996 19:14:37	537.7	73
I34	IH	3IH	4	13-Jun-1996 19:14:43	537.7	27
I42	IH	4IH	2	13-Jun-1996 19:14:43	537.7	48
I34	IH	3IH	4	13-Jun-1996 19:14:49	537.7	38

Table A.1 continued

Corr	Detection		Antenna	Date	RKM	Power
	Dam	Site		Recorded		
I42	IH	4IH	2	13-Jun-1996 19:14:49	537.7	16
I34	IH	3IH	4	13-Jun-1996 19:14:55	537.7	84
IT2	IH	TIH	2	13-Jun-1996 19:15:42	537.7	14
IT3	IH	TIH	3	13-Jun-1996 19:16:51	537.7	10
IT2	IH	TIH	2	13-Jun-1996 19:18:12	537.7	97
IT3	IH	TIH	3	13-Jun-1996 19:18:19	537.7	102
IT4	IH	TIH	4	13-Jun-1996 19:19:35	537.7	31
IT5	IH	TIH	5	13-Jun-1996 19:25:13	537.7	9
LP	IH	TIH	5	13-Jun-1996 19:28:38	537.7	17
FT	IH	9IH	1	13-Jun-1996 20:36:45	537.7	31
LT	IH	9IH	1	13-Jun-1996 20:41:07	537.7	50
EFB	IH	9IH	1	13-Jun-1996 20:41:08	537.7	999
F	IH	9IH	2	13-Jun-1996 20:41:14	537.7	75
L	IH	9IH	2	13-Jun-1996 20:53:32	537.7	18
F	IH	9IH	2	14-Jun-1996 02:09:45	537.7	15
L	IH	9IH	2	14-Jun-1996 03:34:05	537.7	15
F		2CH	1	14-Jun-1996 04:45:41	538.9	119
L		1CH	1	14-Jun-1996 05:19:06	539.4	130
F1	LM	1LM	1	14-Jun-1996 21:51:55	588.6	118
L	LM	1LM	1	14-Jun-1996 22:14:04	588.6	116
F	LM	1LM	1	15-Jun-1996 06:47:16	588.6	141
L	LM	1LM	1	15-Jun-1996 06:56:16	588.6	140
F	LM	1LM	1	15-Jun-1996 20:56:11	588.6	134
L	LM	1LM	1	15-Jun-1996 21:13:22	588.6	147
F	LM	1LM	1	16-Jun-1996 07:03:25	588.6	136
L1	LM	1LM	1	16-Jun-1996 07:24:25	588.6	122
WMBT		TUC	8	21-Jun-1996 12:40:00	661.6	3310
WMBT-T		TUC	8	23-Jun-1996 10:00:00	641.9	3330
WMBT		TUC	8	26-Jun-1996 13:08:00	651.3	3334
WMBT		TUC	8	28-Jun-1996 13:30:00	653.9	3338
WMBT		TUC	8	1-Jul-1996 11:00:00	661.6	3320
WMBT		TUC	8	5-Jul-1996 12:15:00	674.1	3325
WMBT		TUC	8	8-Jul-1996 10:02:00	678.9	3327
WMBT		TUC	8	11-Jul-1996 15:15:00	678.9	3407
WMBT		TUC	8	15-Jul-1996 12:20:00	679.0	3406
WMBT		TUC	8	22-Jul-1996 12:37:00	679.0	3401
WMBT		TUC	8	25-Jul-1996 12:19:00	679.0	3398
WMBT		TUC	8	29-Jul-1996 15:36:00	679.0	3397
WMBT		TUC	8	5-Aug-1996 11:20:00	679.0	3377
WMBT		TUC	8	19-Aug-1996 10:41:00	679.0	3380

Table A.1 continued

Corr	Dam	Detection		Date		RKM	Power
		Site	Antenna	Recorded			
WMBT		TUC	8	19-Aug-1996 12:13:00		679.0	3384
WMBT		TUC	8	21-Aug-1996 12:15:00		679.0	3381
WMBT		TUC	8	22-Aug-1996 08:57:00		679.0	3387
WMBT		TUC	8	28-Aug-1996 14:30:00		685.5	3271
WMBT		TUC	8	29-Aug-1996 15:30:00		681.7	3295
WMBT		TUC	8	3-Sep-1996 15:35:00		681.1	3280
WMBT		TUC	8	4-Sep-1996 14:35:00		681.1	3283
WMBT		TUC	8	5-Sep-1996 12:10:00		681.1	3286
WMBT		TUC	8	9-Sep-1996 13:00:00		680.4	3289
WMBT		TUC	8	10-Sep-1996 12:35:00		680.3	3292
WMBT		TUC	8	11-Sep-1996 13:45:00		679.8	3277
WMBT		TUC	8	12-Sep-1996 13:14:00		680.0	3274
WMBT		TUC	8	13-Sep-1996 12:35:00		680.7	3258
WMBT-T		TUC	8	16-Sep-1996 10:00:00		679.8	3260
RCP		TUC	8	16-Sep-1996 23:59:00		679.8	320

Appendix B

VARIANCE FORMULAS FOR \hat{S}_{SYS} AND $\hat{\mu}_R$ **B.1 Variance formulas for \hat{S}_{sys}**

The parameter S_{sys} is the perceived system survival, or the probability of surviving and remaining in the migrating population from the release to the top of the final dam. For all models, S_{sys} is defined in terms of the recursive parameters η_i . In general,

$$S_{sys} = \eta_R.$$

Variance estimators and partial derivatives will be given in terms of the η_i parameters.

B.1.1 Model 0

For Model 0, η_R is a function of the parameters $\phi_{R,D_{1T}}$ and $\phi_{D_{kT},D_{k+1,T}}$ for $k = 1, \dots, K-1$. The variance of $\hat{\eta}_R$ can be estimated by the following equation:

$$\begin{aligned} \widehat{Var}(\hat{\eta}_R) = \hat{\eta}_R^2 \left\{ \widehat{CV}^2(\hat{\phi}_{R,D_{1T}}) + 2 \sum_{k=1}^{K-1} \frac{\widehat{Cov}(\hat{\phi}_{R,D_{1T}}, \hat{\phi}_{D_{kT},D_{k+1,T}})}{\hat{\phi}_{R,D_{1T}} \hat{\phi}_{D_{kT},D_{k+1,T}}} + \right. \\ \left. \sum_{k=1}^{K-1} \sum_{j=1}^{K-1} \frac{\widehat{Cov}(\hat{\phi}_{D_{kT},D_{k+1,T}}, \hat{\phi}_{D_{jT},D_{j+1,T}})}{\hat{\phi}_{D_{kT},D_{k+1,T}} \hat{\phi}_{D_{jT},D_{j+1,T}}} \right\}, \end{aligned} \quad (B.1)$$

where $\widehat{CV}(\hat{\phi}_{R,D_{1T}}) = \frac{SE(\hat{\phi}_{R,D_{1T}})}{\hat{\phi}_{R,D_{1T}}}$ is the coefficient of variation of $\hat{\phi}_{R,D_{1T}}$. Under the assumption of 100% detection at site D_{KT} , $\phi_{D_{KT},D_{KT}} = \lambda$.

B.1.2 Models 1 and 2

For Models 1 and 2, η_R is a function of the parameters $\phi_{R,D_{1B}}$, $\phi_{D_{kB},D_{kT}}$ ($k = 1, \dots, K$), and $\phi_{D_{kT},D_{k+1,B}}$ ($k = 1, \dots, K-1$). The variance of $\hat{\eta}_R$ can be estimated by the following

equation:

$$\begin{aligned} \widehat{Var}(\widehat{\eta}_R) = \widehat{\eta}_R^2 & \left\{ \widehat{CV}^2(\widehat{\phi}_{R,D_{1B}}) + \sum_{k=1}^{K-1} \sum_{j=1}^{K-1} \frac{\widehat{Cov}(\widehat{\phi}_{D_{kB},D_{kT}}, \widehat{\phi}_{D_{jB},D_{jT}})}{\widehat{\phi}_{D_{kB},D_{kT}} \widehat{\phi}_{D_{jB},D_{jT}}} + \right. \\ & \sum_{k=1}^{K-1} \sum_{j=1}^{K-1} \left\{ \frac{\widehat{Cov}(\widehat{\phi}_{D_{kT},D_{k+1,B}}, \widehat{\phi}_{D_{jT},D_{j+1,B}})}{\widehat{\phi}_{D_{kT},D_{k+1,B}} \widehat{\phi}_{D_{jT},D_{j+1,B}}} + 2 \frac{\widehat{Cov}(\widehat{\phi}_{D_{kB},D_{kT}}, \widehat{\phi}_{D_{jT},D_{j+1,B}})}{\widehat{\phi}_{D_{kB},D_{kT}} \widehat{\phi}_{D_{jT},D_{j+1,B}}} \right\} + \\ & \left. 2 \sum_{k=1}^{K-1} \left\{ \frac{\widehat{Cov}(\widehat{\phi}_{R,D_{1B}}, \widehat{\phi}_{D_{kB},D_{kT}})}{\widehat{\phi}_{R,D_{1B}} \widehat{\phi}_{D_{kB},D_{kT}}} + \frac{\widehat{Cov}(\widehat{\phi}_{R,D_{1B}}, \widehat{\phi}_{D_{kT},D_{k+1,B}})}{\widehat{\phi}_{R,D_{1B}} \widehat{\phi}_{D_{kT},D_{k+1,B}}} \right\} \right\}, \quad (B.2) \end{aligned}$$

where $CV(\widehat{\phi}_{R,D_{1B}}) = \frac{SE(\widehat{\phi}_{R,D_{1B}})}{\widehat{\phi}_{R,D_{1B}}}$ is the coefficient of variation of $\widehat{\phi}_{R,D_{1B}}$. For Model 1, $\phi_{D_{kB},D_{kT}} = \lambda$ under the assumption of 100% detection at site D_{kT} .

B.1.3 Model 3a

Define $\Theta_{3a(\eta_R)}$ to be the set composed of the following parameters:

$$\begin{array}{llll} \phi_{D_{kB},D_{kT}} & k = 2, \dots, K; & \phi_{D_{kT},T_k} & k = 1, \dots, K-1; \\ \phi_{D_{kT},D_{k+1,B}} & k = 1, \dots, K-1; & \phi_{T_k,D_{k+1,B}} & k = 1, \dots, K-1. \end{array}$$

For Model 3a, η_R is a function of the parameters ϕ_{R,T_0} , $\phi_{R,D_{1B}}$, $\phi_{D_{1B},D_{1T}}$, and $\phi_{T_0,D_{1B}}$, and the parameters in the set $\Theta_{3a(\eta_R)}$. The variance of $\widehat{\eta}_R$ can be estimated by the following:

$$\begin{aligned} \widehat{Var}(\widehat{\eta}_R) = & \left(\frac{\partial \eta_R}{\partial \phi_{R,T_0}} \right)^2 \widehat{Var}(\widehat{\phi}_{R,T_0}) + \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} \right)^2 \widehat{Var}(\widehat{\phi}_{R,D_{1B}}) \\ & + \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right)^2 \widehat{Var}(\widehat{\phi}_{D_{1B},D_{1T}}) + \left(\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} \right)^2 \widehat{Var}(\widehat{\phi}_{T_0,D_{1B}}) \\ & + \sum_{\theta \in \Theta_{3a(\eta_R)}} \sum_{\psi \in \Theta_{3a(\eta_R)}} \left(\frac{\partial \eta_R}{\partial \theta} \right) \left(\frac{\partial \eta_R}{\partial \psi} \right) \widehat{Cov}(\widehat{\theta}, \widehat{\psi}) \\ & + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} \right) \widehat{Cov}(\widehat{\phi}_{R,T_0}, \widehat{\phi}_{R,D_{1B}}) \\ & + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\phi}_{R,T_0}, \widehat{\phi}_{D_{1B},D_{1T}}) \end{aligned}$$

$$\begin{aligned}
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{R_0,D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R,T_0}, \hat{\phi}_{T_0,D_{1B}}) \\
& + 2 \sum_{\theta \in \Theta_{3a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R,T_0}, \hat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\phi}_{R,D_{1B}}, \hat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R,D_{1B}}, \hat{\phi}_{T_0,D_{1B}}) \\
& + 2 \sum_{\theta \in \Theta_{3a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R,D_{1B}}, \hat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{D_{1B},D_{1T}}, \hat{\phi}_{T_0,D_{1B}}) \\
& + 2 \sum_{\theta \in \Theta_{3a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{D_{1B},D_{1T}}, \hat{\theta}) \\
& + 2 \sum_{\theta \in \Theta_{3a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{T_0,D_{1B}}, \hat{\theta}), \tag{B.3}
\end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The necessary partial derivatives are the following:

$$\begin{aligned}
\frac{\partial \eta_R}{\partial \phi_{R,T_0}} &= \phi_{T_0,D_{1B}} \phi_{D_{1B},D_{1T}} \eta_{D_{1T}}; \\
\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} &= \phi_{R,T_0} \phi_{D_{1B},D_{1T}} \eta_{D_{1T}}; \\
\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} &= \phi_{D_{1B},D_{1T}} \eta_{D_{1T}}; \\
\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} &= \frac{\eta_R}{\phi_{D_{1B},D_{1T}}};
\end{aligned}$$

for $\theta \in \Theta_{3a}(\eta_R)$,

$$\frac{\partial \eta_R}{\partial \theta} = \frac{\eta_R}{\eta_{D_{1T}}} \frac{\partial \eta_{D_{1T}}}{\partial \theta},$$

where $\frac{\partial \eta_{D_{kT}}}{\partial \theta}$ is defined below.

Define $\Theta_{3a(\eta_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1, B}} & \quad j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1, B}} & \quad j = k+1, \dots, K-1. \end{aligned}$$

For $k = 1, \dots, K-1$, the parameter $\eta_{D_{kT}}$ is a function of the parameters $\phi_{D_{k+1, B}, D_{k+1, T}}$, ϕ_{D_{kT}, T_k} , $\phi_{D_{kT}, D_{k+1, B}}$, and $\phi_{T_k, D_{k+1, B}}$; for $k = 1, \dots, K-2$, $\eta_{D_{kT}}$ is also a function of the parameters in the set $\Theta_{3a(\eta_{D_{kT}})}$. The partial derivatives necessary for Equation (B.3) that involve $\eta_{D_{kT}}$ are below:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1, B}, D_{k+1, T}}} &= \frac{\eta_{D_{kT}}}{\phi_{D_{k+1, B}, D_{k+1, T}}}; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}} &= \phi_{T_k, D_{k+1, B}} \phi_{D_{k+1, B}, D_{k+1, T}} \eta_{D_{k+1, T}}; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1, B}}} &= \phi_{D_{k+1, B}, D_{k+1, T}} \eta_{D_{k+1, T}}; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{T_k, D_{k+1, B}}} &= \phi_{D_{kT}, T_k} \phi_{D_{k+1, B}, D_{k+1, T}} \eta_{D_{k+1, T}}; \end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{3a(\eta_{D_{kT}})}$,

$$\frac{\partial \eta_{D_{kT}}}{\partial \theta} = \frac{\eta_{D_{kT}}}{\eta_{D_{k+1, T}}} \frac{\partial \eta_{D_{k+1, T}}}{\partial \theta}.$$

B.1.4 Model 3b

Define the set $\Theta_{3b(\eta_R)}$ to be the following parameters:

$$\begin{array}{llll}
 \phi_{D_{kB}, D_{kT}} & k = 2, \dots, K; & \phi_{D_{kB}, D_{kT}}^T & k = 2, \dots, K; \\
 \phi_{D_{kT}, T_k} & k = 1, \dots, K-1; & \phi_{D_{kT}, T_k}^T & k = 1, \dots, K-1; \\
 \phi_{D_{kT}, D_{k+1, B}} & k = 1, \dots, K-1; & \phi_{D_{kT}, D_{k+1, B}}^T & k = 1, \dots, K-1; \\
 \phi_{T_k, D_{k+1, B}} & k = 1, \dots, K-1; & \phi_{T_k, D_{k+1, B}}^T & k = 1, \dots, K-1.
 \end{array}$$

For Model 3b, η_R is a function of the parameters ϕ_{R, T_0} , $\phi_{R, D_{1B}}$, $\phi_{T_0, D_{1B}}$, $\phi_{D_{1B}, D_{1T}}$, $\phi_{D_{1B}, D_{1T}}^T$, and the parameters in the set $\Theta_{3b(\eta_R)}$. The variance of $\hat{\eta}_R$ can be estimated by the following:

$$\begin{aligned}
 \widehat{Var}(\hat{\eta}_R) = & \left(\frac{\partial \eta_R}{\partial \phi_{R, T_0}} \right)^2 \widehat{Var}(\hat{\phi}_{R, T_0}) + \left(\frac{\partial \eta_R}{\partial \phi_{R, D_{1B}}} \right)^2 \widehat{Var}(\hat{\phi}_{R, D_{1B}}) \\
 & + \left(\frac{\partial \eta_R}{\partial \phi_{T_0, D_{1B}}} \right)^2 \widehat{Var}(\hat{\phi}_{T_0, D_{1B}}) + \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}) \\
 & + \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}^T} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}^T) + \sum_{\theta \in \Theta_{3b(\eta_R)}} \sum_{\psi \in \Theta_{3b(\eta_R)}} \left(\frac{\partial \eta_R}{\partial \theta} \right) \left(\frac{\partial \eta_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\
 & + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{R, D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\phi}_{R, D_{1B}}) \\
 & + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{T_0, D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\phi}_{T_0, D_{1B}}) \\
 & + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\phi}_{D_{1B}, D_{1T}}) \\
 & + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}^T} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\phi}_{D_{1B}, D_{1T}}^T) \\
 & + 2 \sum_{\theta \in \Theta_{3b(\eta_R)}} \left(\frac{\partial \eta_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\theta}) \\
 & + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R, D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{T_0, D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R, D_{1B}}, \hat{\phi}_{T_0, D_{1B}})
 \end{aligned}$$

$$\begin{aligned}
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\phi}_{R,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^T} \right) \widehat{Cov}(\widehat{\phi}_{R,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}^T) \\
& + 2 \sum_{\theta \in \Theta_{3b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{R,D_{1B}}, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\phi}_{T_0,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^T} \right) \widehat{Cov}(\widehat{\phi}_{T_0,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}^T) \\
& + 2 \sum_{\theta \in \Theta_{3b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{T_0,D_{1B}}, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^T} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\phi}_{D_{1B},D_{1T}}^T) \\
& + 2 \sum_{\theta \in \Theta_{3b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\theta}) \\
& + 2 \sum_{\theta \in \Theta_{3b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^T} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}^T, \widehat{\theta}), \tag{B.4}
\end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The partial derivatives necessary for Equation (B.4) are:

$$\begin{aligned}
\frac{\partial \eta_R}{\partial \phi_{R,T_0}} &= \phi_{T_0,D_{1B}} \phi_{D_{1B},D_{1T}}^T \eta_{D_{1T}}^T; \\
\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}} &= \phi_{D_{1B},D_{1T}} \eta_{D_{1T}}; \\
\frac{\partial \eta_R}{\partial \phi_{T_0,D_{1B}}} &= \phi_{R,T_0} \phi_{D_{1B},D_{1T}}^T \eta_{D_{1T}}^T; \\
\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} &= \phi_{R,D_{1B}} \eta_{D_{1T}}; \\
\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^T} &= \phi_{R,T_0}, \phi_{T_0,D_{1B}} \eta_{D_{1T}}^T;
\end{aligned}$$

$$\frac{\partial \eta_R}{\partial \eta_{D_{1T}}} = \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}};$$

$$\frac{\partial \eta_R}{\partial \eta_{D_{1T}}^T} = \phi_{R,T_0} \phi_{T_0,D_{1B}} \phi_{D_{1B},D_{1T}}^T;$$

for $\theta \in \Theta_{3b(\eta_R)}$,

$$\frac{\partial \eta_R}{\partial \theta} = \frac{\partial \eta_R}{\partial \eta_{D_{1T}}^T} \frac{\partial \eta_{D_{1T}}^T}{\partial \theta} + \frac{\partial \eta_R}{\partial \eta_{D_{1T}}} \frac{\partial \eta_{D_{1T}}}{\partial \theta},$$

where $\frac{\partial \eta_{D_{1T}}^T}{\partial \theta}$ and $\frac{\partial \eta_{D_{1T}}}{\partial \theta}$ are defined below. Define the set $\Theta_{3b(\eta_{D_{kT}})}$ to be the following parameters:

$$\begin{array}{llll} \phi_{D_{jB},D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jB},D_{jT}}^T & j = k+2, \dots, K; \\ \phi_{D_{jT},T_j} & j = k+1, \dots, K-1; & \phi_{D_{jT},T_j}^T & j = k+1, \dots, K-1; \\ \phi_{D_{jT},D_{j+1,B}} & j = k+1, \dots, K-1; & \phi_{D_{jT},D_{j+1,B}}^T & j = k+1, \dots, K-1; \\ \phi_{T_j,D_{j+1,B}} & j = k+1, \dots, K-1; & \phi_{T_j,D_{j+1,B}}^T & j = k+1, \dots, K-1. \end{array}$$

The parameter $\eta_{D_{kT}}$ is a function of the parameters $\phi_{D_{k+1,B},D_{k+1,T}}$, $\phi_{D_{k+1,B},D_{k+1,T}}^T$, ϕ_{D_{kT},T_k} , $\phi_{D_{kT},D_{k+1,B}}$, and $\phi_{T_k,D_{k+1,B}}$ for $k = 1, \dots, K-1$; for $k = 1, \dots, K-2$, $\eta_{D_{kT}}$ is also a function of the parameters in the set $\Theta_{3b(\eta_{D_{kT}})}$. The partial derivatives involving $\eta_{D_{kT}}$ that are necessary for Equation (B.4) are the following:

for $k = 1, \dots, K-1$:

$$\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1,B},D_{k+1,T}}} = \phi_{D_{kT},D_{k+1,B}} \eta_{D_{k+1,T}};$$

$$\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1,B},D_{k+1,T}}^T} = \phi_{D_{kT},T_k} \phi_{T_k,D_{k+1,B}} \eta_{D_{k+1,T}}^T;$$

$$\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k,T},T_k}} = \phi_{T_k,D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}}^T \eta_{D_{k+1,T}}^T;$$

$$\begin{aligned}
\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1}, B}} &= \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \phi_{T_k, D_{k+1}, B}} &= \phi_{D_{kT}, T_k} \phi_{D_{k+1}, B, D_{k+1}, T}^T \eta_{D_{k+1}, T}^T; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, T}} &= \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, T}^T} &= \phi_{D_{kT}, T_k} \phi_{T_k, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^T.
\end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{3b(\eta_{D_{kT}})}$,

$$\frac{\partial \eta_{D_{kT}}}{\partial \theta} = \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, T}} \frac{\partial \eta_{D_{k+1}, T}}{\partial \theta} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, T}^T} \frac{\partial \eta_{D_{k+1}, T}^T}{\partial \theta},$$

where $\frac{\partial \eta_{D_{k+1}, T}^T}{\partial \theta}$ is defined below.

The parameter $\eta_{D_{kT}}^T$ is a function of the parameters $\phi_{D_{k+1}, B, D_{k+1}, T}$, $\phi_{D_{k+1}, B, D_{k+1}, T}^T$, ϕ_{D_{kT}, T_k}^T , $\phi_{D_{kT}, D_{k+1}, B}^T$, and $\phi_{T_k, D_{k+1}, B}^T$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\eta_{D_{kT}}^T$ is also a function of the parameters in the set $\Theta_{3b(\eta_{D_{kT}})}$. The partial derivatives involving $\eta_{D_{kT}}^T$ that are necessary for Equation (B.4) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned}
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= \phi_{D_{kT}, D_{k+1}, B}^T \eta_{D_{k+1}, T}^T; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^T} &= \phi_{D_{kT}, T_k}^T \phi_{T_k, D_{k+1}, B}^T \eta_{D_{k+1}, T}^T; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{T_k, D_{k+1}, B}^T} &= \phi_{T_k, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T}^T \eta_{D_{k+1}, T}^T; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{kT}, D_{k+1}, B}^T} &= \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T}; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{T_k, D_{k+1}, B}^T} &= \phi_{D_{kT}, T_k}^T \phi_{D_{k+1}, B, D_{k+1}, T}^T \eta_{D_{k+1}, T}^T;
\end{aligned}$$

$$\frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{D_{k+1,T}}} = \phi_{D_{kT}, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T}^T;$$

$$\frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{D_{k+1,T}}^T} = \phi_{D_{kT}, T_k}^T \phi_{T_k, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T}^T;$$

for $k = 1, \dots, K - 2$ and $\theta \in \Theta_{3b(\eta_{D_{kT}})}$,

$$\frac{\partial \eta_{D_{kT}}^T}{\partial \theta} = \frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{D_{k+1,T}}} \frac{\partial \eta_{D_{k+1,T}}}{\partial \theta} + \frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{D_{k+1,T}}^T} \frac{\partial \eta_{D_{k+1,T}}^T}{\partial \theta},$$

where $\frac{\partial \eta_{D_{k+1,T}}}{\partial \theta}$ is defined above.

B.1.5 Model 4

Define the set $\Theta_{4(\eta_R)}$ to contain the following parameters:

$$\begin{array}{llll} \phi_{D_{kB}, D_{kT}} & k = 2, \dots, K; & \phi_{D_{kB}, D_{kT}}^F & k = 2, \dots, K; \\ \phi_{D_{kT}, D_{k+1}, B} & k = 1, \dots, K - 1; & \phi_{D_{kT}, D_{k+1}, B}^F & k = 1, \dots, K - 1; \\ f_{D_{kT}} & k = 1, \dots, K - 1. & & \end{array}$$

For Model 4, η_R is a function of the parameters in set $\Theta_{4(\eta_R)}$, as well as $\Phi_{R, D_{1B}}$, $\Phi_{R, D_{1B}}^F$, $\phi_{D_{1B}, D_{1T}}$, and $\phi_{D_{1B}, D_{1T}}^F$. The variance of $\hat{\eta}_R$ can be estimated by the following expression:

$$\begin{aligned} \widehat{Var}(\hat{\eta}_R) &= \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}) + \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}^F) \\ &+ \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}) + \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}^F) \\ &+ \sum_{\theta \in \Theta_{4(\eta_R)}} \sum_{\psi \in \Theta_{4(\eta_R)}} \left(\frac{\partial \eta_R}{\partial \theta} \right) \left(\frac{\partial \eta_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\ &+ 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R, D_{1B}}, \hat{\Phi}_{R, D_{1B}}^F) \\ &+ 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R, D_{1B}}, \hat{\phi}_{D_{1B}, D_{1T}}) \end{aligned}$$

$$\begin{aligned}
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_4(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\phi}_{R,D_{1B}}^F, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\phi}_{R,D_{1B}}^F, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_4(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{R,D_{1B}}^F, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_4(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\theta}) \\
& + 2 \sum_{\theta \in \Theta_4(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}^F, \widehat{\theta}), \tag{B.5}
\end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The partial derivatives necessary for Equation (B.5) are:

$$\begin{aligned}
\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} &= \phi_{D_{1B},D_{1T}} \eta_{D_{1T}}; & \frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} &= \phi_{D_{1B},D_{1T}}^F \eta_{D_{1T}}^F; \\
\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} &= \Phi_{R,D_{1B}} \eta_{D_{1T}}; & \frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} &= \Phi_{R,D_{1B}}^F \eta_{D_{1T}}^F;
\end{aligned}$$

for $\theta \in \Theta_4(\eta_R)$,

$$\frac{\partial \eta_R}{\partial \theta} = \Phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \frac{\partial \eta_{D_{1T}}}{\partial \theta} + \Phi_{R,D_{1B}}^F \phi_{D_{1B},D_{1T}}^F \frac{\partial \eta_{D_{1T}}^F}{\partial \theta},$$

where $\frac{\partial \eta_{D_{1T}}}{\partial \theta}$ and $\frac{\partial \eta_{D_{1T}}^F}{\partial \theta}$ are defined below. Define the set $\Theta_{4(\eta_{D_{kT}})}$ to contain the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jB}, D_{jT}}^F & \quad j = k+2, \dots, K; \\ \phi_{D_{jT}, D_{j+1, B}} & \quad j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1, B}}^F & \quad j = k+1, \dots, K-1; \\ f_{D_{jT}} & \quad j = k+1, \dots, K-1. \end{aligned}$$

The parameter $\eta_{D_{kT}}$ is a function of the models parameters $\phi_{D_{k+1, B}, D_{k+1, T}}$, $\phi_{D_{k+1, B}, D_{k+1, T}}^F$, $\phi_{D_{kT}, D_{k+1, B}}$, $\phi_{D_{kT}, D_{k+1, B}}^F$, and $f_{D_{kT}}$ for $k = 1, \dots, K-1$; for $k = 1, \dots, K-2$, $\eta_{D_{kT}}$ is also a function of the parameters in the set $\Theta_{4(\eta_{D_{kT}})}$. The partial derivatives involving $\eta_{D_{kT}}$ that are necessary for Equation (B.5) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1, B}, D_{k+1, T}}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, D_{k+1, B}} \eta_{D_{k+1, T}}; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1, B}, D_{k+1, T}}^F} &= f_{D_{kT}} \phi_{D_{kT}, D_{k+1, B}}^F \eta_{D_{k+1, T}}^F; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1, B}}} &= (1 - f_{D_{kT}}) \phi_{D_{k+1, B}, D_{k+1, T}} \eta_{D_{k+1, T}}; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1, B}}^F} &= f_{D_{kT}} \phi_{D_{k+1, B}, D_{k+1, T}}^F \eta_{D_{k+1, T}}^F; \\ \frac{\partial \eta_{D_{kT}}}{\partial f_{D_{kT}}} &= -\phi_{D_{kT}, D_{k+1, B}} \phi_{D_{k+1, B}, D_{k+1, T}} \eta_{D_{k+1, T}} + \phi_{D_{kT}, D_{k+1, B}}^F \phi_{D_{k+1, B}, D_{k+1, T}}^F \eta_{D_{k+1, T}}^F; \end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{4(\eta_{D_{kT}})}$,

$$\frac{\partial \eta_{D_{kT}}}{\partial \theta} = \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1, T}}} \frac{\partial \eta_{D_{k+1, T}}}{\partial \theta} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1, T}}^F} \frac{\partial \eta_{D_{k+1, T}}^F}{\partial \theta},$$

where

$$\begin{aligned}\frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1,T}}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}, & k = 1, \dots, K-1; \\ \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, t}^F} &= f_{D_{kT}} \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F, & k = 1, \dots, K-1;\end{aligned}$$

and $\frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta}$ is defined below. Define the set $\Theta_{4(\eta_{D_{kT}}^F)}$ to contain the following parameters:

$$\phi_{D_{jB}, D_{jT}}^F \quad j = k+2, \dots, K; \quad \phi_{D_{jT}, D_{j+1}, B}^F \quad j = k+1, \dots, K-1.$$

The parameter $\eta_{D_{kT}}^F$ ($k = 1, \dots, K-1$) is a function of the model parameters $\phi_{D_{k+1}, B, D_{k+1}, T}^F$ and $\phi_{D_{kT}, D_{k+1}, B}^F$ for $k = 1, \dots, K-1$, and also of the parameters in the set $\Theta_{4(\eta_{D_{kT}}^F)}$ for $k = 1, \dots, K-2$. The partial derivatives involving $\eta_{D_{kT}}^F$ that are necessary for Equation (B.5) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned}\frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= \phi_{D_{kT}, D_{k+1}, B}^F \eta_{D_{k+1}, T}^F; \\ \frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{D_{kT}, D_{k+1}, B}^F} &= \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F; \\ \frac{\partial \eta_{D_{kT}}^F}{\partial \eta_{D_{k+1}, T}^F} &= \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F;\end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{4(\eta_{D_{kT}}^F)}$,

$$\frac{\partial \eta_{D_{kT}}^F}{\partial \theta} = \frac{\partial \eta_{D_{kT}}^F}{\partial \eta_{D_{k+1}, T}^F} \frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta}.$$

B.1.6 Model 5a

Define $\Theta_{5a(\eta_R)}$ to be the set composed of the following model parameters:

$$\begin{array}{llll}
 \phi_{D_{kB}, D_{kT}} & k = 2, \dots, K; & \phi_{D_{kB}, D_{kT}}^F & k = 2, \dots, K; \\
 \phi_{D_{kT}, T_k} & k = 1, \dots, K-1; & \phi_{D_{kT}, T_k}^F & k = 1, \dots, K-1; \\
 \phi_{D_{kT}, D_{k+1, B}} & k = 1, \dots, K-1; & \phi_{D_{kT}, D_{k+1, B}}^F & k = 1, \dots, K-1; \\
 \phi_{T_k, D_{k+1, B}} & k = 0, \dots, K-1; & \phi_{T_k, D_{k+1, B}}^F & k = 0, \dots, K-1; \\
 f_{D_{kT}} & k = 1, \dots, K-1. & f_{T_k} & k = 0, \dots, K-1.
 \end{array}$$

For Model 5a, η_R is a function of the parameters Φ_{R, T_0} , Φ_{R, T_0}^F , $\Phi_{R, D_{1B}}$, $\Phi_{R, D_{1B}}^F$, $\phi_{D_{1B}, D_{1T}}$, and $\phi_{D_{1B}, D_{1T}}^F$, and the parameters in set $\Theta_{5a(\eta_R)}$. The variance of $\hat{\eta}_R$ can be estimated by the following expression for Model 5a:

$$\begin{aligned}
 \widehat{Var}(\hat{\eta}_R) &= \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, T_0}) + \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, T_0}^F) \\
 &+ \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}) + \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}^F) \\
 &+ \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}) + \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}^F) \\
 &+ \sum_{\theta \in \Theta_{5a(\eta_R)}} \sum_{\psi \in \Theta_{5a(\eta_R)}} \left(\frac{\partial \eta_R}{\partial \theta} \right) \left(\frac{\partial \eta_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\
 &+ 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}^F} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\Phi}_{R, T_0}^F) \\
 &+ 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\Phi}_{R, D_{1B}}) \\
 &+ 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\Phi}_{R, D_{1B}}^F) \\
 &+ 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\phi}_{D_{1B}, D_{1T}}) \\
 &+ 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\phi}_{D_{1B}, D_{1T}}^F)
 \end{aligned}$$

$$\begin{aligned}
& + 2 \sum_{\theta \in \Theta_{\delta a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\Phi}_{R,D_{1B}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{\delta a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{\delta a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{\delta a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{\delta a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\theta})
\end{aligned}$$

$$+ 2 \sum_{\theta \in \Theta_{5a}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{D_{1B}, D_{1T}}^F, \hat{\theta}), \quad (\text{B.6})$$

where the partial derivatives are evaluated at their MLEs. The partial derivatives necessary for Equation (B.6) are the following:

$$\begin{aligned} \frac{\partial \eta_R}{\partial \Phi_{R, T_0}} &= \eta_{T_0}; & \frac{\partial \eta_R}{\partial \Phi_{R, T_0}^F} &= \eta_{T_0}^F; \\ \frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}} &= \phi_{D_{1B}, D_{1T}} \eta_{D_{1T}}; & \frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}^F} &= \phi_{D_{1B}, D_{1T}}^F \eta_{D_{1T}}^F; \end{aligned}$$

and

$$\begin{aligned} \frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}} &= \Phi_{R, T_0} \frac{\partial \eta_{T_0}}{\partial \phi_{D_{1B}, D_{1T}}} + \Phi_{R, D_{1B}} \eta_{D_{1T}}; \\ \frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}^F} &= \Phi_{R, T_0} \frac{\partial \eta_{T_0}}{\partial \phi_{D_{1B}, D_{1T}}^F} + \Phi_{R, T_0}^F \frac{\partial \eta_{T_0}^F}{\partial \phi_{D_{1B}, D_{1T}}^F} + \Phi_{R, D_{1B}}^F \eta_{D_{1T}}^F; \\ \frac{\partial \eta_R}{\partial \theta} &= \Phi_{R, T_0} \frac{\partial \eta_{T_0}}{\partial \theta} + \Phi_{R, D_{1B}} \phi_{D_{1B}, D_{1T}} \frac{\partial \eta_{D_{1T}}}{\partial \theta} + \Phi_{R, T_0}^F \frac{\partial \eta_{T_0}^F}{\partial \theta} + \Phi_{R, D_{1B}}^F \phi_{D_{1B}, D_{1T}}^F \frac{\partial \eta_{D_{1T}}^F}{\partial \theta}, \end{aligned}$$

for any parameter $\theta \in \Theta_{5a}(\eta_R)$.

The partial derivatives involving η_{T_0} , $\eta_{T_0}^F$, $\eta_{D_{kT}}$, and $\eta_{D_{1T}}^F$ are defined below.

Define $\Theta_{5a(\eta_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{T_j, D_{j+1}, B} & \quad j = k, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^F & \quad j = k, \dots, K-1; \\ f_{T_j} & \quad j = k, \dots, K-1. \end{aligned}$$

Define $\Theta'_{5a(\eta_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{array}{llll} \phi_{D_{jB}, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jB}, D_{jT}}^F & j = k+2, \dots, K; \\ \phi_{D_{jT}, T_j} & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^F & j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B} & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B}^F & j = k+1, \dots, K-1; \\ f_{D_{jT}} & j = k+1, \dots, K-1. & & \end{array}$$

The parameter $\eta_{D_{kT}}$ is a function of the model parameters $\phi_{D_{k+1}, B, D_{k+1}, T}$, $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, ϕ_{D_{kT}, T_k} , ϕ_{D_{kT}, T_k}^F , $\phi_{D_{kT}, D_{k+1}, B}$, $\phi_{D_{kT}, D_{k+1}, B}^F$, $f_{D_{kT}}$ and the parameters in the set $\Theta_{5a(\eta_{D_{kT}})}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\eta_{D_{kT}}$ is also a function of the parameters in the set $\Theta'_{5a(\eta_{D_{kT}})}$. The partial derivatives involving $\eta_{D_{kT}}$ that are necessary for Equation (B.6) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= (1 - f_{D_{kT}}) \left\{ \phi_{D_{kT}, T_k} \frac{\partial \eta_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} + \phi_{D_{kT}, D_{k+1}, B} \eta_{D_{k+1}, T} \right\}; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= \frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}} \frac{\partial \eta_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}^F} \frac{\partial \eta_{T_k}^F}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} \\ &\quad + f_{D_{kT}} \phi_{D_{kT}, D_{k+1}, B}^F \eta_{D_{k+1}, T}^F; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}} &= (1 - f_{D_{kT}}) \eta_{T_k}; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}^F} &= f_{D_{kT}} \eta_{T_k}^F; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1}, B}} &= (1 - f_{D_{kT}}) \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T}; \\ \frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1}, B}^F} &= f_{D_{kT}} \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F; \end{aligned}$$

$$\begin{aligned}
\frac{\partial \eta_{D_{kT}}}{\partial f_{D_{kT}}} &= -\left\{ \phi_{D_{kT}, T_k} \eta_{T_k} + \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T} \right\} \\
&\quad + \phi_{D_{kT}, T_k}^F \eta_{T_k}^F + \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, T_k}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}^F} &= f_{D_{kT}} \phi_{D_{kT}, T_k}^F; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, T}} &= (1 - f_{D_{kT}}) \left\{ \phi_{D_{kT}, T_k} \frac{\partial \eta_{T_k}}{\partial \eta_{D_{k+1}, T}} + \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} \right\}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, T}^F} &= \frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}} \frac{\partial \eta_{T_k}}{\partial \eta_{D_{k+1}, T}^F} + f_{D_{kT}} \left\{ \phi_{D_{kT}, T_k}^F \frac{\partial \eta_{T_k}^F}{\partial \eta_{D_{k+1}, T}^F} + \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \right\};
\end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{5a(\eta_{D_{kT}})}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta'_{5a(\eta_{D_{kT}})}$,

$$\frac{\partial \eta_{D_{kT}}}{\partial \theta} = \frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}} \frac{\partial \eta_{T_k}}{\partial \theta} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, T}} \frac{\partial \eta_{D_{k+1}, T}}{\partial \theta} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}^F} \frac{\partial \eta_{T_k}^F}{\partial \theta} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1}, T}^F} \frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta}.$$

Define $\Theta_{5a(\eta_{D_{kT}}^F)}$ to contain the following parameters:

$$\begin{aligned}
\phi_{D_{jB}, D_{jT}}^F & \quad j = k+2, \dots, K; & \phi_{D_{jT}, T_j}^F & \quad j = k+1, \dots, K-1; \\
\phi_{D_{jT}, D_{j+1}, B}^F & \quad j = k+1, \dots, K-1. & \phi_{T_j, D_{j+1}, B}^F & \quad j = k+1, \dots, K-1.
\end{aligned}$$

For $k = 1, \dots, K-1$, the parameter $\eta_{D_{kT}}^F$ is a function of the parameters $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, ϕ_{D_{kT}, T_k}^F , and $\phi_{D_{kT}, D_{k+1}, B}^F$. For $k = 1, \dots, K-2$, $\eta_{D_{kT}}^F$ is also a function of the parameters in the set $\Theta_{5a(\eta_{D_{kT}}^F)}$. The necessary partial derivatives involving $\eta_{D_{kT}}^F$ are:

for $k = 1, \dots, K-1$:

$$\begin{aligned}
\frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= \phi_{D_{kT}, D_{k+1}, B}^F \eta_{D_{k+1}, T}^F; \\
\frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{D_{kT}, T_k}^F} &= \eta_{T_k}^F;
\end{aligned}$$

$$\frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{D_{kT}, D_{k+1}, B}^F} = \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F.$$

For $k = 1, \dots, K-2$ and $\theta \in \Theta_{5a(\eta_{D_{kT}}^F)}$,

$$\frac{\partial \eta_{D_{kT}}^F}{\partial \theta} = \phi_{D_{kT}, T_k}^F \frac{\partial \eta_{T_k}^F}{\partial \theta} + \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta}.$$

Define $\Theta_{5a(\eta_{T_k})}$ to be the set composed of the following parameters:

$$\begin{array}{ll} \phi_{D_{jB}, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jB}, D_{jT}}^F & j = k+2, \dots, K; \\ \phi_{D_{jT}, T_j} & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^F & j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B} & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B}^F & j = k+1, \dots, K-1; \\ \phi_{T_j, D_{j+1}, B} & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^F & j = k+1, \dots, K-1; \\ f_{D_{jT}} & j = k+1, \dots, K-1; & f_{T_j} & j = k+1, \dots, K-1. \end{array}$$

For $k = 0, \dots, K-1$, the parameter η_{T_k} is a function of the parameters $\phi_{D_{k+1}, B, D_{k+1}, T}$, $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, $\phi_{T_k, D_{k+1}, B}$, $\phi_{T_k, D_{k+1}, B}^F$, and f_{T_k} ; for $k = 0, \dots, K-2$, η_{T_k} is also a function of the parameters in the set $\Theta_{5a(\eta_{T_k})}$. The necessary partial derivatives involving η_{T_k} are:

for $k = 0, \dots, K-1$:

$$\begin{aligned} \frac{\partial \eta_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= (1 - f_{T_k}) \phi_{T_k, D_{k+1}, B} \eta_{D_{k+1}, T}; \\ \frac{\partial \eta_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= f_{T_k} \phi_{T_k, D_{k+1}, B}^F \eta_{D_{k+1}, T}^F; \\ \frac{\partial \eta_{T_k}}{\partial \phi_{T_k, D_{k+1}, B}} &= (1 - f_{T_k}) \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T}; \\ \frac{\partial \eta_{T_k}}{\partial \phi_{T_k, D_{k+1}, B}^F} &= f_{T_k} \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F; \\ \frac{\partial \eta_{T_k}}{\partial f_{T_k}} &= -\phi_{T_k, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T} + \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F; \end{aligned}$$

for $k = 0, \dots, K - 2$ and $\theta \in \Theta_{5a(\eta_{T_k}^F)}$,

$$\frac{\partial \eta_{T_k}^F}{\partial \theta} = (1 - f_{T_k}) \phi_{T_k, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} \frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta} + f_{T_k} \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta}.$$

Define $\Theta_{5a(\eta_{T_k}^F)}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_j, B, D_j, T}^F & \quad j = k + 2, \dots, K; & \phi_{D_j, T, T_j}^F & \quad j = k + 1, \dots, K - 1; \\ \phi_{D_j, T, D_{j+1}, B}^F & \quad j = k + 1, \dots, K - 1; & \phi_{T_j, D_{j+1}, B}^F & \quad j = k + 1, \dots, K - 1; \end{aligned}$$

For $k = 0, \dots, K - 1$, the parameter $\eta_{T_k}^F$ is a function of the parameters $\phi_{D_{k+1}, B, D_{k+1}, T}^F$ and $\phi_{T_k, D_{k+1}, B}^F$. For $k = 0, \dots, K - 2$, $\eta_{T_k}^F$ is also a function of the parameters in the set $\Theta_{5a(\eta_{T_k}^F)}$. The necessary partial derivatives involving $\eta_{T_k}^F$ are:

for $k = 0, \dots, K - 1$:

$$\begin{aligned} \frac{\partial \eta_{T_k}^F}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= \phi_{T_k, D_{k+1}, B}^F \eta_{D_{k+1}, T}^F; \\ \frac{\partial \eta_{T_k}^F}{\partial \phi_{T_k, D_{k+1}, B}^F} &= \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F; \end{aligned}$$

for $k = 0, \dots, K - 2$ and $\theta \in \Theta_{5a(\eta_{T_k}^F)}$,

$$\frac{\partial \eta_{T_k}^F}{\partial \theta} = \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta}.$$

B.1.7 Models 5b and 6

Define $\Theta_{5b(\eta_R)}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{kB}, D_{kT}} & k = 2, \dots, K; & \phi_{D_{kB}, D_{kT}}^F & k = 2, \dots, K; \\
 \phi_{D_{kB}, D_{kT}}^T & k = 1, \dots, K; & \phi_{D_{kT}, T_k} & k = 1, \dots, K-1; \\
 \phi_{D_{kT}, T_k}^F & k = 1, \dots, K-1; & \phi_{D_{kT}, T_k}^T & k = 1, \dots, K-1; \\
 \phi_{D_{kT}, T_k}^{FT} & k = 1, \dots, K-1; & \phi_{D_{kT}, D_{k+1}, B} & k = 1, \dots, K-1; \\
 \phi_{D_{kT}, D_{k+1}, B}^F & k = 1, \dots, K-1; & \phi_{D_{kT}, D_{k+1}, B}^T & k = 1, \dots, K-1; \\
 \phi_{D_{kT}, D_{k+1}, B}^{FT} & k = 1, \dots, K-1; & \phi_{T_k, D_{k+1}, B} & k = 0, \dots, K-1; \\
 \phi_{T_k, D_{k+1}, B}^F & k = 0, \dots, K-1 & \phi_{T_k, D_{k+1}, B}^T & k = 1, \dots, K-1; \\
 \phi_{T_k, D_{k+1}, B}^{FT} & k = 1, \dots, K-1; & f_{D_{kT}} & k = 1, \dots, K-1; \\
 f_{D_{kT}}^T & k = 1, \dots, K-1; & f_{T_k} & k = 0, \dots, K-1; \\
 f_{T_k}^T & k = 1, \dots, K-1. & &
 \end{array}$$

For Model 5b, the parameter η_R is a function of the parameters Φ_{R, T_0} , Φ_{R, T_0}^F , $\Phi_{R, D_{1B}}$, $\Phi_{R, D_{1B}}^F$, $\phi_{D_{1B}, D_{1T}}$, $\phi_{D_{1B}, D_{1T}}^F$, and the parameters in the set $\Theta_{5b(\eta_R)}$. The variance of $\hat{\eta}_R$ can be estimated by the following for Model 5b:

$$\begin{aligned}
 \widehat{Var}(\hat{\eta}_R) = & \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, T_0}) + \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, T_0}^F) \\
 & + \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}) + \left(\frac{\partial \eta_R}{\partial \Phi_{R, D_{1B}}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}^F) \\
 & + \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}) + \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}^F) \\
 & + \sum_{\theta \in \Theta_{5b(\eta_R)}} \sum_{\psi \in \Theta_{5b(\eta_R)}} \left(\frac{\partial \eta_R}{\partial \theta} \right) \left(\frac{\partial \eta_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\
 & + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R, T_0}^F} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\Phi}_{R, T_0}^F)
 \end{aligned}$$

$$\begin{aligned}
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\Phi}_{R,D_{1B}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\Phi}_{R,D_{1B}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,D_{1B}}, \hat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R,D_{1B}}, \hat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,D_{1B}}, \hat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\hat{\Phi}_{R,D_{1B}}, \hat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R,D_{1B}}^F, \hat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,D_{1B}}^F, \hat{\phi}_{D_{1B},D_{1T}}^F)
\end{aligned}$$

$$\begin{aligned}
& + 2 \sum_{\theta \in \Theta_{5b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \Phi_{R,D_1B}^F} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_1B}^F, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \eta_R}{\partial \phi_{D_1B,D_1T}} \right) \left(\frac{\partial \eta_R}{\partial \phi_{D_1B,D_1T}^F} \right) \widehat{Cov}(\widehat{\phi}_{D_1B,D_1T}, \widehat{\phi}_{D_1B,D_1T}^F) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_1B,D_1T}} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_1B,D_1T}, \widehat{\theta}) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\eta_R)} \left(\frac{\partial \eta_R}{\partial \phi_{D_1B,D_1T}^F} \right) \left(\frac{\partial \eta_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_1B,D_1T}^F, \widehat{\theta}), \tag{B.7}
\end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The partial derivatives necessary for Equation (B.7) are the following:

$$\begin{aligned}
\frac{\partial \eta_R}{\partial \Phi_{R,T_0}} &= \eta_{T_0}; & \frac{\partial \eta_R}{\partial \Phi_{R,T_0}^F} &= \eta_{T_0}^F; \\
\frac{\partial \eta_R}{\partial \Phi_{R,D_1B}} &= \phi_{D_1B,D_1T} \eta_{D_1T}; & \frac{\partial \eta_R}{\partial \Phi_{R,D_1B}^F} &= \phi_{D_1B,D_1T}^F \eta_{D_1T}^F; \\
\frac{\partial \eta_R}{\partial \phi_{D_1B,D_1T}} &= \Phi_{R,D_1B} \eta_{D_1T}; & \frac{\partial \eta_R}{\partial \phi_{D_1B,D_1T}^F} &= \Phi_{R,T_0} \frac{\partial \eta_{T_0}}{\partial \phi_{D_1B,D_1T}^F} + \Phi_{R,D_1B}^F \eta_{D_1T}^F;
\end{aligned}$$

and, for $\theta \in \Theta_{5b}(\eta_R)$,

$$\frac{\partial \eta_R}{\partial \theta} = \Phi_{R,T_0} \frac{\partial \eta_{T_0}}{\partial \theta} + \Phi_{R,T_0}^F \frac{\partial \eta_{T_0}^F}{\partial \theta} + \Phi_{R,D_1B} \phi_{D_1B,D_1T} \frac{\partial \eta_{D_1T}}{\partial \theta} + \Phi_{R,D_1B}^F \phi_{D_1B,D_1T}^F \frac{\partial \eta_{D_1T}^F}{\partial \theta},$$

where $\frac{\partial \eta_{T_0}}{\partial \theta}$, $\frac{\partial \eta_{T_0}^F}{\partial \theta}$, $\frac{\partial \eta_{D_1T}}{\partial \theta}$, and $\frac{\partial \eta_{D_1T}^F}{\partial \theta}$ are defined below.

Define $\Theta_{5b(\eta_{T_k})}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{jB}, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jB}, D_{jT}}^F & j = k+2, \dots, K; \\
 \phi_{D_{jB}, D_{jT}}^T & j = k+2, \dots, K; & \phi_{D_{jT}, T_j}^F & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, T_j}^T & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^{FT} & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1}, B}^F & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B}^T & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1}, B}^{FT} & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^F & j = k+1, \dots, K-1; \\
 \phi_{T_j, D_{j+1}, B}^T & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^{FT} & j = k+1, \dots, K-1; \\
 f_{D_{jT}}^T & j = k+1, \dots, K-1 & f_{T_j}^T & j = k+1, \dots, K-1.
 \end{array}$$

Define $\Theta'_{5b(\eta_{T_k})}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{jT}, T_j} & j = k+2, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & j = k+2, \dots, K-1; \\
 \phi_{T_j, D_{j+1}, B} & j = k+2, \dots, K-1; & f_{D_{jT}} & j = k+2, \dots, K-1; \\
 f_{T_j} & j = k+2, \dots, K-1.
 \end{array}$$

For $k = 0, \dots, K-1$, the parameter η_{T_k} is a function of the parameters $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, $\phi_{D_{k+1}, B, D_{k+1}, T}^T$, $\phi_{T_k, D_{k+1}, B}$, $\phi_{T_k, D_{k+1}, B}^F$, and f_{T_k} . For $k = 0, \dots, K-2$, η_{T_k} is also a function of the parameters in the set $\Theta_{5b(\eta_{T_k})}$; for $k = 0, \dots, K-3$, η_{T_k} is also a function of the parameters in the set $\Theta'_{5b(\eta_{T_k})}$. The partial derivatives necessary for Equation (B.7) that involve η_{T_k} are the following:

For $k = 0, \dots, K-1$:

$$\begin{aligned}
 \frac{\partial \eta_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= f_{T_k} \phi_{T_k, D_{k+1}, B}^F \eta_{D_{k+1}, T}^F; \\
 \frac{\partial \eta_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^T} &= (1 - f_{T_k}) \phi_{T_k, D_{k+1}, B} \eta_{D_{k+1}, T}^T;
 \end{aligned}$$

$$\begin{aligned}\frac{\partial \eta_{T_k}}{\partial \phi_{T_k, D_{k+1}, B}} &= (1 - f_{T_k}) \phi_{D_{k+1}, B, D_{k+1}, T}^T \eta_{D_{k+1}, T}^T; \\ \frac{\partial \eta_{T_k}}{\partial \phi_{T_k, D_{k+1}, B}^F} &= f_{T_k} \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F; \\ \frac{\partial \eta_{T_k}}{\partial f_{T_k}} &= -\phi_{T_k, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^T \eta_{D_{k+1}, T}^T + \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \eta_{D_{k+1}, T}^F;\end{aligned}$$

for $k = 0, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{T_k})}$, and separately for $k = 0, \dots, K-3$ and $\theta \in \Theta'_{5b(\eta_{T_k})}$:

$$\frac{\partial \eta_{T_k}}{\partial \theta} = \frac{\partial \eta_{T_k}}{\partial \eta_{D_{k+1}, T}^T} \frac{\partial \eta_{D_{k+1}, T}^T}{\partial \theta} + \frac{\partial \eta_{T_k}}{\partial \eta_{D_{k+1}, T}^F} \frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta},$$

where

$$\begin{aligned}\frac{\partial \eta_{T_k}}{\partial \eta_{D_{k+1}, T}^T} &= (1 - f_{T_k}) \phi_{T_k, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^T; \\ \frac{\partial \eta_{T_k}}{\partial \eta_{D_{k+1}, T}^F} &= f_{T_k} \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F;\end{aligned}$$

and the partial derivatives $\frac{\partial \eta_{D_{k+1}, T}^T}{\partial \theta}$ and $\frac{\partial \eta_{D_{k+1}, T}^F}{\partial \theta}$ are defined below.

Define $\Theta_{5b(\eta_{T_k}^F)}$ to be the set composed of the following parameters:

$$\begin{aligned}\phi_{D_j B, D_j T} & \quad j = k+2, \dots, K; & \phi_{D_j B, D_j T}^T & \quad j = k+2, \dots, K; \\ \phi_{D_j T, T_j}^T & \quad j = k+1, \dots, K-1; & \phi_{D_j T, D_{j+1}, B}^T & \quad j = k+1, \dots, K-1; \\ \phi_{T_j, D_{j+1}, B}^T & \quad j = k+1, \dots, K-1.\end{aligned}$$

Define $\Theta'_{5b(\eta_{T_k}^F)}$ to be the set composed of the following parameters:

$$\begin{aligned}\phi_{D_j T, T_j} & \quad j = k+2, \dots, K-1; & \phi_{D_j T, D_{j+1}, B} & \quad j = k+2, \dots, K-1; \\ \phi_{T_j, D_{j+1}, B} & \quad j = k+2, \dots, K-1.\end{aligned}$$

For Model 5b, the parameter $\eta_{T_k}^F$ is a function of the two parameters $\phi_{D_{k+1}, B, D_{k+1}, T}^T$ and $\phi_{T_k, D_{k+1}, B}^F$ for $k = 0, \dots, K-1$, and of the parameters in the set $\Theta_{5b(\eta_{T_k}^F)}$ for $k = 0, \dots, K-2$,

and of the parameters in the set $\Theta'_{5b(\eta_{T_k}^F)}$ for $k = 0, \dots, K-3$. The necessary partial derivatives involving $\eta_{T_k}^F$ are the following:

For $k = 0, \dots, K-1$:

$$\frac{\partial \eta_{T_k}^F}{\partial \phi_{D_{k+1,B}, D_{k+1,T}}^T} = \phi_{T_k, D_{k+1,B}}^F \eta_{D_{k+1,T}}^{fT}; \quad \frac{\partial \eta_{T_k}^F}{\partial \phi_{T_k, D_{k+1,B}}^F} = \phi_{D_{k+1,B}, D_{k+1,T}}^T \eta_{D_{k+1,T}}^{fT};$$

for $k = 0, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{T_k}^F)}$, and separately for $k = 0, \dots, K-3$ and $\theta \in \Theta'_{5b(\eta_{T_k}^F)}$,

$$\frac{\partial \eta_{T_k}^F}{\partial \theta} = \frac{\eta_{T_k}^F}{\eta_{D_{k+1,T}}^{fT}} \frac{\partial \eta_{D_{k+1,T}}^{fT}}{\partial \theta},$$

where $\frac{\partial \eta_{D_{k+1,T}}^{fT}}{\partial \theta}$ is defined below.

Define $\Theta_{5b(\eta_{T_k}^T)}$ to be the set composed of the following parameters:

$\phi_{D_{jB}, D_{jT}}$	$j = k+2, \dots, K;$	$\phi_{D_{jB}, D_{jT}}^F$	$j = k+2, \dots, K;$
$\phi_{D_{jB}, D_{jT}}^T$	$j = k+2, \dots, K;$	ϕ_{D_{jT}, T_j}^F	$j = k+1, \dots, K-1;$
ϕ_{D_{jT}, T_j}^T	$j = k+1, \dots, K-1;$	ϕ_{D_{jT}, T_j}^{FT}	$j = k+1, \dots, K-1;$
$\phi_{D_{jT}, D_{j+1,B}}^F$	$j = k+1, \dots, K-1;$	$\phi_{D_{jT}, D_{j+1,B}}^T$	$j = k+1, \dots, K-1;$
$\phi_{D_{jT}, D_{j+1,B}}^{FT}$	$j = k+1, \dots, K-1;$	$\phi_{T_j, D_{j+1,B}}^F$	$j = k+1, \dots, K-1;$
$\phi_{T_j, D_{j+1,B}}^T$	$j = k+1, \dots, K-1;$	$\phi_{T_j, D_{j+1,B}}^{FT}$	$j = k+1, \dots, K-1;$
$f_{D_{jT}}^T$	$j = k+1, \dots, K-1;$	$f_{T_j}^T$	$j = k+1, \dots, K-1.$

Define $\Theta'_{5b(\eta_{T_k}^T)}$ to be the set composed of the following parameters:

ϕ_{D_{jT}, T_j}	$j = k+2, \dots, K-1;$	$\phi_{D_{jT}, D_{j+1,B}}$	$j = k+2, \dots, K-1;$
$\phi_{T_j, D_{j+1,B}}$	$j = k+2, \dots, K-1;$	$f_{D_{jT}}$	$j = k+2, \dots, K-1;$
f_{T_j}	$j = k+2, \dots, K-1.$		

For Model 5b, the parameter $\eta_{T_k}^T$ is a function of $\phi_{D_{k+1},B,D_{k+1},T}^F$, $\phi_{D_{k+1},B,D_{k+1},T}^T$, $\phi_{T_k,D_{k+1},B}^T$, $\phi_{T_k,D_{k+1},B}^{FT}$, and $f_{T_k}^T$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\eta_{T_k}^T$ is also a function of the parameters in the set $\Theta_{5b(\eta_{T_k}^T)}$; for $k = 1, \dots, K-3$, $\eta_{T_k}^T$ is also a function of the parameters in the set $\Theta'_{5b(\eta_{T_k}^T)}$. The partial derivatives involving $\eta_{T_k}^T$ that are necessary for Equation (B.7) are the following:

For $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \eta_{T_k}^T}{\partial \phi_{D_{k+1},B,D_{k+1},T}^F} &= f_{T_k}^T \phi_{T_k,D_{k+1},B}^{FT} \eta_{D_{k+1},T}^F; \\ \frac{\partial \eta_{T_k}^T}{\partial \phi_{D_{k+1},B,D_{k+1},T}^T} &= (1 - f_{T_k}^T) \phi_{T_k,D_{k+1},B}^T \eta_{D_{k+1},T}^T; \\ \frac{\partial \eta_{T_k}^T}{\partial \phi_{T_k,D_{k+1},B}^T} &= (1 - f_{T_k}^T) \phi_{D_{k+1},B,D_{k+1},T}^T \eta_{D_{k+1},T}^T; \\ \frac{\partial \eta_{T_k}^T}{\partial \phi_{T_k,D_{k+1},B}^{FT}} &= f_{T_k}^T \phi_{D_{k+1},B,D_{k+1},T}^F \eta_{D_{k+1},T}^F; \\ \frac{\partial \eta_{T_k}^T}{\partial f_{T_k}^T} &= -\phi_{T_k,D_{k+1},B}^T \phi_{D_{k+1},B,D_{k+1},T}^T \eta_{D_{k+1},T}^T + \phi_{T_k,D_{k+1},B}^{FT} \phi_{D_{k+1},B,D_{k+1},T}^F \eta_{D_{k+1},T}^F; \end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{T_k}^T)}$, and separately for $k = 1, \dots, K-3$ and $\theta \in \Theta'_{5b(\eta_{T_k}^T)}$,

$$\frac{\partial \eta_{T_k}^T}{\partial \theta} = \frac{\partial \eta_{T_k}^T}{\partial \eta_{D_{k+1},T}^T} \frac{\partial \eta_{D_{k+1},T}^T}{\partial \theta} + \frac{\partial \eta_{T_k}^T}{\partial \eta_{D_{k+1},T}^F} \frac{\partial \eta_{D_{k+1},T}^F}{\partial \theta},$$

where

$$\begin{aligned} \frac{\partial \eta_{T_k}^T}{\partial \eta_{D_{k+1},T}^T} &= (1 - f_{T_k}^T) \phi_{T_k,D_{k+1},B}^T \phi_{D_{k+1},B,D_{k+1},T}^T; \\ \frac{\partial \eta_{T_k}^T}{\partial \eta_{D_{k+1},T}^F} &= f_{T_k}^T \phi_{T_k,D_{k+1},B}^{FT} \phi_{D_{k+1},B,D_{k+1},T}^F, \end{aligned}$$

and where the partial derivatives $\frac{\partial \eta_{D_{k+1},T}^T}{\partial \theta}$ and $\frac{\partial \eta_{D_{k+1},T}^F}{\partial \theta}$ are defined below.

The parameter $\eta_{T_k}^f$ is a function of the two parameters $\phi_{D_{k+1},B,D_{k+1},T}^T$ and $\phi_{T_k,D_{k+1},B}$ for $k = 2, \dots, K-1$. The parameter $\eta_{T_k}^f$ is also a function of the parameters in the set $\Theta_{5b(\eta_{T_k}^F)}$ for $k = 2, \dots, K-2$, and in the set $\Theta'_{5b(\eta_{T_k}^F)}$ for $k = 2, \dots, K-3$. The partial derivatives involving $\eta_{T_k}^f$ that are necessary for Equation (B.7) are the following:

For $k = 2, \dots, K-1$:

$$\frac{\partial \eta_{T_k}^f}{\partial \phi_{D_{k+1},B,D_{k+1},T}^T} = \frac{\eta_{T_k}^f}{\phi_{D_{k+1},B,D_{k+1},T}^T}; \quad \frac{\partial \eta_{T_k}^f}{\partial \phi_{T_k,D_{k+1},B}} = \frac{\eta_{T_k}^f}{\phi_{T_k,D_{k+1},B}};$$

for $k = 2, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{T_k}^F)}$, and separately for $k = 2, \dots, K-3$ and $\theta \in \Theta'_{5b(\eta_{T_k}^F)}$,

$$\frac{\partial \eta_{T_k}^f}{\partial \theta} = \frac{\eta_{T_k}^f}{\eta_{D_{k+1},T}^{fT}} \frac{\partial \eta_{D_{k+1},T}^{fT}}{\partial \theta},$$

where $\frac{\partial \eta_{D_{k+1},T}^{fT}}{\partial \theta}$ is defined below.

The parameter $\eta_{T_k}^{fT}$ is a function of the parameters $\phi_{D_{k+1},B,D_{k+1},T}^T$ and $\phi_{T_k,D_{k+1},B}^T$ for $k = 1, \dots, K-1$, as well as the parameters in the set $\Theta_{5b(\eta_{T_k}^F)}$ for $k = 1, \dots, K-2$ and the parameters in the set $\Theta'_{5b(\eta_{T_k}^F)}$ for $k = 1, \dots, K-3$. The necessary partial derivatives involving $\eta_{T_k}^{fT}$ are the following:

For $k = 1, \dots, K-1$:

$$\frac{\partial \eta_{T_k}^{fT}}{\partial \phi_{D_{k+1},B,D_{k+1},T}^T} = \frac{\eta_{T_k}^{fT}}{\phi_{D_{k+1},B,D_{k+1},T}^T}; \quad \frac{\partial \eta_{T_k}^{fT}}{\partial \phi_{T_k,D_{k+1},B}^T} = \frac{\eta_{T_k}^{fT}}{\phi_{T_k,D_{k+1},B}^T};$$

for $k = 1, \dots, K - 2$ and $\theta \in \Theta_{5b(\eta_{T_k}^F)}$, and separately for $k = 1, \dots, K - 3$ and $\theta \in \Theta'_{5b(\eta_{T_k}^F)}$,

$$\frac{\partial \eta_{T_k}^{fT}}{\partial \theta} = \frac{\eta_{T_k}^{fT}}{\eta_{D_{k+1},T}^{fT}} \frac{\partial \eta_{D_{k+1},T}^{fT}}{\partial \theta},$$

where $\frac{\partial \eta_{D_{k+1},T}^{fT}}{\partial \theta}$ is defined below.

Define $\Theta_{5b(\eta_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{array}{llll} \phi_{D_{jB}, D_{jT}} & j = k + 2, \dots, K; & \phi_{D_{jT}, T_j} & j = k + 1, \dots, K - 1; \\ \phi_{D_{jT}, T_j}^F & j = k + 1, \dots, K - 1; & \phi_{D_{jT}, T_j}^T & j = k + 1, \dots, K - 1; \\ \phi_{D_{jT}, T_j}^{FT} & j = k + 1, \dots, K - 1; & \phi_{D_{jT}, D_{j+1}, B} & j = k + 1, \dots, K - 1; \\ \phi_{D_{jT}, D_{j+1}, B}^F & j = k + 1, \dots, K - 1; & \phi_{D_{jT}, D_{j+1}, B}^T & j = k + 1, \dots, K - 1; \\ \phi_{D_{jT}, D_{j+1}, B}^{FT} & j = k + 1, \dots, K - 1; & \phi_{T_j, D_{j+1}, B}^T & j = k + 1, \dots, K - 1; \\ \phi_{T_j, D_{j+1}, B}^{FT} & j = k + 1, \dots, K - 1; & f_{D_{jT}} & j = k + 1, \dots, K - 1; \\ f_{T_j}^T & j = k + 1, \dots, K - 1; & f_{D_{jT}}^T & j = k + 1, \dots, K - 1. \end{array}$$

Define $\Theta'_{5b(\eta_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{array}{llll} \phi_{D_{jB}, D_{jT}}^F & j = k + 1, \dots, K; & \phi_{D_{jB}, D_{jT}}^T & j = k + 1, \dots, K; \\ \phi_{T_j, D_{j+1}, B}^F & j = k, \dots, K - 1; & \phi_{T_j, D_{j+1}, B}^F & j = k, \dots, K - 1; \\ f_{T_j} & j = k, \dots, K - 1. & & \end{array}$$

For Model 5b, the parameter $\eta_{D_{kT}}$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, ϕ_{D_{kT}, T_k} , ϕ_{D_{kT}, T_k}^F , $\phi_{D_{kT}, D_{k+1}, B}$, $\phi_{D_{kT}, D_{k+1}, B}^F$, and $f_{D_{kT}}$ for $k = 1, \dots, K - 1$. The parameter $\eta_{D_{kT}}$ is also a function of the parameters in the set $\Theta_{5b(\eta_{D_{kT}})}$ for $k = 1, \dots, K - 2$, and of the parameters in the set $\Theta'_{5b(\eta_{D_{kT}})}$ for $k = 1, \dots, K - 1$. The partial derivatives involving $\eta_{D_{kT}}$ that are necessary for Equation (B.7) are the following:

For $k = 1, \dots, K-1$:

$$\begin{aligned}
\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1,B}, D_{k+1,T}}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, D_{k+1,B}} \eta_{D_{k+1,T}}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{k+1,B}, D_{k+1,T}}^F} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, T_k} \frac{\partial \eta_{T_k}}{\partial \phi_{D_{k+1,B}, D_{k+1,T}}^F} + f_{D_{kT}} \phi_{D_{kT}, D_{k+1,B}}^F \eta_{D_{k+1,T}}^F; \\
\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}} &= (1 - f_{D_{kT}}) \eta_{T_k}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}^F} &= f_{D_{kT}} \eta_{T_k}^F; \\
\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1,B}}} &= (1 - f_{D_{kT}}) \phi_{D_{k+1,B}, D_{k+1,T}} \eta_{D_{k+1,T}}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1,B}}^F} &= f_{D_{kT}} \phi_{D_{k+1,B}, D_{k+1,T}}^F \eta_{D_{k+1,T}}^F; \\
\frac{\partial \eta_{D_{kT}}}{\partial f_{D_{kT}}} &= -[\phi_{D_{kT}, T_k} \eta_{T_k} + \phi_{D_{kT}, D_{k+1,B}} \phi_{D_{k+1,B}, D_{k+1,T}} \eta_{D_{k+1,T}}] + \\
&\quad \phi_{D_{kT}, T_k}^F \eta_{T_k}^F + \phi_{D_{kT}, D_{k+1,B}}^F \phi_{D_{k+1,B}, D_{k+1,T}}^F \eta_{D_{k+1,T}}^F;
\end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{D_{kT}})}$, and separately for $k = 1, \dots, K-1$ and $\theta \in \Theta'_{5b(\eta_{D_{kT}})}$,

$$\frac{\partial \eta_{D_{kT}}}{\partial \theta} = \frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}} \frac{\partial \eta_{T_k}}{\partial \theta} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}^F} \frac{\partial \eta_{T_k}^F}{\partial \theta} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1,T}}} \frac{\partial \eta_{D_{k+1,T}}}{\partial \theta} + \frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1,T}}^F} \frac{\partial \eta_{D_{k+1,T}}^F}{\partial \theta},$$

where

$$\begin{aligned}
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, T_k}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{T_k}^F} &= f_{D_{kT}} \phi_{D_{kT}, T_k}^F; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1,T}}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, D_{k+1,B}} \phi_{D_{k+1,B}, D_{k+1,T}}; \\
\frac{\partial \eta_{D_{kT}}}{\partial \eta_{D_{k+1,T}}^F} &= f_{D_{kT}} \phi_{D_{kT}, D_{k+1,B}}^F \phi_{D_{k+1,B}, D_{k+1,T}}^F.
\end{aligned}$$

The partial derivatives $\frac{\partial \eta_{T_k}}{\partial \theta}$ and $\frac{\partial \eta_{T_k}^F}{\partial \theta}$ are defined above, and $\frac{\partial \eta_{D_{k+1},T}^F}{\partial \theta}$ is defined below.

Define $\Theta_{5b(\eta_{D_{kT}}^F)}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, T_j}^T & \quad j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B}^T & \quad j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B} & \quad j = k+1, \dots, K-1; \\ \phi_{T_j, D_{j+1}, B}^T & \quad j = k+1, \dots, K-1. \end{aligned}$$

Define $\Theta'_{5b(\eta_{D_{kT}}^F)}$ to be the set composed of the parameters $\phi_{D_{jB}, D_{jT}}^T$ for $j = k+1, \dots, K$. For Model 5b, the parameter $\eta_{D_{kT}}^F$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, ϕ_{D_{kT}, T_k}^F , $\phi_{D_{kT}, D_{k+1}, B}^F$, $\phi_{T_k, D_{k+1}, B}^F$, and the parameters in the set $\Theta'_{5b(\eta_{D_{kT}}^F)}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\eta_{D_{kT}}^F$ is also a function of the parameters in the set $\Theta_{5b(\eta_{D_{kT}}^F)}$. The partial derivatives involving $\eta_{D_{kT}}^F$ that are necessary for Equation (B.7) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= \phi_{D_{kT}, D_{k+1}, B}^F \eta_{D_{k+1}, T}^f; \\ \frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{D_{kT}, T_k}^F} &= \eta_{T_k}^F; \\ \frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{D_{kT}, D_{k+1}, B}^F} &= \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T}^f; \\ \frac{\partial \eta_{D_{kT}}^F}{\partial \phi_{T_k, D_{k+1}, B}^F} &= \phi_{D_{kT}, T_k}^F \phi_{D_{k+1}, B, D_{k+1}, T}^T \eta_{D_{k+1}, T}^{fT}; \end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{D_{kT}}^F)}$, and separately for $k = 1, \dots, K-1$ and $\theta \in \Theta'_{5b(\eta_{D_{kT}}^F)}$,

$$\frac{\partial \eta_{D_{kT}}^F}{\partial \theta} = \phi_{D_{kT}, T_k}^F \frac{\partial \eta_{T_k}^F}{\partial \theta} + \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^T \frac{\partial \eta_{D_{k+1}, T}^f}{\partial \theta},$$

where $\frac{\partial \eta_{T_k}^F}{\partial \theta}$ is defined above and $\frac{\partial \eta_{D_{k+1},T}^f}{\partial \theta}$ is defined below.

Define $\Theta_{5b(\eta_{D_{kT}}^T)}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{jB}, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, T_j}^F & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^T & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, T_j}^{FT} & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1}, B}^F & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B}^T & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1}, B}^{FT} & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B} & j = k+1, \dots, K-1; \\
 \phi_{T_j, D_{j+1}, B}^F & j = k+1, \dots, K-1; & f_{D_{jT}} & j = k+1, \dots, K-1; \\
 f_{D_{jT}}^T & j = k+1, \dots, K-1; & f_{T_j} & j = k+1, \dots, K-1.
 \end{array}$$

Define $\Theta'_{5b(\eta_{D_{kT}}^T)}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{jB}, D_{jT}}^F & j = k+1, \dots, K; & \phi_{D_{jB}, D_{jT}}^T & j = k+1, \dots, K; \\
 \phi_{T_j, D_{j+1}, B}^T & j = k, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^{FT} & j = k, \dots, K-1; \\
 f_{T_j}^T & j = k, \dots, K-1.
 \end{array}$$

For Model 5b, the parameter $\eta_{D_{kT}}^T$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, ϕ_{D_{kT}, T_k}^T , ϕ_{D_{kT}, T_k}^{FT} , $\phi_{D_{kT}, D_{k+1}, B}^T$, $\phi_{D_{kT}, D_{k+1}, B}^{FT}$, $f_{D_{kT}}^T$, and the parameters in the set $\Theta'_{5b(\eta_{D_{kT}}^T)}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\eta_{D_{kT}}^T$ is also a function of the parameters in the set $\Theta_{5b(\eta_{D_{kT}}^T)}$. The partial derivatives involving $\eta_{D_{kT}}^T$ necessary for Equation (B.7) are the following:

For $k = 1, \dots, K-1$:

$$\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} = (1 - f_{D_{kT}}^T) \phi_{D_{kT}, D_{k+1}, B}^T \eta_{D_{k+1}, T};$$

$$\begin{aligned}
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{k+1,B},D_{k+1,T}}^F} &= (1 - f_{D_{kT}}^T) \phi_{D_{kT},T_k}^T \frac{\partial \eta_{T_k}^T}{\partial \phi_{D_{k+1,B},D_{k+1,T}}^F} + f_{D_{kT}}^T \phi_{D_{kT},D_{k+1,B}}^{FT} \eta_{D_{k+1,T}}^F; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{kT},T_k}^T} &= (1 - f_{D_{kT}}^T) \eta_{T_k}^T; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{kT},T_k}^{FT}} &= f_{D_{kT}}^T \eta_{T_k}^F; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{kT},D_{k+1,B}}^T} &= (1 - f_{D_{kT}}^T) \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}}; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \phi_{D_{kT},D_{k+1,B}}^{FT}} &= f_{D_{kT}}^T \phi_{D_{k+1,B},D_{k+1,T}}^F \eta_{D_{k+1,T}}^F; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial f_{D_{kT}}^T} &= -\phi_{D_{kT},T_k}^T \eta_{T_k}^T - \phi_{D_{kT},D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}} \eta_{D_{k+1,T}} \\
&\quad + \phi_{D_{kT},T_k}^{FT} \eta_{T_k}^F + \phi_{D_{kT},D_{k+1,B}}^{FT} \phi_{D_{k+1,B},D_{k+1,T}}^F \eta_{D_{k+1,T}}^F;
\end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{D_{kT}}^T)}$, and separately for $k = 1, \dots, K-1$ and $\theta \in \Theta'_{5b(\eta_{D_{kT}}^T)}$,

$$\frac{\partial \eta_{D_{kT}}^T}{\partial \theta} = \frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{T_k}^T} \frac{\partial \eta_{T_k}^T}{\partial \theta} + \frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{T_k}^F} \frac{\partial \eta_{T_k}^F}{\partial \theta} + \frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{D_{k+1,T}}^F} \frac{\partial \eta_{D_{k+1,T}}^F}{\partial \theta} + \frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{D_{k+1,T}}^F} \frac{\partial \eta_{D_{k+1,T}}^F}{\partial \theta},$$

where

$$\begin{aligned}
\frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{T_k}^T} &= (1 - f_{D_{kT}}^T) \phi_{D_{kT},T_k}^T; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{T_k}^F} &= f_{D_{kT}}^T \phi_{D_{kT},T_k}^{FT}; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{D_{k+1,T}}^F} &= (1 - f_{D_{kT}}^T) \phi_{D_{kT},D_{k+1,B}}^T \phi_{D_{k+1,B},D_{k+1,T}}; \\
\frac{\partial \eta_{D_{kT}}^T}{\partial \eta_{D_{k+1,T}}^F} &= f_{D_{kT}}^T \phi_{D_{kT},D_{k+1,B}}^{FT} \phi_{D_{k+1,B},D_{k+1,T}}^F;
\end{aligned}$$

and where $\frac{\partial \eta_{T_k}^T}{\partial \theta}$, $\frac{\partial \eta_{T_k}^F}{\partial \theta}$, $\frac{\partial \eta_{D_{k+1,T}}^F}{\partial \theta}$, and $\frac{\partial \eta_{D_{k+1,T}}^F}{\partial \theta}$ are defined above.

Define $\Theta_{5b(\eta_{D_{kT}}^f)}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, T_j}^T & \quad j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1, B}} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1, B}}^T & = j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1, B}}^T & \quad j = k+1, \dots, K-1. \end{aligned}$$

Define $\Theta'_{5b(\eta_{D_{kT}}^f)}$ to be the set composed of the following parameters:

$$\phi_{D_{jB}, D_{jT}}^T \quad j = k+1, \dots, K; \quad \phi_{T_j, D_{j+1, B}} \quad j = k, \dots, K-1.$$

The parameter $\eta_{D_{kT}}^f$ is a function of the parameters $\phi_{D_{k+1, B}, D_{k+1, T}}$, ϕ_{D_{kT}, T_k} , and $\phi_{D_{kT}, D_{k+1, B}}$ and the parameters in the set $\Theta'_{5b(\eta_{D_{kT}}^f)}$ for $k = 2, \dots, K-1$. For $k = 2, \dots, K-2$, $\eta_{D_{kT}}^f$ is a function of the parameters in the set $\Theta_{5b(\eta_{D_{kT}}^f)}$. The partial derivatives involving $\eta_{D_{kT}}^f$ that are necessary for Equation (B.7) are the following:

for $k = 2, \dots, K-1$:

$$\begin{aligned} \frac{\partial \eta_{D_{kT}}^f}{\partial \phi_{D_{k+1, B}, D_{k+1, T}}} &= \phi_{D_{kT}, D_{k+1, B}} \eta_{D_{k+1, T}}^f; \\ \frac{\partial \eta_{D_{kT}}^f}{\partial \phi_{D_{kT}, T_k}} &= \eta_{T_k}^f; \\ \frac{\partial \eta_{D_{kT}}^f}{\partial \phi_{D_{kT}, D_{k+1, B}}} &= \phi_{D_{k+1, B}, D_{k+1, T}} \eta_{D_{k+1, T}}^f; \end{aligned}$$

for $k = 2, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{D_{kT}}^f)}$, and separately for $k = 2, \dots, K-1$ and $\theta \in \Theta'_{5b(\eta_{D_{kT}}^f)}$,

$$\frac{\partial \eta_{D_{kT}}^f}{\partial \theta} = \phi_{D_{kT}, T_k} \frac{\partial \eta_{T_k}^f}{\partial \theta} + \phi_{D_{kT}, D_{k+1, B}} \phi_{D_{k+1, B}, D_{k+1, T}} \frac{\partial \eta_{D_{k+1, T}}^f}{\partial \theta},$$

where $\frac{\partial \eta_{T_k}^f}{\partial \theta}$ is defined above.

Define $\Theta_{5b(\eta_{D_{kT}}^{fT})}$ to be the set composed of the following parameters:

$$\begin{array}{llll} \phi_{D_{jB}, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & j = k+1, \dots, K-1; \\ \phi_{D_{jT}, T_j}^T & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B}^T & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B} & j = k+1, \dots, K-1. \end{array}$$

Define $\Theta'_{5b(\eta_{D_{kT}}^{fT})}$ to be the set composed of the following parameters:

$$\phi_{D_{jB}, D_{jT}}^T \quad j = k+1, \dots, K; \quad \phi_{T_j, D_{j+1}, B}^T \quad j = k, \dots, K-1.$$

The parameter $\eta_{D_{kT}}^{fT}$ is a function of the parameters $\phi_{D_{k+1}, B, D_{k+1}, T}$, ϕ_{D_{kT}, T_k}^T , and $\phi_{D_{kT}, D_{k+1}, B}^T$, and of the parameters in the set $\Theta'_{5b(\eta_{D_{kT}}^{fT})}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\eta_{D_{kT}}^{fT}$ is a function of the parameters in the set $\Theta_{5b(\eta_{D_{kT}}^{fT})}$. The partial derivatives involving $\eta_{D_{kT}}^{fT}$ that are necessary for Equation (B.7) are:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \eta_{D_{kT}}^{fT}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= \phi_{D_{kT}, D_{k+1}, B}^T \eta_{D_{k+1}, T}^f; \\ \frac{\partial \eta_{D_{kT}}^{fT}}{\partial \phi_{D_{kT}, T_k}^T} &= \eta_{T_k}^{fT}; \\ \frac{\partial \eta_{D_{kT}}^{fT}}{\partial \phi_{D_{kT}, D_{k+1}, B}^T} &= \phi_{D_{k+1}, B, D_{k+1}, T} \eta_{D_{k+1}, T}^f; \end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{5b(\eta_{D_{kT}}^{fT})}$, and separately for $k = 1, \dots, K-1$ and $\theta \in \Theta'_{5b(\eta_{D_{kT}}^{fT})}$,

$$\frac{\partial \eta_{D_{kT}}^{fT}}{\partial \theta} = \phi_{D_{kT}, T_k}^T \frac{\partial \eta_{T_k}^{fT}}{\partial \theta} + \phi_{D_{kT}, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T} \frac{\partial \eta_{D_{k+1}, T}^f}{\partial \theta},$$

where $\frac{\partial \eta_{T_k}^{fT}}{\partial \theta}$ and $\frac{\partial \eta_{D_{k+1}, T}^f}{\partial \theta}$ are defined above.

B.2 Variance formulas for $\hat{\mu}_R$

The parameter μ_R is the unaccountable loss rate, i.e., the probability of *not* ending either in a tributary or at the top of the final dam (K). For all models, μ_R is defined in terms of the recursive parameters μ_i , which are in turn defined in terms of the basic model parameters.

B.2.1 Model 0

Because $\mu_R = 1 - \eta_R$ for Model 0,

$$\widehat{Var}(\hat{\mu}_R) = \widehat{Var}(\hat{\eta}_R);$$

(see Equation (B.1)).

B.2.2 Model 1

Because $\mu_R = 1 - \eta_R$ for Model 1,

$$\widehat{Var}(\hat{\mu}_R) = \widehat{Var}(\hat{\eta}_R);$$

see Equation (B.2).

B.2.3 Model 2

Define $\Theta_{2(\mu_R)}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{kB}, D_{kT}} & \quad k = 2, \dots, K; & \phi_{D_{kT}, T_k} & \quad k = 1, \dots, K-1; \\ \phi_{D_{kT}, D_{k+1, B}} & \quad k = 1, \dots, K-1. \end{aligned}$$

Define $\Theta_{2(\mu_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1, B}} & \quad j = k+1, \dots, K-1. \end{aligned}$$

For Model 2, μ_R is a function of ϕ_{R,T_0} , $\phi_{R,D_{1B}}$, and $\phi_{D_{1B},D_{1T}}$, and the parameters in the set $\Theta_{2(\eta_R)}$. The variance of $\hat{\mu}_R$ can be estimated by the following:

$$\begin{aligned}
\widehat{Var}(\hat{\mu}_R) &= \widehat{Var}(\hat{\phi}_{R,T_0}) + \left(\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} \right)^2 \widehat{Var}(\hat{\phi}_{R,D_{1B}}) + \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B},D_{1T}}) \\
&+ \sum_{\theta \in \Theta_{2(\mu_R)}} \sum_{\psi \in \Theta_{2(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \theta} \right) \left(\frac{\partial \mu_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\
&- 2 \left(\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R,T_0}, \hat{\phi}_{R,D_{1B}}) - 2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\phi}_{R,T_0}, \hat{\phi}_{D_{1B},D_{1T}}) \\
&- 2 \sum_{\theta \in \Theta_{2(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R,T_0}, \hat{\theta}) \\
&+ 2 \left(\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\phi}_{R,D_{1B}}, \hat{\phi}_{D_{1B},D_{1T}}) \\
&+ 2 \sum_{\theta \in \Theta_{2(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R,D_{1B}}, \hat{\theta}) \\
&+ 2 \sum_{\theta \in \Theta_{2(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{D_{1B},D_{1T}}, \hat{\theta}), \tag{B.8}
\end{aligned}$$

where the partial derivatives are all evaluated at the maximum likelihood estimates (MLEs).

The necessary partial derivatives are:

$$\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} = -\phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}); \quad \frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} = -\phi_{R,D_{1B}}(1 - \mu_{D_{1T}})$$

for $\theta \in \Theta_{2(\mu_R)}$,

$$\frac{\partial \mu_R}{\partial \theta} = \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \frac{\partial \mu_{D_{1T}}}{\partial \theta},$$

where $\frac{\partial \mu_{D_{1T}}}{\partial \theta}$ is defined below. The parameter $\mu_{D_{kT}}$ is a function of $\phi_{D_{k+1,B},D_{k+1,T}}$, ϕ_{D_{kT},T_k} , and $\phi_{D_{kT},D_{k+1,B}}$ for $k = 1, \dots, K-1$, and also of the parameters in the set $\Theta_{2(\mu_{D_{kT}})}$ for $k = 1, \dots, K-2$. The partial derivatives involving $\mu_{D_{kT}}$ that are necessary for Equation (B.8) are the following:

for $k = 1, \dots, K - 1$:

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1,B}, D_{k+1,T}}} &= -\phi_{D_{kT}, D_{k+1,B}}(1 - \mu_{D_{k+1,T}}); \\ \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}} &= -1; \\ \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1,B}}} &= -\phi_{D_{k+1,B}, D_{k+1,T}}(1 - \mu_{D_{k+1,T}});\end{aligned}$$

for $k = 1, \dots, K - 2$ and $\theta \in \Theta_{2(\mu_{D_{kT}})}$,

$$\frac{\partial \mu_{D_{kT}}}{\partial \theta} = \phi_{D_{kT}, D_{k+1,B}} \phi_{D_{k+1,B}, D_{k+1,T}} \frac{\partial \mu_{D_{k+1,T}}}{\partial \theta}.$$

B.2.4 Model 3a

Define $\Theta_{3a(\mu_R)}$ to be the set composed of the following parameters:

$$\begin{array}{llll}\phi_{D_{kB}, D_{kT}} & k = 2, \dots, K; & \phi_{D_{kT}, T_k} & k = 1, \dots, K - 1; \\ \phi_{D_{kT}, D_{k+1,B}} & k = 1, \dots, K - 1; & \phi_{T_k, D_{k+1,B}} & k = 1, \dots, K - 1.\end{array}$$

The parameter μ_R is a function of ϕ_{R, T_0} , $\phi_{R, D_{1B}}$, $\phi_{D_{1B}, D_{1T}}$, $\phi_{T_0, D_{1B}}$, and the parameters in the set $\Theta_{3a(\mu_R)}$. The variance of $\hat{\mu}_R$ can be estimated by the following:

$$\begin{aligned}\widehat{Var}(\hat{\mu}_R) &= \left(\frac{\partial \mu_R}{\partial \phi_{R, T_0}} \right)^2 \widehat{Var}(\hat{\phi}_{R, T_0}) + \left(\frac{\partial \mu_R}{\partial \phi_{R, D_{1B}}} \right)^2 \widehat{Var}(\hat{\phi}_{R, D_{1B}}) \\ &+ \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}) + \left(\frac{\partial \mu_R}{\partial \phi_{T_0, D_{1B}}} \right)^2 \widehat{Var}(\hat{\phi}_{T_0, D_{1B}}) \\ &+ \sum_{\theta \in \Theta_{3a(\mu_R)}} \sum_{\psi \in \Theta_{3a(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \theta} \right) \left(\frac{\partial \mu_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\ &+ 2 \left(\frac{\partial \mu_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{R, D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\phi}_{R, D_{1B}}) \\ &+ 2 \left(\frac{\partial \mu_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\phi}_{D_{1B}, D_{1T}})\end{aligned}$$

$$\begin{aligned}
& + 2 \left(\frac{\partial \mu_R}{\partial \phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{T_0,D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R,T_0}, \hat{\phi}_{T_0,D_{1B}}) \\
& + 2 \sum_{\theta \in \Theta_{3a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R,T_0}, \hat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\phi}_{R,D_{1B}}, \hat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{T_0,D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R,D_{1B}}, \hat{\phi}_{T_0,D_{1B}}) \\
& + 2 \sum_{\theta \in \Theta_{3a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R,D_{1B}}, \hat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{T_0,D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{D_{1B},D_{1T}}, \hat{\phi}_{T_0,D_{1B}}) \\
& + 2 \sum_{\theta \in \Theta_{3a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{D_{1B},D_{1T}}, \hat{\theta}) \\
& + 2 \sum_{\theta \in \Theta_{3a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{T_0,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{T_0,D_{1B}}, \hat{\theta}), \tag{B.9}
\end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The necessary partial derivatives are as follows:

$$\begin{aligned}
\frac{\partial \mu_R}{\partial \phi_{R,T_0}} &= \phi_{T_0,D_{1B}} [1 - \phi_{D_{1B},D_{1T}} (1 - \mu_{D_{1T}})] - 1; \\
\frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} &= -\phi_{D_{1B},D_{1T}} (1 - \mu_{D_{1T}}); \\
\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} &= -(\phi_{R,T_0} \phi_{T_0,D_{1B}} + \phi_{R,D_{1B}}) (1 - \mu_{D_{1T}}); \\
\frac{\partial \mu_R}{\partial \phi_{T_0,D_{1B}}} &= \phi_{R,T_0} [1 - \phi_{D_{1B},D_{1T}} (1 - \mu_{D_{1T}})];
\end{aligned}$$

for $\theta \in \Theta_{3a}(\mu_R)$,

$$\frac{\partial \mu_R}{\partial \theta} = (\phi_{R,T_0} \phi_{T_0,D_{1B}} + \phi_{R,D_{1B}}) \phi_{D_{1B},D_{1T}} \frac{\partial \mu_{D_{1T}}}{\partial \theta},$$

where $\frac{\partial \mu_{D_{kT}}}{\partial \theta}$ is defined below. Define $\Theta_{3a(\mu_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1, B}} & \quad j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1, B}} & \quad j = k+1, \dots, K-1. \end{aligned}$$

For $k = 1, \dots, K-1$, the parameter $\mu_{D_{kT}}$ is a function of the parameters $\phi_{D_{k+1, B}, D_{k+1, T}}$, ϕ_{D_{kT}, T_k} , $\phi_{D_{kT}, D_{k+1, B}}$, and $\phi_{T_k, D_{k+1, B}}$; for $k = 1, \dots, K-2$, $\mu_{D_{kT}}$ is also a function of the parameters in the set $\Theta_{3a(\mu_{D_{kT}})}$. The partial derivatives necessary for Equation (B.9) that involve $\mu_{D_{kT}}$ are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1, B}, D_{k+1, T}}} &= -(\phi_{D_{kT}, T_k} \phi_{T_k, D_{k+1, B}} + \phi_{D_{kT}, D_{k+1, B}})(1 - \mu_{D_{k+1, T}}); \\ \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}} &= \phi_{T_k, D_{k+1, B}}[1 - \phi_{D_{k+1, B}, D_{k+1, T}}(1 - \mu_{D_{k+1, T}})] - 1; \\ \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1, B}}} &= -\phi_{D_{k+1, B}, D_{k+1, T}}(1 - \mu_{D_{k+1, T}}); \\ \frac{\partial \mu_{D_{kT}}}{\partial \phi_{T_k, D_{k+1, B}}} &= \phi_{D_{kT}, T_k}[1 - \phi_{D_{k+1, B}, D_{k+1, T}}(1 - \mu_{D_{k+1, T}})]; \end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{3a(\mu_{D_{kT}})}$,

$$\frac{\partial \mu_{D_{kT}}}{\partial \theta} = (\phi_{D_{kT}, T_k} \phi_{T_k, D_{k+1, B}} + \phi_{D_{kT}, D_{k+1, B}}) \phi_{D_{k+1, B}, D_{k+1, T}} \frac{\partial \mu_{D_{k+1, T}}}{\partial \theta}.$$

B.2.5 Model 3b

Define $\Theta_{3b(\mu_R)}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{kB}, D_{kT}} & k = 2, \dots, K; & \phi_{D_{kB}, D_{kT}}^T & k = 1, \dots, K; \\
 \phi_{D_{kT}, T_k} & k = 1, \dots, K-1; & \phi_{D_{kT}, T_k}^T & k = 1, \dots, K-1; \\
 \phi_{D_{kT}, D_{k+1, B}} & k = 1, \dots, K-1; & \phi_{D_{kT}, D_{k+1, B}}^T & k = 1, \dots, K-1; \\
 \phi_{T_k, D_{k+1, B}} & k = 0, \dots, K-1; & \phi_{T_k, D_{k+1, B}}^T & k = 1, \dots, K-1.
 \end{array}$$

For Model 3b, the parameter μ_R is a function of ϕ_{R, T_0} , $\phi_{R, D_{1B}}$, $\phi_{D_{1B}, D_{1T}}$, and the parameters in the set $\Theta_{3b(\mu_R)}$. The variance of $\hat{\mu}_R$ can be estimated by the following expression:

$$\begin{aligned}
 \widehat{Var}(\hat{\mu}_R) &= \left(\frac{\partial \mu_R}{\partial \phi_{R, T_0}} \right)^2 \widehat{Var}(\hat{\phi}_{R, T_0}) + \left(\frac{\partial \mu_R}{\partial \phi_{R, D_{1B}}} \right)^2 \widehat{Var}(\hat{\phi}_{R, D_{1B}}) \\
 &+ \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}) \\
 &+ \sum_{\theta \in \Theta_{3b(\mu_R)}} \sum_{\psi \in \Theta_{3b(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \theta} \right) \left(\frac{\partial \mu_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\
 &+ 2 \left(\frac{\partial \mu_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{R, D_{1B}}} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\phi}_{R, D_{1B}}) \\
 &+ 2 \left(\frac{\partial \mu_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\phi}_{D_{1B}, D_{1T}}) \\
 &+ 2 \sum_{\theta \in \Theta_{3b(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \phi_{R, T_0}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R, T_0}, \hat{\theta}) \\
 &+ 2 \left(\frac{\partial \mu_R}{\partial \phi_{R, D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right) \widehat{Cov}(\hat{\phi}_{R, D_{1B}}, \hat{\phi}_{D_{1B}, D_{1T}}) \\
 &+ 2 \sum_{\theta \in \Theta_{3b(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \phi_{R, D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{R, D_{1B}}, \hat{\theta}) \\
 &+ 2 \sum_{\theta \in \Theta_{3b(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\phi}_{D_{1B}, D_{1T}}, \hat{\theta}), \tag{B.10}
 \end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The necessary partial derivatives are defined as follows:

$$\begin{aligned}\frac{\partial \mu_R}{\partial \phi_{R,T_0}} &= -(1 - \mu_{T_0}); & \frac{\partial \mu_R}{\partial \phi_{R,D_{1B}}} &= -\phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}); \\ \frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} &= -\phi_{R,D_{1B}}(1 - \mu_{D_{1T}}); & &\end{aligned}$$

for $\theta \in \Theta_{3b(\mu_R)}$,

$$\frac{\partial \mu_R}{\partial \theta} = \phi_{R,T_0} \frac{\partial \mu_{T_0}}{\partial \theta} + \phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \frac{\partial \mu_{D_{1T}}}{\partial \theta},$$

where $\frac{\partial \mu_{T_0}}{\partial \theta}$ and $\frac{\partial \mu_{D_{1T}}}{\partial \theta}$ are defined below.

Define $\Theta_{3b(\mu_{T_k})}$ to be the set composed of the following parameters:

$$\phi_{D_{jB},D_{jT}}^T \quad j = k+1, \dots, K; \quad \phi_{T_j,D_{j+1,B}} \quad j = k, \dots, K-1.$$

Define $\Theta'_{3b(\mu_{T_k})}$ to be the set composed of the following parameters:

$$\begin{aligned}\phi_{D_{jB},D_{jT}} \quad j = k+2, \dots, K; & \quad \phi_{D_{jT},T_j}^T \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT},D_{j+1,B}}^T \quad j = k+1, \dots, K-1; & \quad \phi_{T_j,D_{j+1,B}}^T \quad j = k+1, \dots, K-1.\end{aligned}$$

Define $\Theta''_{3b(\mu_{T_k})}$ to be the set composed of the following parameters:

$$\phi_{D_{jT},T_j} \quad j = k+2, \dots, K-1; \quad \phi_{D_{jT},D_{j+1,B}} \quad j = k+2, \dots, K-1.$$

For $k = 0, \dots, K-1$, μ_{T_k} is a function of $\phi_{T_k,D_{k+1,B}}$, $\phi_{D_{k+1,B},D_{k+1,T}}^T$, and the parameters in the set $\Theta_{3b(\mu_{T_k})}$. For $k = 0, \dots, K-2$, μ_{T_k} is also a function of the parameters in the set $\Theta'_{3b(\mu_{T_k})}$; for $k = 0, \dots, K-3$, μ_{T_k} is also a function of the parameters in the set $\Theta''_{3b(\mu_{T_k})}$. For partial derivatives involving μ_{T_k} that are necessary for Equation (B.10) are the following:

for $k = 0, \dots, K - 1$:

$$\begin{aligned}\frac{\partial \mu_{T_k}}{\partial \phi_{D_{k+1,B}, D_{k+1,T}}} &= -\phi_{T_k, D_{k+1,B}}(1 - \mu_{D_{k+1,T}}^T); \\ \frac{\partial \mu_{T_k}}{\partial \phi_{T_k, D_{k+1,B}}} &= 1 - \phi_{D_{k+1,B}, D_{k+1,T}}^T(1 - \mu_{D_{k+1,T}}^T);\end{aligned}$$

for $k = 0, \dots, K - 1$ and $\theta \in \Theta_{3b(\mu_{T_k})}$, for $k = 0, \dots, K - 2$ and $\theta \in \Theta'_{3b(\mu_{T_k})}$, or for $k = 0, \dots, K - 3$ and $\theta \in \Theta''_{3b(\mu_{T_k})}$,

$$\frac{\partial \mu_{T_k}}{\partial \theta} = \phi_{T_k, D_{k+1,B}} \phi_{D_{k+1,B}, D_{k+1,T}}^T \frac{\partial \mu_{D_{k+1,T}}^T}{\partial \theta},$$

where $\frac{\partial \mu_{D_{k+1,T}}^T}{\partial \theta}$ is defined below.

Define $\Theta_{3b(\mu_{T_k})}$ to be the set composed of the following parameters:

$$\begin{aligned}\phi_{D_jB, D_jT} & \quad j = k + 2, \dots, K; & \phi_{D_jB, D_jT}^T & \quad j = k + 2, \dots, K; \\ \phi_{D_jT, T_j}^T & \quad j = k + 1, \dots, K - 1; & \phi_{D_jT, D_{j+1,B}}^T & \quad j = k + 1, \dots, K - 1; \\ \phi_{T_j, D_{j+1,B}}^T & \quad j = k + 1, \dots, K - 1.\end{aligned}$$

Define $\Theta'_{3b(\mu_{T_k})}$ to be the set composed of the following parameters:

$$\begin{aligned}\phi_{D_jT, T_j} & \quad j = k + 2, \dots, K - 1; & \phi_{D_jT, D_{j+1,B}} & \quad j = k + 2, \dots, K - 1; \\ \phi_{T_j, D_{j+1,B}} & \quad j = k + 2, \dots, K - 1.\end{aligned}$$

The parameter $\mu_{T_k}^T$ is a function of $\phi_{D_{k+1,B}, D_{k+1,T}}^T$ and $\phi_{T_k, D_{k+1,B}}^T$ for $k = 1, \dots, K - 1$. For $k = 1, \dots, K - 2$, $\mu_{T_k}^T$ is also a function of the parameters in the set $\Theta_{3b(\mu_{T_k})}$, and for $k = 1, \dots, K - 3$, $\mu_{T_k}^T$ is also a function of the parameters in the set $\Theta'_{3b(\mu_{T_k})}$. The partial derivatives involving $\mu_{T_k}^T$ that are necessary for Equation (B.10) are the following:

for $k = 1, \dots, K - 1$:

$$\begin{aligned}\frac{\partial \mu_{T_k}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^T} &= -\phi_{T_k, D_{k+1}, B}^T (1 - \mu_{D_{k+1}, T}^T); \\ \frac{\partial \mu_{T_k}^T}{\partial \phi_{T_k, D_{k+1}, B}^T} &= 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T}^T);\end{aligned}$$

for $k = 1, \dots, K - 2$ and $\theta \in \Theta_{3b(\mu_{T_k}^T)}$, and separately for $k = 1, \dots, K - 3$ and $\theta \in \Theta'_{3b(\mu_{T_k}^T)}$,

$$\frac{\partial \mu_{T_k}^T}{\partial \theta} = \phi_{T_k, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T}^T \frac{\partial \mu_{D_{k+1}, T}^T}{\partial \theta},$$

where $\frac{\partial \mu_{D_{k+1}, T}^T}{\partial \theta}$ is defined below.

Define $\Theta_{3b(\mu_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{array}{lll} \phi_{D_{jB}, D_{jT}} & j = k + 2, \dots, K; & \phi_{D_{jT}, T_j} \quad j = k + 1, \dots, K - 1; \\ \phi_{D_{jT}, T_j}^T & j = k + 1, \dots, K - 1; & \phi_{D_{jT}, D_{j+1}, B} \quad j = k + 1, \dots, K - 1; \\ \phi_{D_{jT}, D_{j+1}, B}^T & j = k + 1, \dots, K - 1; & \phi_{T_j, D_{j+1}, B}^T \quad j = k + 1, \dots, K - 1.\end{array}$$

The parameter $\mu_{D_{kT}}$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, ϕ_{D_{kT}, T_k} , $\phi_{D_{kT}, D_{k+1}, B}$, and the parameters in the set $\Theta_{3b(\mu_{T_k}^T)}$ for $k = 1, \dots, K - 1$. For $k = 1, \dots, K - 2$, $\mu_{D_{kT}}$ is also a function of the parameters in the set $\Theta_{3b(\mu_{D_{kT}})}$. The partial derivatives involving $\mu_{D_{kT}}$ that are necessary for Equation (B.10) are the following:

for $k = 1, \dots, K - 1$:

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= -\phi_{D_{kT}, D_{k+1}, B} (1 - \mu_{D_{k+1}, T}); \\ \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}} &= -(1 - \mu_{T_k}); \\ \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1}, B}} &= -\phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T});\end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{3b(\mu_{T_k})}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta_{3b(\mu_{D_{kT}})}$,

$$\frac{\partial \mu_{D_{kT}}}{\partial \theta} = \phi_{D_{kT}, T_k} \frac{\partial \mu_{T_k}}{\partial \theta} + \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} \frac{\partial \mu_{D_{k+1}, T}}{\partial \theta},$$

where $\frac{\partial \mu_{T_k}}{\partial \theta}$ is defined above.

Define $\Theta_{3b(\mu_{D_{kT}}^T)}$ to be the set composed of the following parameters:

$$\phi_{D_{jB}, D_{jT}}^T \quad j = k+1, \dots, K; \quad \phi_{T_j, D_{j+1}, B}^T \quad j = k, \dots, K-1.$$

Define $\Theta'_{3b(\mu_{D_{kT}}^T)}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, T_j}^T & \quad j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B}^T & \quad j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B} & \quad j = k+1, \dots, K-1. \end{aligned} \tag{B.11}$$

The parameters $\mu_{D_{kT}}^T$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, ϕ_{D_{kT}, T_k}^T , $\phi_{D_{kT}, D_{k+1}, B}^T$, and the parameters in the set $\Theta_{3b(\mu_{D_{kT}}^T)}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\mu_{D_{kT}}^T$ is also a function of the parameters in the set $\Theta'_{3b(\mu_{D_{kT}}^T)}$. The partial derivatives involving $\mu_{D_{kT}}^T$ that are necessary for Equation (B.10) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= -\phi_{D_{kT}, D_{k+1}, B}^T (1 - \mu_{D_{k+1}, T}); \\ \frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{kT}, T_k}^T} &= -(1 - \mu_{T_k}^T); \\ \frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{kT}, D_{k+1}, B}^T} &= -\phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}); \end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{3b(\mu_{D_{kT}}^T)}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta'_{3b(\mu_{D_{kT}}^T)}$,

$$\frac{\partial \mu_{D_{kT}}^T}{\partial \theta} = \phi_{D_{kT}, T_k}^T \frac{\partial \mu_{T_k}^T}{\partial \theta} + \phi_{D_{kT}, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T} \frac{\partial \mu_{D_{k+1}, T}}{\partial \theta},$$

where $\frac{\partial \mu_{T_k}^T}{\partial \theta}$ and $\frac{\partial \mu_{D_{k+1}, T}}{\partial \theta}$ are defined above.

B.2.6 Model 4

Define $\Theta_{4(\mu_R)}$ to be the set composed of the following parameters:

$$\begin{array}{llll} \phi_{D_{kB}, D_{kT}} & k = 2, \dots, K; & \phi_{D_{kB}, D_{kT}}^F & k = 2, \dots, K; \\ \phi_{D_{kT}, T_k} & k = 1, \dots, K-1; & \phi_{D_{kT}, T_k}^F & k = 1, \dots, K-1; \\ \phi_{D_{kT}, D_{k+1}, B} & k = 1, \dots, K-1; & \phi_{D_{kT}, D_{k+1}, B}^F & k = 1, \dots, K-1; \\ f_{D_{kT}} & k = 1, \dots, K-1. & & \end{array}$$

The parameter μ_R is a function of the Φ_{R, T_0} , Φ_{R, T_0}^F , $\Phi_{R, D_{1B}}$, $\Phi_{R, D_{1B}}^F$, $\phi_{D_{1B}, D_{1T}}$, $\phi_{D_{1B}, D_{1T}}^F$, and the parameters in the set $\Theta_{4(\mu_R)}$. The variance of $\hat{\mu}_R$ can be estimated by the following expression for Model 4:

$$\begin{aligned} \widehat{Var}(\hat{\mu}_R) &= \widehat{Var}(\hat{\Phi}_{R, T_0}) + \widehat{Var}(\hat{\Phi}_{R, T_0}^F) \\ &+ \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}) + \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}^F) \\ &+ \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}) + \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}^F) \\ &+ \sum_{\theta \in \Theta_{4(\mu_R)}} \sum_{\psi \in \Theta_{4(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \theta} \right) \left(\frac{\partial \mu_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\ &+ 2 \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\Phi}_{R, T_0}^F) - 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\Phi}_{R, D_{1B}}) \\ &- 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\Phi}_{R, D_{1B}}^F) - 2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\phi}_{D_{1B}, D_{1T}}) \\ &- 2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\phi}_{D_{1B}, D_{1T}}^F) \end{aligned}$$

$$\begin{aligned}
& -2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, T_0}, \widehat{\phi}_{D_{1B}, D_{1T}}^F) - 2 \sum_{\theta \in \Theta_4(\mu_R)} \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R, T_0}, \widehat{\theta}) \\
& -2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, T_0}^F, \widehat{\Phi}_{R, D_{1B}}^F) - 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, T_0}^F, \widehat{\Phi}_{R, D_{1B}}^F) \\
& -2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, T_0}^F, \widehat{\phi}_{D_{1B}, D_{1T}}^F) - 2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, T_0}^F, \widehat{\phi}_{D_{1B}, D_{1T}}^F) \\
& -2 \sum_{\theta \in \Theta_4(\mu_R)} \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R, T_0}^F, \widehat{\theta}) \\
& +2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, D_{1B}}^F, \widehat{\Phi}_{R, D_{1B}}^F) \\
& +2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, D_{1B}}^F, \widehat{\phi}_{D_{1B}, D_{1T}}^F) \\
& +2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, D_{1B}}^F, \widehat{\phi}_{D_{1B}, D_{1T}}^F) \\
& +2 \sum_{\theta \in \Theta_4(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R, D_{1B}}^F, \widehat{\theta}) \\
& +2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, D_{1B}}^F, \widehat{\phi}_{D_{1B}, D_{1T}}^F) \\
& +2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R, D_{1B}}^F, \widehat{\phi}_{D_{1B}, D_{1T}}^F) \\
& +2 \sum_{\theta \in \Theta_4(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R, D_{1B}}^F, \widehat{\theta}) \\
& +2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B}, D_{1T}}^F, \widehat{\phi}_{D_{1B}, D_{1T}}^F) \\
& +2 \sum_{\theta \in \Theta_4(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B}, D_{1T}}^F, \widehat{\theta}) \\
& +2 \sum_{\theta \in \Theta_4(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B}, D_{1T}}^F, \widehat{\theta}), \tag{B.12}
\end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The partial derivatives necessary for Equation (B.12) are the following:

$$\begin{aligned}\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} &= -\phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}); & \frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} &= -\phi_{D_{1B},D_{1T}}^F(1 - \mu_{D_{1T}}^F); \\ \frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} &= -\Phi_{R,D_{1B}}(1 - \mu_{D_{1T}}); & \frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} &= -\Phi_{R,D_{1B}}^F(1 - \mu_{D_{1T}}^F);\end{aligned}$$

for $\theta \in \Theta_{4(\mu_R)}$,

$$\frac{\partial \mu_R}{\partial \theta} = \Phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \frac{\partial \mu_{D_{1T}}}{\partial \theta} + \Phi_{R,D_{1B}}^F \phi_{D_{1B},D_{1T}}^F \frac{\partial \mu_{D_{1T}}^F}{\partial \theta},$$

where $\frac{\partial \mu_{D_{1T}}}{\partial \theta}$ and $\frac{\partial \mu_{D_{1T}}^F}{\partial \theta}$ are defined below. Define $\Theta_{4(\mu_{D_{kT}})}$ to be the sets composed of the following parameters:

$$\begin{aligned}\phi_{D_{jB},D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jB},D_{jT}}^F & \quad j = k+2, \dots, K; \\ \phi_{D_{jT},T_j} & \quad j = k+1, \dots, K-1; & \phi_{D_{jT},T_j}^F & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT},D_{j+1,B}} & \quad j = k+1, \dots, K-1; & \phi_{D_{jT},D_{j+1,B}}^F & \quad j = k+1, \dots, K-1; \\ f_{D_{jT}} & \quad j = k+1, \dots, K-1.\end{aligned}$$

The parameter $\mu_{D_{kT}}$ is a function of the parameters $\phi_{D_{k+1,B},D_{k+1,T}}$, $\phi_{D_{k+1,B},D_{k+1,T}}^F$, ϕ_{D_{kT},T_k} , ϕ_{D_{kT},T_k}^F , $\phi_{D_{kT},D_{k+1,B}}$, $\phi_{D_{kT},D_{k+1,B}}^F$, and $f_{D_{kT}}$ for $k = 1, \dots, K-1$; for $k = 1, \dots, K-2$, $\mu_{D_{kT}}$ is also a function of the parameters in the set $\Theta_{4(\mu_{D_{kT}})}$. The partial derivatives involving $\mu_{D_{kT}}$ that are necessary for Equation (B.12) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1,B},D_{k+1,T}}} &= -(1 - f_{D_{kT}}) \phi_{D_{kT},D_{k+1,B}}(1 - \mu_{D_{k+1,T}}); \\ \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1,B},D_{k+1,T}}^F} &= -f_{D_{kT}} \phi_{D_{kT},D_{k+1,B}}^F(1 - \mu_{D_{k+1,T}}^F);\end{aligned}$$

$$\begin{aligned}
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}} &= -(1 - f_{D_{kT}}); \\
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}^F} &= -f_{D_{kT}}; \\
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1}, B}} &= -(1 - f_{D_{kT}}) \phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}); \\
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1}, B}^F} &= -f_{D_{kT}} \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F); \\
\frac{\partial \mu_{D_{kT}}}{\partial f_{D_{kT}}} &= \phi_{D_{kT}, T_k} + \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}) - \phi_{D_{kT}, T_k}^F \\
&\quad - \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F);
\end{aligned}$$

for $k = 1, \dots, K - 2$ and $\theta \in \Theta_{4(\mu_{D_{kT}})}$,

$$\frac{\partial \mu_{D_{kT}}}{\partial \theta} = \frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1}, T}} \frac{\partial \mu_{D_{k+1}, T}}{\partial \theta} + \frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1}, T}^F} \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta},$$

where

$$\begin{aligned}
\frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1}, T}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}, \\
\frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1}, T}^F} &= f_{D_{kT}} \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F,
\end{aligned}$$

and $\frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta}$ is defined below. Define $\Theta_{4(\mu_{D_{kT}}^F)}$ to be the set composed of the following parameters:

$$\begin{aligned}
\phi_{D_{jB}, D_{jT}}^F \quad j = k + 2, \dots, K; \quad \phi_{D_{jT}, T_j}^F \quad j = k + 1, \dots, K - 1; \\
\phi_{D_{jT}, D_{j+1}, B}^F \quad j = k + 1, \dots, K - 1.
\end{aligned}$$

The parameter $\mu_{D_{kT}}^F$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, ϕ_{D_{kT}, T_k}^F , and $\phi_{D_{kT}, D_{k+1}, B}^F$ for $k = 1, \dots, K - 1$. For $k = 1, \dots, K - 2$, $\mu_{D_{kT}}^F$ is also a function of the parameters in the set $\Theta_{4(\mu_{D_{kT}}^F)}$. The partial derivatives involving $\mu_{D_{kT}}^F$ that are necessary for Equation (B.12) are

the following:

for $k = 1, \dots, K - 1$:

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{k+1,B}, D_{k+1,T}}^F} &= -\phi_{D_{kT}, D_{k+1,B}}^F (1 - \mu_{D_{k+1,T}}^F); \\ \frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{kT}, T_k}^F} &= -1; \\ \frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{kT}, D_{k+1,B}}^F} &= -\phi_{D_{k+1,B}, D_{k+1,T}}^F (1 - \mu_{D_{k+1,T}}^F);\end{aligned}$$

for $k = 1, \dots, K - 2$ and $\theta \in \Theta_{4(\mu_{D_{kT}}^F)}$,

$$\frac{\partial \mu_{D_{kT}}^F}{\partial \theta} = \phi_{D_{kT}, D_{k+1,B}}^F \phi_{D_{k+1,B}, D_{k+1,T}}^F \frac{\mu_{D_{k+1,T}}^F}{\partial \theta}.$$

B.2.7 Model 5a

Define $\Theta_{5a(\mu_R)}$ to be the set composed of the following parameters:

$\phi_{D_{kB}, D_{kT}}$	$k = 2, \dots, K;$	$\phi_{D_{kB}, D_{kT}}^F$	$k = 2, \dots, K;$
ϕ_{D_{kT}, T_k}	$k = 1, \dots, K - 1;$	ϕ_{D_{kT}, T_k}^F	$k = 1, \dots, K - 1;$
$\phi_{D_{kT}, D_{k+1,B}}$	$k = 1, \dots, K - 1;$	$\phi_{D_{kT}, D_{k+1,B}}^F$	$k = 1, \dots, K - 1;$
$\phi_{T_k, D_{k+1,B}}$	$k = 0, \dots, K - 1;$	$\phi_{T_k, D_{k+1,B}}^F$	$k = 0, \dots, K - 1;$
$f_{D_{kT}}$	$k = 1, \dots, K - 1;$	f_{T_k}	$k = 0, \dots, K - 1.$

For Model 5a, the parameter μ_R is a function of Φ_{R, T_0} , ϕ_{R, T_0}^F , $\Phi_{R, D_{1B}}$, $\Phi_{R, D_{1B}}^F$, $\phi_{D_{1B}, D_{1T}}$, $\phi_{D_{1B}, D_{1T}}^F$, and the parameters in the set $\Theta_{5a(\mu_R)}$. The variance of $\hat{\mu}_R$ can be estimated by the following expression for Model 5a:

$$\widehat{Var}(\hat{\mu}_R) = \left(\frac{\partial \mu_R}{\partial \Phi_{R, T_0}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, T_0}) + \left(\frac{\partial \mu_R}{\partial \Phi_{R, T_0}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, T_0}^F)$$

$$\begin{aligned}
& + \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right)^2 \widehat{Var}(\hat{\phi}_{R,D_{1B}}) + \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R,D_{1B}}^F) \\
& + \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B},D_{1T}}) + \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B},D_{1T}}^F) \\
& + \sum_{\theta \in \Theta_{5a}(\mu_R)} \sum_{\psi \in \Theta_{5a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \theta} \right) \left(\frac{\partial \mu_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\Phi}_{R,T_0}^F) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\Phi}_{R,D_{1B}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}, \hat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\Phi}_{R,D_{1B}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\hat{\Phi}_{R,T_0}^F, \hat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\hat{\Phi}_{R,D_{1B}}, \hat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\hat{\Phi}_{R,D_{1B}}, \hat{\phi}_{D_{1B},D_{1T}})
\end{aligned}$$

$$\begin{aligned}
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\theta}) \\
& + 2 \sum_{\theta \in \Theta_{5a}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}^F, \widehat{\theta}), \tag{B.13}
\end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The partial derivatives necessary for Equation (B.13) are the following:

$$\begin{aligned}
\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} &= -(1 - \mu_{T_0}); \\
\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} &= -(1 - \mu_{T_0}^F); \\
\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} &= -\phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}); \\
\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} &= -\phi_{D_{1B},D_{1T}}^F(1 - \mu_{D_{1T}}^F); \\
\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} &= \Phi_{R,T_0} \frac{\partial \mu_{T_0}}{\partial \phi_{D_{1B},D_{1T}}} - \Phi_{R,D_{1B}}(1 - \mu_{D_{1T}}); \\
\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} &= \Phi_{R,T_0} \frac{\partial \mu_{T_0}}{\partial \phi_{D_{1B},D_{1T}}^F} + \Phi_{R,T_0}^F \frac{\partial \mu_{T_0}^F}{\partial \phi_{D_{1B},D_{1T}}^F} - \Phi_{R,D_{1B}}^F(1 - \mu_{D_{1T}}^F);
\end{aligned}$$

for $\theta \in \Theta_{5a(\mu_R)}$,

$$\frac{\partial \mu_R}{\partial \theta} = \Phi_{R,T_0} \frac{\partial \mu_{T_0}}{\partial \theta} + \Phi_{R,T_0}^F \frac{\partial \mu_{T_0}^F}{\partial \theta} + \Phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \frac{\partial \mu_{D_{1T}}}{\partial \theta} + \Phi_{R,D_{1B}}^F \phi_{D_{1B},D_{1T}}^F \frac{\partial \mu_{D_{1T}}^F}{\partial \theta},$$

where the partial derivatives involving μ_{T_0} , $\mu_{T_0}^F$, $\mu_{D_{1T}}$, and $\mu_{D_{1T}}^F$ are defined below.

Define $\Theta_{5a(\mu_{T_k})}$ to be the set composed of the following parameters:

$$\begin{array}{llll} \phi_{D_{jB},D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jB},D_{jT}}^F & j = k+2, \dots, K; \\ \phi_{D_{jT},T_j} & j = k+1, \dots, K-1; & \phi_{D_{jT},T_k}^F & j = k+1, \dots, K-1; \\ \phi_{D_{jT},D_{j+1,B}} & j = k+1, \dots, K-1; & \phi_{D_{jT},D_{j+1,B}}^F & j = k+1, \dots, K-1; \\ \phi_{T_j,D_{j+1,B}} & j = k+1, \dots, K-1; & \phi_{T_j,D_{j+1,B}}^F & j = k+1, \dots, K-1; \\ f_{D_{jT}} & j = k+1, \dots, K-1; & f_{T_j} & j = k+1, \dots, K-1. \end{array}$$

The parameter μ_{T_k} is a function of the parameters $\phi_{D_{k+1,B},D_{k+1,T}}$, $\phi_{D_{k+1,B},D_{k+1,T}}^F$, $\phi_{T_k,D_{k+1,B}}$, $\phi_{T_k,D_{k+1,B}}^F$, and f_{T_k} for $k = 0, \dots, K-1$. For $k = 0, \dots, K-2$, μ_{T_k} is also a function of the parameters in the set $\Theta_{5a(\mu_{T_k})}$. The partial derivatives involving μ_{T_k} that are necessary for Equation (B.13) are the following:

for $k = 0, \dots, K-1$:

$$\begin{aligned} \frac{\partial \mu_{T_k}}{\partial \phi_{D_{k+1,B},D_{k+1,T}}} &= -(1 - f_{T_k}) \phi_{T_k,D_{k+1,B}} (1 - \mu_{D_{k+1,T}}); \\ \frac{\partial \mu_{T_k}}{\partial \phi_{D_{k+1,B},D_{k+1,T}}^F} &= -f_{T_k} \phi_{T_k,D_{k+1,B}}^F (1 - \mu_{D_{k+1,T}}^F); \\ \frac{\partial \mu_{T_k}}{\partial \phi_{T_k,D_{k+1,B}}} &= (1 - f_{T_k}) [1 - \phi_{D_{k+1,B},D_{k+1,T}} (1 - \mu_{D_{k+1,T}})]; \\ \frac{\partial \mu_{T_k}}{\partial \phi_{T_k,D_{k+1,B}}^F} &= f_{T_k} [1 - \phi_{D_{k+1,B},D_{k+1,T}}^F (1 - \mu_{D_{k+1,T}}^F)]; \end{aligned}$$

$$\begin{aligned} \frac{\partial \mu_{T_k}}{\partial f_{T_k}} &= -\phi_{T_k, D_{k+1}, B} [1 - \phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T})] \\ &\quad + \phi_{T_k, D_{k+1}, B}^F [1 - \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F)]; \end{aligned} \quad (\text{B.14})$$

for $k = 0, \dots, K-2$ and $\theta \in \Theta_{5a}(\mu_{T_k})$,

$$\frac{\partial \mu_{T_k}}{\partial \theta} = \frac{\partial \mu_{T_k}}{\partial \mu_{D_{k+1}, T}} \frac{\partial \mu_{D_{k+1}, T}}{\partial \theta} + \frac{\partial \mu_{T_k}}{\partial \mu_{D_{k+1}, T}^F} \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta},$$

where

$$\begin{aligned} \frac{\partial \mu_{T_k}}{\partial \mu_{D_{k+1}, T}} &= (1 - f_{T_k}) \phi_{T_k, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}; \\ \frac{\partial \mu_{T_k}}{\partial \mu_{D_{k+1}, T}^F} &= f_{T_k} \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F; \end{aligned}$$

and $\frac{\partial \mu_{D_{k+1}, T}}{\partial \theta}$ and $\frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta}$ are defined below.

Define $\Theta_{5a}(\mu_{T_k}^F)$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}}^F & \quad j = k+2, \dots, K-1; & \phi_{D_{jT}, T_j}^F & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B}^F & \quad j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^F & \quad j = k+1, \dots, K-1. \end{aligned}$$

For Model 5a, the parameter $\mu_{T_k}^F$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}^F$ and $\phi_{T_k, D_{k+1}, B}^F$ for $k = 0, \dots, K-1$, and also of the parameters in the set $\Theta_{5a}(\mu_{T_k}^F)$ for $k = 0, \dots, K-2$. The partial derivatives involving $\mu_{T_k}^F$ that are necessary for Equation (B.13) are the following:

for $k = 0, \dots, K-1$:

$$\frac{\partial \mu_{T_k}^F}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} = -\phi_{T_k, D_{k+1}, B}^F (1 - \mu_{D_{k+1}, T}^F);$$

$$\frac{\partial \mu_{T_k}^F}{\partial \phi_{T_k, D_{k+1}, B}^F} = 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F);$$

for $k = 0, \dots, K-2$ and $\theta \in \Theta_{5a(\mu_{T_k}^F)}$,

$$\frac{\partial \mu_{T_k}^F}{\partial \theta} = \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta},$$

where $\frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta}$ is defined below.

Define $\Theta_{5a(\mu_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{T_j, D_{j+1}, B} & \quad j = k, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^F & \quad j = k, \dots, K-1; \\ f_{T_j} & \quad j = k, \dots, K-1. \end{aligned}$$

Define $\Theta'_{5a(\mu_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jB}, D_{jT}}^F & \quad j = k+2, \dots, K; \\ \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^F & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B} & \quad j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B}^F & \quad j = k+1, \dots, K-1; \\ f_{D_{jT}} & \quad j = k+1, \dots, K-1. \end{aligned}$$

For Model 5a, the parameter $\mu_{D_{kT}}$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, ϕ_{D_{kT}, T_k} , ϕ_{D_{kT}, T_k}^F , $\phi_{D_{kT}, D_{k+1}, B}$, $\phi_{D_{kT}, D_{k+1}, B}^F$, $f_{D_{kT}}$, and the parameters in the set $\Theta_{5a(\mu_{D_{kT}})}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\mu_{D_{kT}}$ is also a function of the parameters in the set $\Theta'_{5a(\mu_{D_{kT}})}$. The partial derivatives involving $\mu_{D_{kT}}$ that are necessary for Equation (B.13) are the following:

for $k = 1, \dots, K-1$:

$$\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} = (1 - f_{D_{kT}}) [\phi_{D_{kT}, T_k} \frac{\partial \mu_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} - \phi_{D_{kT}, D_{k+1}, B} (1 - \mu_{D_{k+1}, T})];$$

$$\begin{aligned}
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1,B},D_{k+1,T}}^F} &= (1 - f_{D_{kT}}) \phi_{D_{kT},T_k} \frac{\partial \mu_{T_k}}{\partial \phi_{D_{k+1,B},D_{k+1,T}}^F} + f_{D_{kT}} \phi_{D_{kT},T_k}^F \frac{\partial \mu_{T_k}^F}{\partial \phi_{D_{k+1,B},D_{k+1,T}}^F} \\
&\quad - f_{D_{kT}} \phi_{D_{kT},D_{k+1,B}}^F (1 - \mu_{D_{k+1,T}}^F); \\
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT},T_k}} &= -(1 - f_{D_{kT}})(1 - \mu_{T_k}); \\
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT},T_k}^F} &= -f_{D_{kT}}(1 - \mu_{T_k}^F); \\
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT},D_{k+1,B}}} &= -(1 - f_{D_{kT}}) \phi_{D_{k+1,B},D_{k+1,T}} (1 - \mu_{D_{k+1,T}}); \\
\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT},D_{k+1,B}}^F} &= -f_{D_{kT}} \phi_{D_{k+1,B},D_{k+1,T}}^F (1 - \mu_{D_{k+1,T}}^F); \\
\frac{\partial \mu_{D_{kT}}}{\partial f_{D_{kT}}} &= \phi_{D_{kT},T_k} (1 - \mu_{T_k}) + \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}} (1 - \mu_{D_{k+1,T}}) \\
&\quad - \phi_{D_{kT},T_k}^F (1 - \mu_{T_k}^F) - \phi_{D_{kT},D_{k+1,B}}^F \phi_{D_{k+1,B},D_{k+1,T}}^F (1 - \mu_{D_{k+1,T}}^F);
\end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{5a(\mu_{D_{kT}})}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta'_{5a(\mu_{D_{kT}})}$,

$$\frac{\partial \mu_{D_{kT}}}{\partial \theta} = \frac{\partial \mu_{D_{kT}}}{\partial \mu_{T_k}} \frac{\partial \mu_{T_k}}{\partial \theta} + \frac{\partial \mu_{D_{kT}}}{\partial \mu_{T_k}^F} \frac{\partial \mu_{T_k}^F}{\partial \theta} + \frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1,T}}} \frac{\partial \mu_{D_{k+1,T}}}{\partial \theta} + \frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1,T}}^F} \frac{\partial \mu_{D_{k+1,T}}^F}{\partial \theta},$$

where

$$\begin{aligned}
\frac{\partial \mu_{D_{kT}}}{\partial \mu_{T_k}} &= (1 - f_{D_{kT}}) \phi_{D_{kT},T_k}; \\
\frac{\partial \mu_{D_{kT}}}{\partial \mu_{T_k}^F} &= f_{D_{kT}} \phi_{D_{kT},T_k}^F; \\
\frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1,T}}} &= (1 - f_{D_{kT}}) \phi_{D_{kT},D_{k+1,B}} \phi_{D_{k+1,B},D_{k+1,T}}; \\
\frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1,T}}^F} &= f_{D_{kT}} \phi_{D_{kT},D_{k+1,B}}^F \phi_{D_{k+1,B},D_{k+1,T}}^F.
\end{aligned}$$

The partial derivatives $\frac{\partial \mu_{T_k}}{\partial \theta}$ and $\frac{\partial \mu_{T_k}^F}{\partial \theta}$ are defined above, and $\frac{\partial \mu_{D_{k+1,T}}^F}{\partial \theta}$ is defined below.

Define $\Theta_{5a(\mu_{D_{kT}}^F)}$ to be the set composed of the parameters $\phi_{T_j, D_{j+1}, B}^T$ ($j = k, \dots, K-1$). Define $\Theta'_{5a(\mu_{D_{kT}}^F)}$ to be set composed of the following parameters:

$$\begin{aligned} \phi_{D_j B, D_j T}^F & \quad j = k+2, \dots, K; & \phi_{D_j T, T_j}^F & \quad j = k+1, \dots, K-1; \\ \phi_{D_j T, D_{j+1}, B}^F & \quad j = k+1, \dots, K-1. \end{aligned}$$

For Model 5a, the parameter $\mu_{D_{k+1}, T}^F$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, ϕ_{D_{kT}, T_k}^F , $\phi_{D_{kT}, D_{k+1}, B}^F$, and the parameters in the set $\Theta_{5a(\mu_{D_{kT}}^F)}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\mu_{D_{k+1}, T}^F$ is also a function of the parameters in the set $\Theta'_{5a(\mu_{D_{kT}}^F)}$. The partial derivatives involving $\mu_{D_{kT}}^F$ that are necessary for Equation (B.13) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= -\phi_{D_{kT}, D_{k+1}, B}^F (1 - \mu_{D_{k+1}, T}^F); \\ \frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{kT}, T_k}^F} &= -(1 - \mu_{T_k}^F); \\ \frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{kT}, D_{k+1}, B}^F} &= -\phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F); \end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{5a(\mu_{D_{kT}}^F)}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta'_{5a(\mu_{D_{kT}}^F)}$,

$$\frac{\partial \mu_{D_{kT}}^F}{\partial \theta} = \phi_{D_{kT}, T_k}^F \frac{\partial \mu_{T_k}^F}{\partial \theta} + \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta},$$

where $\frac{\partial \mu_{T_k}^F}{\partial \theta}$ is defined above.

B.2.8 Models 5b and 6

Define $\Theta_{5b(\mu_R)}$ to be the set composed of the following parameters:

$\phi_{D_{kB}, D_{kT}}$	$k = 2, \dots, K;$	$\phi_{D_{kB}, D_{kT}}^F$	$k = 2, \dots, K;$
$\phi_{D_{kB}, D_{kT}}^T$	$k = 1, \dots, K;$	ϕ_{D_{kT}, T_k}	$k = 1, \dots, K - 1;$
ϕ_{D_{kT}, T_k}^F	$k = 1, \dots, K - 1;$	ϕ_{D_{kT}, T_k}^T	$k = 1, \dots, K - 1;$
ϕ_{D_{kT}, T_k}^{FT}	$k = 1, \dots, K - 1;$	$\phi_{D_{kT}, D_{k+1}, B}$	$k = 1, \dots, K - 1;$
$\phi_{D_{kT}, D_{k+1}, B}^F$	$k = 1, \dots, K - 1;$	$\phi_{D_{kT}, D_{k+1}, B}^T$	$k = 1, \dots, K - 1;$
$\phi_{D_{kT}, D_{k+1}, B}^{FT}$	$k = 1, \dots, K - 1;$	$\phi_{T_k, D_{k+1}, B}$	$k = 0, \dots, K - 1;$
$\phi_{T_k, D_{k+1}, B}^F$	$k = 0, \dots, K - 1;$	$\phi_{T_k, D_{k+1}, B}^T$	$k = 1, \dots, K - 1;$
$\phi_{T_k, D_{k+1}, B}^{FT}$	$k = 1, \dots, K - 1;$	$f_{D_{kT}}$	$k = 1, \dots, K - 1;$
$f_{D_{kT}}^T$	$k = 1, \dots, K - 1;$	f_{T_k}	$k = 0, \dots, K - 1;$
$f_{T_k}^T$	$k = 1, \dots, K - 1.$		

For Model 5b, the parameter μ_R is a function of Φ_{R, T_0} , Φ_{R, T_0}^F , $\Phi_{R, D_{1B}}$, $\Phi_{R, D_{1B}}^F$, $\phi_{D_{1B}, D_{1T}}$, $\phi_{D_{1B}, D_{1T}}^F$, and the parameters in the set $\Theta_{5b(\mu_R)}$. The variance of $\hat{\mu}_R$ can be estimated by the following expression for Model 5b:

$$\begin{aligned}
 \widehat{Var}(\hat{\mu}_R) &= \left(\frac{\partial \mu_R}{\partial \Phi_{R, T_0}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, T_0}) + \left(\frac{\partial \mu_R}{\partial \Phi_{R, T_0}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, T_0}^F) \\
 &+ \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}) + \left(\frac{\partial \mu_R}{\partial \Phi_{R, D_{1B}}^F} \right)^2 \widehat{Var}(\hat{\Phi}_{R, D_{1B}}^F) \\
 &+ \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}) + \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B}, D_{1T}}^F} \right)^2 \widehat{Var}(\hat{\phi}_{D_{1B}, D_{1T}}^F) \\
 &+ \sum_{\theta \in \Theta_{5b(\mu_R)}} \sum_{\psi \in \Theta_{5b(\mu_R)}} \left(\frac{\partial \mu_R}{\partial \theta} \right) \left(\frac{\partial \mu_R}{\partial \psi} \right) \widehat{Cov}(\hat{\theta}, \hat{\psi}) \\
 &+ 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R, T_0}} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R, T_0}^F} \right) \widehat{Cov}(\hat{\Phi}_{R, T_0}, \hat{\Phi}_{R, T_0}^F)
 \end{aligned}$$

$$\begin{aligned}
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}, \widehat{\Phi}_{R,D_{1B}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}, \widehat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\Phi}_{R,D_{1B}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,T_0}^F, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\Phi}_{R,D_{1B}}^F) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\phi}_{D_{1B},D_{1T}}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\phi}_{D_{1B},D_{1T}}^F)
\end{aligned}$$

$$\begin{aligned}
& + 2 \sum_{\theta \in \Theta_{5b}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\Phi}_{R,D_{1B}}^F, \widehat{\theta}) \\
& + 2 \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\phi}_{D_{1B},D_{1T}}^F) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}, \widehat{\theta}) \\
& + 2 \sum_{\theta \in \Theta_{5b}(\mu_R)} \left(\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} \right) \left(\frac{\partial \mu_R}{\partial \theta} \right) \widehat{Cov}(\widehat{\phi}_{D_{1B},D_{1T}}^F, \widehat{\theta}), \tag{B.15}
\end{aligned}$$

where the partial derivatives are evaluated at their MLEs. The partial derivatives necessary for Equation (B.15) are the following:

$$\begin{aligned}
\frac{\partial \mu_R}{\partial \Phi_{R,T_0}} &= -(1 - \mu_{T_0}); \\
\frac{\partial \mu_R}{\partial \Phi_{R,T_0}^F} &= -(1 - \mu_{T_0}^F); \\
\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}} &= -\phi_{D_{1B},D_{1T}}(1 - \mu_{D_{1T}}); \\
\frac{\partial \mu_R}{\partial \Phi_{R,D_{1B}}^F} &= -\phi_{D_{1B},D_{1T}}^F(1 - \mu_{D_{1T}}^F); \\
\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}} &= -\Phi_{R,D_{1B}}(1 - \mu_{D_{1T}}); \\
\frac{\partial \mu_R}{\partial \phi_{D_{1B},D_{1T}}^F} &= \Phi_{R,T_0} \frac{\partial \mu_{T_0}}{\partial \phi_{D_{1B},D_{1T}}^F} - \Phi_{R,D_{1B}}^F(1 - \mu_{D_{1T}}^F);
\end{aligned}$$

and for $\theta \in \Theta_{5b}(\mu_R)$,

$$\frac{\partial \mu_R}{\partial \theta} = \Phi_{R,T_0} \frac{\partial \mu_{T_0}}{\partial \theta} + \Phi_{R,T_0}^F \frac{\partial \mu_{T_0}^F}{\partial \theta} + \Phi_{R,D_{1B}} \phi_{D_{1B},D_{1T}} \frac{\partial \mu_{D_{1T}}}{\partial \theta} + \Phi_{R,D_{1B}}^F \phi_{D_{1B},D_{1T}}^F \frac{\partial \mu_{D_{1T}}^F}{\partial \theta},$$

where the partial derivatives involving μ_{T_0} , $\mu_{T_0}^F$, $\mu_{D_{1T}}$, and $\mu_{D_{1T}}^F$ are defined below.

Define $\Theta_{5b(\mu_{T_k})}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{jB}, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jB}, D_{jT}}^F & j = k+2, \dots, K; \\
 \phi_{D_{jB}, D_{jT}}^T & j = k+2, \dots, K; & \phi_{D_{jT}, T_j}^F & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, T_j}^T & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^{FT} & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1}, B}^F & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B}^T & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1}, B}^{FT} & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^F & j = k+1, \dots, K-1; \\
 \phi_{T_j, D_{j+1}, B}^T & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^{FT} & j = k+1, \dots, K-1; \\
 f_{D_{jT}}^T & j = k+1, \dots, K-1; & f_{T_j}^T & j = k+1, \dots, K-1.
 \end{array}$$

Define $\Theta'_{5b(\mu_{T_k})}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{jT}, T_j} & j = k+2, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & j = k+2, \dots, K-1; \\
 \phi_{T_j, D_{j+1}, B} & j = k+2, \dots, K-1; & f_{D_{jT}} & j = k+2, \dots, K-1; \\
 f_{T_j} & j = k+2, \dots, K-1.
 \end{array}$$

For Model 5b, the parameter μ_{T_k} is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, $\phi_{D_{k+1}, B, D_{k+1}, T}^T$, $\phi_{T_k, D_{k+1}, B}$, $\phi_{T_k, D_{k+1}, B}^F$, and f_{T_k} for $k = 0, \dots, K-1$. For $k = 0, \dots, K-2$, μ_{T_k} is also a function of the parameters in the set $\Theta_{5b(\mu_{T_k})}$; for $k = 0, \dots, K-3$, μ_{T_k} is also a function of the parameters in the set $\Theta'_{5b(\mu_{T_k})}$. The partial derivatives involving μ_{T_k} that are necessary for Equation (B.15) are the following:

for $k = 0, \dots, K-1$:

$$\begin{aligned}
 \frac{\partial \mu_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= -f_{T_k} \phi_{T_k, D_{k+1}, B}^F (1 - \mu_{D_{k+1}, T}^F); \\
 \frac{\partial \mu_{T_k}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^T} &= -(1 - f_{T_k}) \phi_{T_k, D_{k+1}, B} (1 - \mu_{D_{k+1}, T}^T);
 \end{aligned}$$

$$\begin{aligned}
\frac{\partial \mu_{T_k}}{\partial \phi_{T_k, D_{k+1}, B}} &= (1 - f_{T_k}) \left\{ 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T}^T) \right\}; \\
\frac{\partial \mu_{T_k}}{\partial \phi_{T_k, D_{k+1}, B}^F} &= f_{T_k} \left\{ 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F) \right\}; \\
\frac{\partial \mu_{T_k}}{\partial f_{T_k}} &= -\phi_{T_k, D_{k+1}, B} \left\{ 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T}^T) \right\} + \phi_{T_k, D_{k+1}, B}^F \\
&\quad - \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F);
\end{aligned}$$

for $k = 0, \dots, K-2$ and $\theta \in \Theta_{5b(\mu_{T_k})}$, and separately for $k = 0, \dots, K-3$ and $\theta \in \Theta'_{5b(\mu_{T_k})}$,

$$\frac{\partial \mu_{T_k}}{\partial \theta} = (1 - f_{T_k}) \phi_{T_k, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}^T \frac{\partial \mu_{D_{k+1}, T}^T}{\partial \theta} + f_{T_k} \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta},$$

where $\frac{\partial \mu_{D_{k+1}, T}^T}{\partial \theta}$ and $\frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta}$ are defined below.

For Model 5b, $\mu_{T_k}^T$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, $\phi_{D_{k+1}, B, D_{k+1}, T}^T$, $\phi_{T_k, D_{k+1}, B}^T$, $\phi_{T_k, D_{k+1}, B}^{FT}$, and $f_{T_k}^T$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\mu_{T_k}^T$ is also a function of the parameters in the set $\Theta_{5b(\mu_{T_k})}$, and for $k = 1, \dots, K-3$, $\mu_{T_k}^T$ is also a function of the parameters in the set $\Theta'_{5b(\mu_{T_k})}$. The partial derivatives involving $\mu_{T_k}^T$ that are necessary for Equation (B.15) are the following:

for $k = 0, \dots, K-1$:

$$\begin{aligned}
\frac{\partial \mu_{T_k}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= -f_{T_k}^T \phi_{T_k, D_{k+1}, B}^{FT} (1 - \mu_{D_{k+1}, T}^F); \\
\frac{\partial \mu_{T_k}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^T} &= -(1 - f_{T_k}^T) \phi_{T_k, D_{k+1}, B}^T (1 - \mu_{D_{k+1}, T}^T); \\
\frac{\partial \mu_{T_k}^T}{\partial \phi_{T_k, D_{k+1}, B}^T} &= (1 - f_{T_k}^T) \left\{ 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T}^T) \right\}; \\
\frac{\partial \mu_{T_k}^T}{\partial \phi_{T_k, D_{k+1}, B}^{FT}} &= f_{T_k}^T \left\{ 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F) \right\};
\end{aligned}$$

$$\begin{aligned} \frac{\partial \mu_{T_k}^T}{\partial f_{T_k}^T} = & -\phi_{T_k, D_{k+1}, B}^T \left\{ 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T}^T) \right\} + \phi_{T_k, D_{k+1}, B}^{FT} \\ & - \phi_{T_k, D_{k+1}, B}^{FT} \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F); \end{aligned}$$

for $k = 1, \dots, K-2$ and $\theta \in \Theta_{5b(\mu_{T_k})}$, and separately for $k = 1, \dots, K-3$ and $\theta \in \Theta'_{5b(\mu_{T_k})}$,

$$\frac{\partial \mu_{T_k}^T}{\partial \theta} = (1 - f_{T_k}^T) \phi_{T_k, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T}^T \frac{\partial \mu_{D_{k+1}, T}^T}{\partial \theta} + f_{T_k}^T \phi_{T_k, D_{k+1}, B}^{FT} \phi_{D_{k+1}, B, D_{k+1}, T}^F \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta},$$

where $\frac{\partial \mu_{D_{k+1}, T}^T}{\partial \theta}$ and $\frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta}$ are defined below.

Define $\Theta_{5b(\mu_{T_k}^F)}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_j B, D_j T} \quad j = k+2, \dots, K; \quad & \phi_{D_j B, D_j T}^T \quad j = k+2, \dots, K; \\ \phi_{D_j T, T_j}^T \quad j = k+1, \dots, K-1; \quad & \phi_{D_j T, D_{j+1}, B}^T \quad j = k+1, \dots, K-1; \\ \phi_{T_j, D_{j+1}, B}^T \quad j = k+1, \dots, K-1. \end{aligned}$$

Define $\Theta'_{5b(\mu_{T_k}^F)}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_j T, T_j} \quad j = k+2, \dots, K-1; \quad & \phi_{D_j T, D_{j+1}, B} \quad j = k+2, \dots, K-1; \\ \phi_{T_j, D_{j+1}, B} \quad j = k+2, \dots, K-1. \end{aligned}$$

For Model 5b, the parameter $\mu_{T_k}^F$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}^T$ and $\phi_{T_k, D_{k+1}, B}^F$ for $k = 0, \dots, K-1$. For $k = 0, \dots, K-2$, $\mu_{T_k}^F$ is also a function of the parameters in the set $\theta \in \Theta_{5b(\mu_{T_k}^F)}$, and for $k = 0, \dots, K-3$, $\mu_{T_k}^F$ is also a function of the parameters in the set $\theta \in \Theta'_{5b(\mu_{T_k}^F)}$. The partial derivatives involving $\mu_{T_k}^F$ that are necessary for Equation (B.15) are the following:

for $k = 0, \dots, K - 1$:

$$\begin{aligned}\frac{\partial \mu_{T_k}^F}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^T} &= -\phi_{T_k, D_{k+1}, B}^F (1 - \mu_{D_{k+1}, T}^{fT}); \\ \frac{\partial \mu_{T_k}^F}{\partial \phi_{T_k, D_{k+1}, B}^F} &= 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T}^{fT});\end{aligned}$$

for $k = 0, \dots, K - 2$ and $\theta \in \Theta_{5b(\mu_{T_k}^F)}$, and separately for $k = 0, \dots, K - 3$ and $\theta \in \Theta'_{5b(\mu_{T_k}^F)}$,

$$\frac{\partial \mu_{T_k}^F}{\partial \theta} = \phi_{T_k, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^T \frac{\partial \mu_{D_{k+1}, T}^{fT}}{\partial \theta},$$

where $\frac{\partial \mu_{D_{k+1}, T}^{fT}}{\partial \theta}$ is defined below.

The parameter $\mu_{T_k}^f$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}^T$ and $\phi_{T_k, D_{k+1}, B}$ for $k = 2, \dots, K - 1$. For $k = 2, \dots, K - 2$, $\mu_{T_k}^f$ is also a function of the parameters in the set $\Theta_{5b(\mu_{T_k}^F)}$; for $k = 2, \dots, K - 3$, $\mu_{T_k}^f$ is also a function of the parameters in the set $\Theta'_{5b(\mu_{T_k}^F)}$. The partial derivatives involving $\mu_{T_k}^f$ that are necessary for Equation (B.15) are the following:

for $k = 2, \dots, K - 1$:

$$\begin{aligned}\frac{\partial \mu_{T_k}^f}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^T} &= -\phi_{T_k, D_{k+1}, B}^f (1 - \mu_{D_{k+1}, T}^{fT}); \\ \frac{\partial \mu_{T_k}^f}{\partial \phi_{T_k, D_{k+1}, B}^f} &= 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T}^{fT});\end{aligned}$$

for $k = 2, \dots, K - 2$ and $\theta \in \Theta_{5b(\mu_{T_k}^F)}$, and separately for $k = 2, \dots, K - 3$ and $\theta \in \Theta'_{5b(\mu_{T_k}^F)}$,

$$\frac{\partial \mu_{T_k}^f}{\partial \theta} = \phi_{T_k, D_{k+1}, B}^f \phi_{D_{k+1}, B, D_{k+1}, T}^T \frac{\partial \mu_{D_{k+1}, T}^{fT}}{\partial \theta},$$

where $\frac{\partial \mu_{D_{k+1}, T}^{fT}}{\partial \theta}$ is defined below.

The parameter $\mu_{T_k}^{fT}$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}^T$ and $\phi_{T_k, D_{k+1}, B}^T$ for $k = 1, \dots, K - 1$.

For $k = 1, \dots, K - 2$, $\mu_{T_k}^{fT}$ is also a function of the parameters in the set $\Theta_{5b(\mu_{T_k}^F)}$; for $k = 1, \dots, K - 3$, $\mu_{T_k}^{fT}$ is also a function of the parameters in the set $\Theta'_{5b(\mu_{T_k}^F)}$. The partial derivatives involving $\mu_{T_k}^{fT}$ that are necessary for Equation (B.15) are the following:

for $k = 1, \dots, K - 1$:

$$\begin{aligned} \frac{\partial \mu_{T_k}^{fT}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^T} &= -\phi_{T_k, D_{k+1}, B}^T (1 - \mu_{D_{k+1}, T}^{fT}); \\ \frac{\partial \mu_{T_k}^{fT}}{\partial \phi_{T_k, D_{k+1}, B}^T} &= 1 - \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T}^{fT}); \end{aligned}$$

for $k = 1, \dots, K - 2$ and $\theta \in \Theta_{5b(\mu_{T_k}^F)}$, and separately for $k = 1, \dots, K - 3$ and $\theta \in \Theta'_{5b(\mu_{T_k}^F)}$,

$$\frac{\partial \mu_{T_k}^{fT}}{\partial \theta} = \phi_{T_k, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T}^T \frac{\partial \mu_{D_{k+1}, T}^{fT}}{\partial \theta},$$

where $\frac{\partial \mu_{D_{k+1}, T}^{fT}}{\partial \theta}$ is defined below.

Define $\Theta_{5b(\mu_{D_k T})}$ to be the set composed of the following parameters:

$$\begin{array}{llll} \phi_{D_j B, D_j T}^T & j = k + 1, \dots, K; & \phi_{T_j, D_{j+1}, B} & j = k, \dots, K - 1; \\ \phi_{T_j, D_{j+1}, B}^F & j = k, \dots, K - 1; & f_{T_j} & j = k, \dots, K - 1. \end{array}$$

Define $\Theta'_{5b(\mu_{D_{kT}})}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{jB}, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jB}, D_{jT}}^F & j = k+2, \dots, K; \\
 \phi_{D_{jT}, T_j} & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^F & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, T_j}^T & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^{FT} & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1, B}} & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1, B}}^F & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1, B}}^T & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1, B}}^{FT} & j = k+1, \dots, K-1; \\
 \phi_{T_j, D_{j+1, B}}^T & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1, B}}^{FT} & j = k+1, \dots, K-1; \\
 f_{D_{jT}} & j = k+1, \dots, K-1; & f_{D_{jT}}^T & j = k+1, \dots, K-1; \\
 f_{T_j}^T & j = k+1, \dots, K-1. & &
 \end{array}$$

For Model 5b, the parameter $\mu_{D_{kT}}$ is a function of $\phi_{D_{k+1, B}, D_{k+1, T}}$, $\phi_{D_{k+1, B}, D_{k+1, T}}^F$, ϕ_{D_{kT}, T_k} , ϕ_{D_{kT}, T_k}^F , $\phi_{D_{kT}, D_{k+1, B}}$, $\phi_{D_{kT}, D_{k+1, B}}^F$, $f_{D_{kT}}$, and the parameters in the set $\Theta_{5b(\mu_{D_{kT}})}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\mu_{D_{kT}}$ is also a function of the parameters in the set $\Theta'_{5b(\mu_{D_{kT}})}$. The partial derivatives involving $\mu_{D_{kT}}$ that are necessary for Equation (B.15) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned}
 \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1, B}, D_{k+1, T}}} &= -(1 - f_{D_{kT}}) \phi_{D_{kT}, D_{k+1, B}} (1 - \mu_{D_{k+1, T}}); \\
 \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{k+1, B}, D_{k+1, T}}^F} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, T_k} \frac{\partial \mu_{T_k}}{\partial \phi_{D_{k+1, B}, D_{k+1, T}}^F} - f_{D_{kT}} \phi_{D_{kT}, D_{k+1, B}}^F (1 - \mu_{D_{k+1, T}}^F); \\
 \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}} &= -(1 - f_{D_{kT}}) (1 - \mu_{T_k}); \\
 \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, T_k}^F} &= -f_{D_{kT}} (1 - \mu_{T_k}^F); \\
 \frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1, B}}} &= -(1 - f_{D_{kT}}) \phi_{D_{k+1, B}, D_{k+1, T}} (1 - \mu_{D_{k+1, T}});
 \end{aligned}$$

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}}{\partial \phi_{D_{kT}, D_{k+1}, B}^F} &= -f_{D_{kT}} \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F); \\ \frac{\partial \mu_{D_{kT}}}{\partial f_{D_{kT}}} &= \phi_{D_{kT}, T_k} (1 - \mu_{T_k}) + \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}) \\ &\quad - \phi_{D_{kT}, T_k}^F (1 - \mu_{T_k}^F) - \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F);\end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{5b(\mu_{D_{kT}})}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta'_{5b(\mu_{D_{kT}})}$,

$$\frac{\partial \mu_{D_{kT}}}{\partial \theta} = \frac{\partial \mu_{D_{kT}}}{\partial \mu_{T_k}} \frac{\partial \mu_{T_k}}{\partial \theta} + \frac{\partial \mu_{D_{kT}}}{\partial \mu_{T_k}^F} \frac{\partial \mu_{T_k}^F}{\partial \theta} + \frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1}, T}} \frac{\partial \mu_{D_{k+1}, T}}{\partial \theta} + \frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1}, T}^F} \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta},$$

where

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}}{\partial \mu_{T_k}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, T_k}; \\ \frac{\partial \mu_{D_{kT}}}{\partial \mu_{T_k}^F} &= f_{D_{kT}} \phi_{D_{kT}, T_k}^F; \\ \frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1}, T}} &= (1 - f_{D_{kT}}) \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T}; \\ \frac{\partial \mu_{D_{kT}}}{\partial \mu_{D_{k+1}, T}^F} &= f_{D_{kT}} \phi_{D_{kT}, D_{k+1}, B}^F \phi_{D_{k+1}, B, D_{k+1}, T}^F.\end{aligned}$$

The partial derivatives involving μ_{T_k} and $\mu_{T_k}^F$ are defined above, and those involving $\mu_{D_{k+1}, T}^F$ are defined below.

Define $\Theta_{5b(\mu_{D_{kT}}^T)}$ to be the set composed of the following parameters:

$$\begin{array}{llll}\phi_{D_j B, D_j T}^T & j = k+1, \dots, K; & \phi_{T_j, D_{j+1}, B}^F & j = k, \dots, K-1; \\ \phi_{T_j, D_{j+1}, B}^T & j = k, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^{FT} & j = k, \dots, K-1; \\ f_{T_j}^T & j = k, \dots, K-1.\end{array}$$

Define $\Theta'_{5b(\mu_{D_{kT}}^T)}$ to be the set composed of the following parameters:

$$\begin{array}{llll}
 \phi_{D_{jB}, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jB}, D_{jT}}^F & j = k+2, \dots, K; \\
 \phi_{D_{jT}, T_j} & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^F & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, T_j}^T & j = k+1, \dots, K-1; & \phi_{D_{jT}, T_j}^{FT} & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1}, B} & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B}^F & j = k+1, \dots, K-1; \\
 \phi_{D_{jT}, D_{j+1}, B}^T & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B}^{FT} & j = k+1, \dots, K-1; \\
 \phi_{T_j, D_{j+1}, B} & j = k+1, \dots, K-1; & f_{D_{jT}} & j = k+1, \dots, K-1; \\
 f_{D_{jT}}^T & j = k+1, \dots, K-1; & f_{T_j} & j = k+1, \dots, K-1.
 \end{array}$$

For Model 5b, the parameter $\mu_{D_{kT}}^T$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, $\phi_{D_{k+1}, B, D_{k+1}, T}^F$, ϕ_{D_{kT}, T_k}^T , ϕ_{D_{kT}, T_k}^{FT} , $\phi_{D_{kT}, D_{k+1}, B}^T$, $\phi_{D_{kT}, D_{k+1}, B}^{FT}$, $f_{D_{kT}}^T$, and the parameters in the set $\Theta_{5b(\mu_{D_{kT}}^T)}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\mu_{D_{kT}}^T$ is also a function of the parameters in the set $\Theta'_{5b(\mu_{D_{kT}}^T)}$. The partial derivatives involving $\mu_{D_{kT}}^T$ that are necessary for Equation (B.15) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned}
 \frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= -(1 - f_{D_{kT}}^T) \phi_{D_{kT}, D_{k+1}, B}^T (1 - \mu_{D_{k+1}, T}); \\
 \frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} &= (1 - f_{D_{kT}}^T) \phi_{D_{kT}, T_k}^T \frac{\partial \mu_{T_k}^T}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}^F} - f_{D_{kT}}^T \phi_{D_{kT}, D_{k+1}, B}^{FT} (1 - \mu_{D_{k+1}, T}^F); \\
 \frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{kT}, T_k}^T} &= -(1 - f_{D_{kT}}^T) (1 - \mu_{T_k}^T); \\
 \frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{kT}, T_k}^{FT}} &= -f_{D_{kT}}^T (1 - \mu_{T_k}^F); \\
 \frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{kT}, D_{k+1}, B}^T} &= -(1 - f_{D_{kT}}^T) \phi_{D_{k+1}, B, D_{k+1}, T}^T (1 - \mu_{D_{k+1}, T});
 \end{aligned}$$

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}^T}{\partial \phi_{D_{kT}, D_{k+1}, B}^{FT}} &= -f_{D_{kT}}^T \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F); \\ \frac{\partial \mu_{D_{kT}}^T}{\partial f_{D_{kT}}^T} &= \phi_{D_{kT}, T_k}^T (1 - \mu_{T_k}^T) + \phi_{D_{kT}, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F) \\ &\quad - \phi_{D_{kT}, T_k}^{FT} (1 - \mu_{T_k}^F) - \phi_{D_{kT}, D_{k+1}, B}^{FT} \phi_{D_{k+1}, B, D_{k+1}, T}^F (1 - \mu_{D_{k+1}, T}^F);\end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{5b(\mu_{D_{kT}}^T)}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta'_{5b(\mu_{D_{kT}}^T)}$,

$$\frac{\partial \mu_{D_{kT}}^T}{\partial \theta} = \frac{\partial \mu_{D_{kT}}^T}{\partial \mu_{T_k}^T} \frac{\partial \mu_{T_k}^T}{\partial \theta} + \frac{\partial \mu_{D_{kT}}^T}{\partial \mu_{T_k}^F} \frac{\partial \mu_{T_k}^F}{\partial \theta} + \frac{\partial \mu_{D_{kT}}^T}{\partial \mu_{D_{k+1}, T}^F} \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta} + \frac{\partial \mu_{D_{kT}}^T}{\partial \mu_{D_{k+1}, T}^F} \frac{\partial \mu_{D_{k+1}, T}^F}{\partial \theta},$$

where

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}^T}{\partial \mu_{T_k}^T} &= (1 - f_{D_{kT}}^T) \phi_{D_{kT}, T_k}^T; \\ \frac{\partial \mu_{D_{kT}}^T}{\partial \mu_{T_k}^F} &= f_{D_{kT}}^T \phi_{D_{kT}, T_k}^{FT}; \\ \frac{\partial \mu_{D_{kT}}^T}{\partial \mu_{D_{k+1}, T}^F} &= (1 - f_{D_{kT}}^T) \phi_{D_{kT}, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T}^F; \\ \frac{\partial \mu_{D_{kT}}^T}{\partial \mu_{D_{k+1}, T}^F} &= f_{D_{kT}}^T \phi_{D_{kT}, D_{k+1}, B}^{FT} \phi_{D_{k+1}, B, D_{k+1}, T}^F.\end{aligned}$$

The partial derivatives involving $\mu_{T_k}^T$, $\mu_{T_k}^F$, and $\mu_{D_{k+1}, T}$ are defined above; those involving $\mu_{D_{k+1}, T}^F$ are defined below.

Define $\Theta_{5b(\mu_{D_{kT}}^F)}$ to be the set composed of the parameters $\phi_{D_j B, D_{jT}}^T$ for $j = k+1, \dots, K$. Define $\Theta'_{5b(\mu_{D_{kT}}^F)}$ to be the set composed of the following parameters:

$$\begin{array}{llll}\phi_{D_j B, D_{jT}} & j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & j = k+1, \dots, K-1; \\ \phi_{D_{jT}, T_j}^T & j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B}^T & j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B} & j = k+1, \dots, K-1; \\ \phi_{T_j, D_{j+1}, B}^T & j = k+1, \dots, K-1.\end{array}$$

For Model 5b, the parameter $\mu_{D_{kT}}^F$ is a function of $\phi_{D_{k+1,B},D_{k+1,T}}$, ϕ_{D_{kT},T_k}^F , $\phi_{D_{kT},D_{k+1,B}}^F$, $\phi_{T_k,D_{k+1,B}}^F$, and the parameters in the set $\Theta_{5b(\mu_{D_{kT}}^F)}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\mu_{D_{kT}}^F$ is also a function of the parameters in the set $\Theta'_{5b(\mu_{D_{kT}}^F)}$. The partial derivatives involving $\mu_{D_{kT}}^F$ that are necessary for Equation (B.15) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned}\frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{k+1,B},D_{k+1,T}}} &= -\phi_{D_{kT},D_{k+1,B}}^F (1 - \mu_{D_{k+1,T}}^f); \\ \frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{kT},T_k}^F} &= -(1 - \mu_{T_k}^F); \\ \frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{D_{kT},D_{k+1,B}}^F} &= -\phi_{D_{k+1,B},D_{k+1,T}} (1 - \mu_{D_{k+1,T}}^f); \\ \frac{\partial \mu_{D_{kT}}^F}{\partial \phi_{T_k,D_{k+1,B}}^F} &= \phi_{D_{kT},T_k}^F \left\{ 1 - \phi_{D_{k+1,B},D_{k+1,T}}^T (1 - \mu_{D_{k+1,T}}^{fT}) \right\};\end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{5b(\mu_{D_{kT}}^F)}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta'_{5b(\mu_{D_{kT}}^F)}$,

$$\frac{\partial \mu_{D_{kT}}^F}{\partial \theta} = \phi_{D_{kT},T_k}^F \frac{\partial \mu_{T_k}^F}{\partial \theta} + \phi_{D_{kT},D_{k+1,B}}^F \phi_{D_{k+1,B},D_{k+1,T}} \frac{\partial \mu_{D_{k+1,T}}^f}{\partial \theta},$$

where $\frac{\partial \mu_{T_k}^F}{\partial \theta}$ is defined above, and $\frac{\partial \mu_{D_{k+1,T}}^f}{\partial \theta}$ is defined below.

Define $\Theta_{5b(\mu_{D_{kT}}^f)}$ to be the set composed of the following parameters:

$$\phi_{D_{jB},D_{jT}}^T \quad j = k+1, \dots, K; \quad \phi_{T_j,D_{j+1,B}} \quad j = k, \dots, K-1.$$

Define $\Theta'_{5b(\mu_{D_{kT}}^f)}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_{jB}, D_{jT}} & \quad j = k+2, \dots, K-1; & \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, T_j}^T & \quad j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B}^T & \quad j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B}^T & \quad j = k+1, \dots, K-1. \end{aligned}$$

The parameter $\mu_{D_{kT}}^f$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, ϕ_{D_{kT}, T_k} , $\phi_{D_{kT}, D_{k+1}, B}$, and the parameters in the set $\Theta_{5b(\mu_{D_{kT}}^f)}$ for $k = 2, \dots, K-1$. For $k = 2, \dots, K-2$, $\mu_{D_{kT}}^f$ is also a function of the parameters in the set $\Theta'_{5b(\mu_{D_{kT}}^f)}$. The partial derivatives involving $\mu_{D_{kT}}^f$ that are necessary for Equation (B.15) are the following:

for $k = 2, \dots, K-1$:

$$\begin{aligned} \frac{\partial \mu_{D_{kT}}^f}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= -\phi_{D_{kT}, D_{k+1}, B} (1 - \mu_{D_{k+1}, T}^f); \\ \frac{\partial \mu_{D_{kT}}^f}{\partial \phi_{D_{kT}, T_k}} &= -(1 - \mu_{T_k}^f); \\ \frac{\partial \mu_{D_{kT}}^f}{\partial \phi_{D_{kT}, D_{k+1}, B}} &= -\phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}^f); \end{aligned}$$

for $k = 2, \dots, K-1$ and $\theta \in \Theta_{5b(\mu_{D_{kT}}^f)}$, and separately for $k = 2, \dots, K-2$ and $\theta \in \Theta'_{5b(\mu_{D_{kT}}^f)}$,

$$\frac{\partial \mu_{D_{kT}}^f}{\partial \theta} = \phi_{D_{kT}, T_k} \frac{\partial \mu_{T_k}^f}{\partial \theta} + \phi_{D_{kT}, D_{k+1}, B} \phi_{D_{k+1}, B, D_{k+1}, T} \frac{\partial \mu_{D_{k+1}, T}^f}{\partial \theta},$$

where $\frac{\partial \mu_{T_k}^f}{\partial \theta}$ is defined above.

Define $\Theta_{5b(\mu_{D_{kT}}^f)}$ to be the set composed of the following parameters:

$$\phi_{D_{jB}, D_{jT}}^T \quad j = k+1, \dots, K; \quad \phi_{T_j, D_{j+1}, B}^T \quad j = k, \dots, K-1.$$

Define $\Theta'_{5b(\mu_{D_{kT}}^{fT})}$ to be the set composed of the following parameters:

$$\begin{aligned} \phi_{D_j B, D_{jT}} & \quad j = k+2, \dots, K; & \phi_{D_{jT}, T_j} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, T_j}^T & \quad j = k+1, \dots, K-1; & \phi_{D_{jT}, D_{j+1}, B} & \quad j = k+1, \dots, K-1; \\ \phi_{D_{jT}, D_{j+1}, B}^T & \quad j = k+1, \dots, K-1; & \phi_{T_j, D_{j+1}, B} & \quad j = k+1, \dots, K-1. \end{aligned}$$

The parameter $\mu_{D_{kT}}^{fT}$ is a function of $\phi_{D_{k+1}, B, D_{k+1}, T}$, ϕ_{D_{kT}, T_k}^T , $\phi_{D_{kT}, D_{k+1}, B}^T$, and the parameters in the set $\Theta_{5b(\mu_{D_{kT}}^{fT})}$ for $k = 1, \dots, K-1$. For $k = 1, \dots, K-2$, $\mu_{D_{kT}}^{fT}$ is also a function of the parameters in the set $\Theta'_{5b(\mu_{D_{kT}}^{fT})}$. The partial derivatives involving $\mu_{D_{kT}}^{fT}$ that are necessary for Equation (B.15) are the following:

for $k = 1, \dots, K-1$:

$$\begin{aligned} \frac{\partial \mu_{D_{kT}}^{fT}}{\partial \phi_{D_{k+1}, B, D_{k+1}, T}} &= -\phi_{D_{kT}, D_{k+1}, B}^T (1 - \mu_{D_{k+1}, T}^f); \\ \frac{\partial \mu_{D_{kT}}^{fT}}{\partial \phi_{D_{kT}, T_k}^T} &= -(1 - \mu_{T_k}^{fT}); \\ \frac{\partial \mu_{D_{kT}}^{fT}}{\partial \phi_{D_{kT}, D_{k+1}, B}^T} &= -\phi_{D_{k+1}, B, D_{k+1}, T} (1 - \mu_{D_{k+1}, T}^f); \end{aligned}$$

for $k = 1, \dots, K-1$ and $\theta \in \Theta_{5b(\mu_{D_{kT}}^{fT})}$, and separately for $k = 1, \dots, K-2$ and $\theta \in \Theta'_{5b(\mu_{D_{kT}}^{fT})}$,

$$\frac{\partial \mu_{D_k}^{fT}}{\partial \theta} = \phi_{D_{kT}, T_k}^T \frac{\partial \mu_{T_k}^{fT}}{\partial \theta} + \phi_{D_{kT}, D_{k+1}, B}^T \phi_{D_{k+1}, B, D_{k+1}, T} \frac{\partial \mu_{D_{k+1}, T}^f}{\partial \theta},$$

where $\frac{\partial \mu_{T_k}^{fT}}{\partial \theta}$ and $\frac{\partial \mu_{D_{k+1}, T}^f}{\partial \theta}$ are defined above.

VITA

Rebecca Buchanan graduated magna cum laude from Bryn Mawr College in 1995 with an A.B. and honors in mathematics. She earned a Master of Science in mathematics education from Syracuse University in 1998, and taught undergraduate mathematics at West Chester University in West Chester, PA, from 1998 to 2000. Rebecca did an internship at Patuxent National Wildlife Refuge in Laurel, MD, in June and July, 2004, and earned a Doctorate of Philosophy in Quantitative Ecology and Resource Management from the University of Washington in 2005. Publications are listed below.

Buchanan, R.A., J.R. Skalski, and S.G. Smith. (in press 2006). Estimating the effects of smolt transportation from different vantage points and management perspectives. *North American Journal of Fisheries Management*.

Buchanan, R.A. and J.R. Skalski. (submitted 2005). A life-cycle release-recapture model for salmonid PIT-tag investigations. *Journal of Agricultural, Biological, and Environmental Statistics*.

Buchanan, R.A., L.L. Conquest, and J.-P. Courbois. 2005. A cost analysis of ranked set sampling to estimate a population mean. *Environmetrics* 16:235-256.