

## Part 2. Protocols for Studies with a Control and One Treatment

Material in Part 2 presents the theory and application for experiments with single treatment and control groups (i.e.,  $v = t$  and  $c$ ). An array of tests are given to assess model assumptions under each of the sampling protocols. The estimation theory for each of the five protocols follows. Data for the general numerical example (provided in Chapter 1.3) are used to illustrate the computations. Other points are illustrated using the output from program RELEASE.

### 2.1. Models, Hypotheses, and Tests: An Overview

#### 2.1.1. Overview of Hypothesis Tests

The strategy we recommend in analysis of release-recapture data is to select the most biologically reasonable, parsimonious, statistical model for the data. This is a generally accepted basis for a good model (see McCullagh and Nelder 1983). Inferences about treatment effects and other parameters are then based on that model. The set of reasonable models to consider is determined by a priori reasoning (logic) based on the nature of the study. In ecological studies, however, logic alone is usually insufficient to specify a single (unique) model as *the* model for the data. Instead, statistical hypothesis tests must be used to determine if a model fits the data and to determine the simplest model, from an a priori sequence of models, that is most appropriate for the data.

Three major tests are used in this process: TEST 1, TEST 2, and TEST 3. Table 2.1 summarizes some aspects of these tests. If sample sizes are large enough, each test statistic is distributed as a chi-square statistic. Each test is computed as a series of independent, chi-square test statistics which, added together, give the overall test; however, the separate test components are often of more interest than their sums.

TEST 1, as an overall test, tests the null hypothesis,  $H_0$ , "there is no treatment effect," versus the alternative,  $H_A$ , "there is a treatment effect." Treatment effects are defined in terms of differences in the parameters  $\phi_i$  and  $p_i$  between treatment and control groups. TEST 1 is computed on the basis of summary statistics from each treatment group.

TESTs 2 and 3 are goodness of fit tests applicable to an individual set of release-recapture data. If there is only one group of releases (e.g., only controls, or only turbine fish, or fish of only one age or sex group), TESTs 2 and 3 are still computable; however, TEST 1 does not exist unless there are two or more treatment groups. The sum of TESTs 2 and 3 is the fully efficient goodness of fit test for Jolly-Seber capture-recapture data.

Table 2.1. - Summary of three types of statistical tests for the four capture history protocols and associated models.

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|        |  |
|--------|--|
| TEST 1 | <p>Summary statistics from the experimental groups are used to test for overall treatment effects. TEST 1 is computed as a series of contingency table tests that allow detailed interpretation of the results. Tests of this form have roots in the publications by Brownie and Robson (1976) and Pollock (1981a). Details of this test are given in Table 2.3.</p> <p><math>H_0</math>: All parameters <math>\phi_i</math> and <math>p_i</math> are the same across treatment groups.<br/> <math>H_A</math>: At least some parameters differ between or among groups.</p>  |
| TEST 2 | <p>Summary statistics from a single treatment group are used to test for goodness of fit of the model to the data. TEST 2 is conducted separately for each group and is computed as a series of tests that allow a detailed interpretation of the results. There are many ways to compute this test sequence; we use contingency tables. This test can be most directly traced back to Robson and Youngs (unpublished report, 1971), but it also appears in papers by Seber (1970), Brownie and Robson (1976), Brownie et al. (1978, 1985), Balsler (1984), and Pollock et al. (1985). Details of this test are given in Table 2.4.</p> <p><math>H_0</math>: The parameters <math>\phi_i</math> and <math>p_i</math> are specific to sampling occasions or sampling sites within each group.<br/> <math>H_A</math>: The model does not fit the data. There may be a wide variety of reasons for this, including tagging effects and differential behavior.</p> |
| TEST 3 | <p>Data from the full <math>m</math>-array for a single group are used to test for parameters that are specific to individual capture histories. TEST 3 is potentially computed as a large series of contingency tables; however, a great deal of pooling is usually required for most data sets. This test was developed by Pollock et al. (1985). Details of this test are given in Table 2.5.</p> <p><math>H_0</math>: The parameters <math>\phi_i</math> and <math>p_i</math> do not depend on the capture histories of fish released on any release occasion.<br/> <math>H_A</math>: Some of the parameters <math>\phi_i</math> and <math>p_i</math> are dependent on the capture histories of fish in a given release; this implies that the corresponding subcohorts among which capture and survival rates differ should not be pooled (Table 1.3 indicates the nature of those subcohorts).</p>   |

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In following sections we elaborate on these tests, outlining their components, how they are computed under any given protocol, and some idea of their meaning. Under the complete capture history protocol, all components of TESTs 1, 2, and 3 can be computed. Under the first capture history protocol, TESTs 2 and 3 do not exist (i.e., cannot be computed) and some components of TEST 1 cannot be computed.

The material presented in Part 2 is complex and extensive. It is difficult to understand fully the various separate ideas until one comprehends the "big picture." Yet, that comprehension requires starting somewhere to learn the various separate components of models, protocols, hypotheses, tests, and estimators. Consequently, readers may find it useful to refer back to Chapter 2.1 as they study the rest of Part 2.

2.1.2. Sequence of Treatment Effects Corresponding to TEST 1

For any study of turbine mortality involving a treatment and control group and  $k$  release-recapture dams, the same types of parameters underlie the sample data:  $\phi_{v1}, \phi_{v2}, \dots, \phi_{v,k-1}$  and  $p_{v2}, \dots, p_{v,k-1}, p_{vk}$ , for  $v = t$  or  $c$ . Only the data collection protocols and the number ( $k$ ) of dams involved may vary. These two factors (i.e., the actual data taken) determine the survival and capture probabilities that that can be estimated, and the statistical tests that can be computed.

In any experiment, one wants to test for the nature and extent of treatment effects. When passage through a dam structure is the treatment, one wants to test hypotheses about equality of treatment and survival rates in the controls. It is also necessary to test for differences in capture probabilities (e.g., does  $p_{t2} = p_{c2}$ ) to reach valid conclusions about effects on survival rates. Because of the spatial ordering of survival rates and recapture sites, there is a logical sequence of hypotheses to test concerning possible treatment effects. Table 2.2 is a representation of the corresponding sequence of possible hypotheses about how the treatment affects the parameters.

Table 2.2. - A summary is shown of specific hypotheses that are relevant to determining the extent of the treatment effect and thereby to selecting an appropriate model. Notation: E means that the parameter is assumed to be equal for  $t$  and  $c$ ; D means that the parameter is allowed to differ for  $t$  and  $c$ .

|                | Dam $j = 1 \rightarrow$ | 2     | $\rightarrow$ | 3     | $\rightarrow$ | 4     | $\rightarrow$ | $k-1 \rightarrow$ | $k$             |
|----------------|-------------------------|-------|---------------|-------|---------------|-------|---------------|-------------------|-----------------|
| Model          | $\phi_1$                | $p_2$ | $\phi_2$      | $p_3$ | $\phi_3$      | $p_4$ | $\rightarrow$ | $p_{k-1}$         | $\phi_{k-1}p_k$ |
| $H_0$          | E                       | E     | E             | E     | E             | E     | $\rightarrow$ | E                 | E               |
| $H_{1\phi}$    | D                       | E     | E             | E     | E             | E     | $\rightarrow$ | E                 | E               |
| $H_{2p}$       | D                       | D     | E             | E     | E             | E     | $\rightarrow$ | E                 | E               |
| $H_{2\phi}$    | D                       | D     | D             | E     | E             | E     | $\rightarrow$ | E                 | E               |
| $H_{3p}$       | D                       | D     | D             | D     | E             | E     | $\rightarrow$ | E                 | E               |
| $H_{3\phi}$    | D                       | D     | D             | D     | D             | E     | $\rightarrow$ | E                 | E               |
| .              | .                       | .     | .             | .     | .             | .     | .             | .                 | .               |
| .              | .                       | .     | .             | .     | .             | .     | .             | .                 | .               |
| .              | .                       | .     | .             | .     | .             | .     | .             | .                 | .               |
| $H_{k-1,p}$    | D                       | D     | D             | D     | D             | D     | $\rightarrow$ | D                 | E               |
| $H_{k-1,\phi}$ | D                       | D     | D             | D     | D             | D     | $\rightarrow$ | D                 | D               |

The simplest model (i.e., statistical) hypothesis, denoted  $H_0$ , specifies that there are no treatment effects; thus, all survival and capture parameters are equal (E) between treatment and control groups. For hypothesis  $H_{1\phi}$  only  $\phi_{t1}$  and  $\phi_{c1}$  differ (D); no other parameters are affected by treatment. In most turbine studies, it has been implicitly assumed that  $H_{1\phi}$  applied, but this hypothesis has rarely been tested because the data that would allow such a test have not been collected. Hypothesis  $H_{2\phi}$  means the underlying parameters

$\phi_{t1}, \phi_{c1}$  may be different, and

$p_{t2}, p_{c2}$  may be different,

while

$\phi_2, \phi_3, \dots, \phi_{k-1}$

and

$p_3, \dots, p_{k-1}, p_k$

are the same for treatment and control.

Hypothesis  $H_{k-1,\phi}$  represents the case where a treatment effect (on survival, capture, or both rates) persists at least to dam  $k$ . We choose to denote the final hypothesis in the sequence this way even though  $\phi_{k-1}$  and  $p_k$  are not separately estimable under any sampling protocol. Thus, technically, we should write  $H_{k-1,\theta}$  and define  $\theta = \phi_{k-1}p_k$ . Instead, we adopt the convention that under  $H_{k-1,\phi}$  one must interpret  $\phi_{k-1}$  as meaning the product  $\phi_{k-1}p_k$ . Under  $H_{k-1,\phi}$  all identifiable parameters are allowed to be different between treatment and control groups.

TEST 1 is conveniently computed as a sequence of simple chi-square tests. Components of TEST 1 are named in Table 2.3 and related hypotheses are given in Table 2.2.

The interpretation of the individual components in TEST 1 could differ from that given here. Other sequences of hypotheses describe possible treatment effects. For example, one might have one or more survival rates differ by treatment but have all capture rates equal; thus, the most general model would be

$$\phi_{ti} \neq \phi_{ci}; \quad i = 1, \dots, k - 1,$$

$$p_{ti} = p_{ci}, \quad i = 2, \dots, k.$$

The same sequence of tests could be carried out, but the corresponding  $H_0$  and  $H_A$  would have a different interpretation. There are no simple closed-form tests or estimators for this model. Efficient inference methods for hypotheses such as those above must be based on numerical optimization procedures (using, e.g., program SURVIV, White 1983). In other contexts, such as testing data sets for male versus female (Brownie et al. 1985, Chapter 5), the separate components of TEST 1 are not of individual interest.

Table 2.2 presents hypotheses about the survival and capture parameters. These hypotheses by themselves do not specify a "model." A model here means a sampling distribution for actual data. Consequently, a model incorporates aspects of both the sampling protocol and a hypothesis about the underlying parameters. All tests of hypotheses take the form of

Table 2.3. - Explanation of TEST 1: its components, their identification, hypotheses tested, and computability of components by capture history (CH) protocol. The index  $v$  ranges over treatment groups, e.g.,  $v = t$  and  $c$  for treatment and control groups, respectively. There are  $2k - 3$  test components ( $k \geq 2$ ).

| Component code | Summary statistics used | Hypothesis     |                | Computability under different protocols |            |                       |                       |                      |
|----------------|-------------------------|----------------|----------------|---|------------|-----------------------|-----------------------|----------------------|
|                |                         |                |                | Complete CH                             | Partial CH |                       |                       | Unk. CH <sup>c</sup> |
|                |                         | Null           | Alternative    |   | Scheme A   | Scheme B <sup>a</sup> | First CH <sup>b</sup> |                      |
| TEST 1.R1      | $R_{v1}, r_{v1}$        | $H_0$          | $H_{1\phi}$    | Yes                                     | Yes        | Yes                   | Yes                   | Yes                  |
| TEST 1.T2      | $T_{v2}, m_{v2}$        | $H_{1\phi}$    | $H_{2p}$       | Yes                                     | Yes        | Yes                   | Yes                   | Yes                  |
| TEST 1.R2      | $R_{v2}, r_{v2}$        | $H_{2p}$       | $H_{2\phi}$    | Yes                                     | Yes        | Yes                   | No                    | No                   |
| TEST 1.T3      | $T_{v3}, m_{v3}$        | $H_{2\phi}$    | $H_{3p}$       | Yes                                     | Yes        | Yes                   | Yes                   | Yes                  |
| TEST 1.R3      | $R_{v3}, r_{v3}$        | $H_{3p}$       | $H_{3\phi}$    | Yes                                     | Yes        | No                    | No                    | No                   |
| .              | .                       | .              | .              | .                                       | .          | .                     | .                     | .                    |
| .              | .                       | .              | .              | .                                       | .          | .                     | .                     | .                    |
| TEST 1.Ti      | $T_{vi}, m_{vi}$        | $H_{i-1,\phi}$ | $H_{ip}$       | Yes                                     | Yes        | Yes                   | Yes                   | Yes                  |
| TEST 1.Ri      | $R_{vi}, r_{vi}$        | $H_{ip}$       | $H_{i\phi}$    | Yes                                     | Yes        | No                    | No                    | No                   |
| .              | .                       | .              | .              | .                                       | .          | .                     | .                     | .                    |
| .              | .                       | .              | .              | .                                       | .          | .                     | .                     | .                    |
| TEST 1.Tk - 1  | $T_{v,k-1}, m_{v,k-1}$  | $H_{k-2,\phi}$ | $H_{k-1,p}$    | Yes                                     | Yes        | Yes                   | Yes                   | Yes                  |
| TEST 1.Rk - 1  | $R_{v,k-1}, r_{v,k-1}$  | $H_{k-1,p}$    | $H_{k-1,\phi}$ | Yes                                     | Yes        | No                    | No                    | No                   |

<sup>a</sup>For partial capture history scheme B, all TESTs 1.Ti are computable, however, only 1.R1 and 1.R2 are computable of the 1.Ri series; also, the exact meanings of the null and alternative hypotheses change when some components of TEST 1 drop out.

<sup>b</sup>For the first capture history protocol, the computable components are 1.R1 and 1.Ti,  $i = 2, \dots, k - 1$ .

<sup>c</sup>For the unknown capture history protocol, the computable components are 1.R1 and 1.Ti,  $i = 2, \dots, k - 1$ ; also, these tests (hence, all of TEST 1) are only approximations under the unknown capture history protocol.

comparing two models: the sampling model under the null hypothesis versus that under the alternative hypothesis. Not all hypotheses in Table 2.2 are testable under all protocols, as shown in Table 2.3.

The simulated treatment-control data summarized in Tables 1.5 and 1.6 are used to illustrate TEST 1. Only the summary statistics  $R_{vi}, r_{vi}$ ,  $i = 1, \dots, k - 1$  and  $m_{vi}, z_{vi}$ ,  $i = 2, \dots, k - 1$  are used in TEST 1. Test components are based on the following tables:

TEST 1.R*i*,  $i = 1, \dots, k - 1$ 

|          |                   |          |
|----------|-------------------|----------|
| $r_{ti}$ | $R_{ti} - r_{ti}$ | totals   |
| $r_{ci}$ | $R_{ci} - r_{ci}$ | $R_{ti}$ |
|          |                   | $R_{ci}$ |

TEST 1.T*i*,  $i = 2, \dots, k - 1$ 

|          |          |          |
|----------|----------|----------|
| $m_{ti}$ | $z_{ti}$ | totals   |
| $m_{ci}$ | $z_{ci}$ | $T_{ti}$ |
|          |          | $T_{ci}$ |

For this example, one can easily construct these  $2 \times 2$  contingency tables with the data from Tables 1.5 and 1.6:

TEST

1.R1

|       |        |
|-------|--------|
| 4,395 | 24,605 |
| 4,075 | 25,925 |

1.R2

|     |     |
|-----|-----|
| 136 | 935 |
| 128 | 872 |

1.R3

|    |     |
|----|-----|
| 31 | 219 |
| 32 | 203 |

1.R4

|     |       |
|-----|-------|
| 102 | 1,760 |
| 93  | 1,584 |

1.R5

|    |     |
|----|-----|
| 26 | 590 |
| 19 | 571 |

TEST

1.T2

|       |       |
|-------|-------|
| 1,104 | 3,291 |
| 1,029 | 3,046 |

1.T3

|     |       |
|-----|-------|
| 260 | 3,167 |
| 249 | 2,925 |

1.T4

|       |       |
|-------|-------|
| 1,924 | 1,274 |
| 1,762 | 1,195 |

1.T5

|     |     |
|-----|-----|
| 644 | 732 |
| 616 | 672 |

The chi-square test statistics and the overall TEST 1 results, in appropriate order, are

| TEST   | Hypothesis  |             | $\chi^2$ | df | P      |
|--------|-------------|-------------|----------|----|--------|
|        | Null        | Alternative |          |    |        |
| 1.R1   | $H_0$       | $H_{1\phi}$ | 29.63    | 1  | 0.000  |
| 1.T2   | $H_{1\phi}$ | $H_{2p}$    | 0.02     | 1  | 0.887  |
| 1.R2   | $H_{2p}$    | $H_{2\phi}$ | 0.01     | 1  | 0.920  |
| 1.T3   | $H_{2\phi}$ | $H_{3p}$    | 0.15     | 1  | 0.699  |
| 1.R3   | $H_{3p}$    | $H_{3\phi}$ | 0.16     | 1  | 0.689  |
| 1.T4   | $H_{3\phi}$ | $H_{4p}$    | 0.21     | 1  | 0.647  |
| 1.R4   | $H_{4p}$    | $H_{4\phi}$ | 0.01     | 1  | 0.920  |
| 1.T5   | $H_{4\phi}$ | $H_{5p}$    | 0.28     | 1  | 0.600  |
| 1.R5   | $H_{5p}$    | $H_{5\phi}$ | 0.84     | 1  | 0.359  |
| TEST 1 | $H_0$       | $H_{5\phi}$ | 31.31    | 9  | <0.001 |

If the individual hypotheses in this sequence make biological sense, this sequential testing is valuable. (This example is discussed further in Chapter 2.4.)

The proportion of  $R_{vi}$  fish released at site  $i$  that are ever recovered is  $r_{vi}/R_{vi}$ . TEST 1.R*i* tests the equality of the expected proportion recaptured for treatment and control. That is, TEST 1.R*i* compares

$$\frac{r_{ti}}{R_{ti}} \text{ and } \frac{r_{ci}}{R_{ci}}$$

to see if they are so different that one should believe different survival or capture rates are applicable to the treatment and control fish after their release at site  $i$ .

TEST 1.T*i* is also comparing two proportions, namely

$$\frac{m_{ti}}{T_{ti}} \text{ and } \frac{m_{ci}}{T_{ci}}$$

The totals  $T_{vi}$  are the numbers of fish known to be alive, at risk of capture, at site  $i$ . Of the total  $T_{vi}$ ,  $m_{vi}$  is the number of fish actually caught at site  $i$ . If treatment and control fish have the same survival and capture rates at, and after, site  $i$ , then these proportions should not differ significantly. Conversely, rejection with TEST 1.7i means there is some treatment effect evident at or after site  $i$ .

### 2.1.3. Goodness of Fit Testing Within a Treatment Group

**2.1.3.1. TEST 1.** – TEST 1 is computed across the different treatment groups. It is also possible to compute separately, for each group, a goodness of fit test to the general assumption of site- (time-) specific parameters. Examples of the types of factors that cause TESTs 2 and 3 to reject are heterogeneity of parameters over fish (caused, e.g., by fish size), failure of the assumption of independent fish fates, and behavioral response to capture and subsequent release (in some types of studies). Goodness of fit is especially critical in studies where new animals are released at each site or time. In such studies, new releases might be different from previously marked animals. This situation is not encountered commonly in fish-turbine survival experiments, but is relevant in studies in which simultaneous estimation of mortality rates at several dams is attempted (i.e., system-wide studies).

**2.1.3.2. TEST 2.** – TEST 2 is based on the  $m$ -array and is computed as a series of linked contingency tables. Table 2.4 gives the names of the separate components of TEST 2 and some information about each component. Program RELEASE computes these tests and labels them by the names listed in Table 2.4. Data required for TESTs 2 and 3 are not available (i.e., do not exist) under the first capture history and unknown capture history protocols. Under the partial capture history protocol scheme B, only TEST 2.C2 exists. TEST 2.C2 is the usual chi-square test of homogeneity based on the following  $2 \times k - 2$  table:

|          |          |     |          |
|----------|----------|-----|----------|
| $m_{13}$ | $m_{14}$ | ... | $m_{1k}$ |
| $m_{23}$ | $m_{24}$ | ... | $m_{2k}$ |



## PART 2. PROTOCOLS FOR STUDIES

Table 2.4. - Explanation of TEST 2: its components, their identification, hypotheses tested, and computability of components by capture history (CH) protocol. TEST 2 is computed separately for each data group; the data used are elements of the  $m$ -array (the  $m_{\tau ij}$ ). There are  $k - 3$  test components ( $k \geq 4$ ).

| TEST          | Summary statistics used  | Null hypothesis   | Computability under different protocols |            |          |          |         |
|---------------|--|---|---|------------|----------|----------|---------|
|               |  |   | Complete CH                             | Partial CH |          | First CH | Unk. CH |
|               |  |   |   | scheme A   | scheme B |          |         |
| TEST 2.C2     | $m_{\tau 13}, \dots, m_{\tau 1k}$<br>$m_{\tau 23}, \dots, m_{\tau 2k}$ | Parameters $(\phi, p)$ are the same for cohort 2 as for survivors at site 2 of cohort 1.                                | Yes                                     | Yes        | Yes      | No       | No      |
| TEST 2.C3     | $m_{\tau i4}, \dots, m_{\tau ik}$<br><br>$i = 1, 2, 3$                 | Parameters $(\phi, p)$ are the same for cohort 3 as for survivors at site 3 of previously released cohorts.             | Yes                                     | Yes        | No       | No       | No      |
| .             | .  | .   | .                                       | .          | .        | .        | .       |
| .             | .  | .   | .                                       | .          | .        | .        | .       |
| .             | .  | .   | .                                       | .          | .        | .        | .       |
| TEST 2.Cj     | $m_{\tau i, j+1}, \dots, m_{\tau ik}$<br><br>$i = 1, \dots, j$         | Parameters $(\phi, p)$ are the same for cohort $j$ as for survivors at site $j$ of previously released cohorts.         | Yes                                     | Yes        | No       | No       | No      |
| .             | .  | .   | .                                       | .          | .        | .        | .       |
| .             | .  | .   | .                                       | .          | .        | .        | .       |
| .             | .  | .   | .                                       | .          | .        | .        | .       |
| TEST 2.Ck - 2 | $m_{\tau i, k-1}, m_{\tau ik}$<br><br>$i = 1, \dots, k - 2$            | Parameters $(\phi, p)$ are the same for cohort $k - 2$ as for survivors at site $k - 1$ of previously released cohorts. | Yes                                     | Yes        | No       | No       | No      |

Notice that  $m_{12}$  was discarded, and that the row and column totals of this table were conditioned. To get TEST 2.C3, take the totals for columns 4 to  $k$  and compare them with recaptures from cohort 4:

|                   |                   |     |                   |
|-------------------|-------------------|-----|-------------------|
| $m_{14} + m_{24}$ | $m_{15} + m_{25}$ | ... | $m_{1k} + m_{2k}$ |
| $m_{34}$          | $m_{35}$          | ... | $m_{3k}$          |

This summing of columns and adjoining of the next cohort continues until one uses cohort  $k - 2$  (thereby getting TEST 2.C $k - 2$ ). Note that for TEST 2.C $i$ , only recaptures downstream from dam  $i$  are used.

TEST 2 is comparing the proportion of counts in rows 1 and 2 across the columns of the contingency table. If these proportions do not differ significantly, then there is no statistical evidence that the underlying survival and capture probabilities differ for the two rows of counts.

The simulated control group data in Table 1.6 are here used for illustration (these are the  $m_{ij}$ ):

| Cohort $i$ | $j = 2$ | 3   | 4     | 5   | 6   |
|------------|---------|-----|-------|-----|-----|
| 1          | 1,104   | 247 | 1,832 | 571 | 641 |
| 2          |         | 13  | 75    | 19  | 29  |
| 3          |         |     | 17    | 4   | 10  |
| 4          |         |     |       | 50  | 52  |
| 5          |         |     |       |     | 26  |

TEST 2.C2 is based on

|     |       |     |     |
|-----|-------|-----|-----|
| 247 | 1,832 | 571 | 641 |
| 13  | 75    | 19  | 29  |

Column  
totals      260    1,907    590    670

Adjoin the cohort 3 recaptures to the above column totals (omitting the leftmost column) to get the table for TEST 2.C3 (note: "C" here denotes cohort, i.e., these tests are based on cohort data):

|       |     |     |
|-------|-----|-----|
| 1,907 | 590 | 670 |
| 17    | 4   | 10  |

Column  
totals      1,924    594    680

In this example, TEST 2.C4 is the final test that can be computed. It is based on the data

|     |     |
|-----|-----|
| 594 | 680 |
| 50  | 52  |

Thus, for the control data, we have

| <u>TEST</u> | <u><math>\chi^2</math></u> | <u>df</u> | <u>P</u>    |
|-------------|----------------------------|-----------|-------------|
| 2.C2        | 1.83                       | 3         | 0.61        |
| 2.C3        | 2.47                       | 2         | 0.32        |
| <u>2.C4</u> | <u>0.22</u>                | <u>1</u>  | <u>0.64</u> |
| TEST 2      | 4.51                       | 6         | 0.61        |

TEST 2 for the controls is the total of these three independent chi-square test statistics. None of these test statistics is significant here; this is expected because these data were generated under model  $H_{1\phi}$ . In a study with two or more groups, TEST 2 is computed for each group separately and the overall TEST 2 is obtained by summing the separate chi-squares and degrees of freedom over groups.

2.1.3.3. TEST 3. - TEST 3 is based on the subcohort information available in the full  $m$ -array. The data for the simulated treatment group example are shown in Table 1.3. Table 2.5 provides our recommendations for computing TEST 3. Basically, TEST 3 has a component for every cohort that has two or more subcohorts. In fish-turbine survival experiments, only cohorts 3 to  $k - 1$  allow a TEST 3 component. In general Jolly-Seber studies, cohort 2 also has two subcohorts.

From Table 1.3, cohort 3, the contingency table of subcohort data on the fates of the releases at dam 3 is:

|     |    |   |   |     |
|-----|----|---|---|-----|
| 224 | 19 | 7 | 5 | 193 |
| 11  | 1  | 0 | 0 | 10  |

Here, 224 fish were rereleased with capture history {101}. The other 11 had history {111}. Numbers of fish never recaptured were 193 and 10, respectively. As often happens, these data are sparse, and some pooling is necessary to enable a test. Because of this pooling, we recommend a routine splitting of these subcohort-fate contingency tables into two test components: TEST 3.SR $i$  and TEST 3.Sm $i$ ,  $i = 3, \dots, k - 2$  (capital  $S$  denotes subcohorts;  $R$  denotes that the test uses the  $R, r$  data; TEST 3.Sm $i$  is based on only the  $m_{i,r}$  data).

The previous table partitions into

|    |     |
|----|-----|
| 31 | 193 |
| 1  | 10  |

for TEST 3.SR3

and into

|    |   |   |
|----|---|---|
| 19 | 7 | 5 |
| 1  | 0 | 0 |

for TEST 3.Sm3.

There are often insufficient data to carry out TEST 3.Smi (as is the case in the previous example), even if that table is further pooled into a simple 2 × 2 contingency table:

|    |    |
|----|----|
| 19 | 12 |
| 1  | 0  |

These 2 × 2 contingency tables are used in program RELEASE for TEST 3 components. Program RELEASE does this pooling automatically because the subcohort data are often sparse. The user can recompute these tests on the basis of less-pooled versions of these tables if that is warranted.

Table 2.5. - Explanation of TEST 3 components as we define them under the default pooling rules, and the (potential) computability of components. TEST 3 is computable only for the complete capture history protocol. Data are the subcohorts within released cohorts. Test components are often not computable if data are sparse.

TEST 3.SR*i*, *i* = 3, ..., *k* - 1.

Components are based on recaptures after time *i*. In RELEASE, the default test is computed from the 2 × 2 contingency table defined below; only data from subcohorts of releases at time *i* are used:

*h* = {10...01}, i.e.,  
 caught at dam *i*, but  
 not at dams 2, ..., *i* - 1

|                |                                   |
|----------------|-----------------------------------|
| $r_{nh}$       | $R_{nh} - r_{nh}$                 |
| $r_n - r_{nh}$ | $(R_n - r_n) - (R_{nh} - r_{nh})$ |

The null hypothesis is that parameters ( $\phi$ ,  $p$ ) for captures at times *i* + 1 to *k* are the same for all capture histories at release time *i*. There are *k* - 3 of these tables (in the fisheries context here where only the first release has newly marked fish). TEST 3 is not computable if *k* < 4.

TEST 3.Smi, *i* = 3, ..., *k* - 2.

Components are based on recaptures at time *i* + 1, given release at time *i* and subsequent recapture. In RELEASE, the default test is computed from the 2 × 2 contingency table defined below; only data from subcohorts of releases at time *i* are used; *h* is as above:

|                           |  |
|---------------------------|--|
| $m_{d,j+1,h}$             | $(r_{nh} - m_{d,j+1,h})$                     |
| $m_{d,j+1} - m_{d,j+1,h}$ | $(r_n - m_{d,j+1}) - (r_{nh} - m_{d,j+1,h})$ |

The null hypothesis is the same as for TEST 3.SR*i*. There are *k* - 4 of these tables (*k* ≥ 5).

Continuing with this example, the subcohort data for controls from Table 1.4 for cohorts 4 and 5 are

| cohort<br>4 |    |       |
|-------------|----|-------|
| 48          | 49 | 1,678 |
| 1           | 2  | 68    |
| 1           | 1  | 14    |

| cohort<br>5 |     |
|-------------|-----|
| 24          | 522 |
| 0           | 18  |
| 0           | 4   |
| 2           | 44  |
| 0           | 1   |
| 0           | 1   |

The  $2 \times 2$  contingency tables for TEST 3 components are

| TEST 3.SR4 |       | TEST 3.SR5 |     | TEST 3.Sm4 |    |
|------------|-------|------------|-----|------------|----|
| 97         | 1,678 | 24         | 522 | 48         | 49 |
| 5          | 82    | 2          | 68  | 2          | 3  |

Note that TEST 3.Sm $k$  - 1 never exists. In general, there is more information in the 3.SR $i$  series of components than in the 3.Sm $i$  series.

Results in this example for the control group are

| <u>TEST</u>  | <u><math>\chi^2</math></u> | <u>df</u> | <u>P</u>    |
|--------------|----------------------------|-----------|-------------|
| 3.SR3        | 0.28                       | 1         | 0.60        |
| 3.SR4        | 0.01                       | 1         | 0.91        |
| 3.SR5        | 0.36                       | 1         | 0.55        |
| 3.Sm3        | 1.25                       | 1         | 0.26        |
| <u>3.Sm4</u> | <u>0.17</u>                | <u>1</u>  | <u>0.68</u> |
| TEST 3       | 2.08                       | 5         | 0.84        |

The overall goodness of fit test for the assumption of site-specific parameters, which are not subcohort dependent (i.e., the Jolly-Seber model), is the sum of TESTs 2 and 3:

| <u>TEST</u> | <u><math>\chi^2</math></u> | <u>df</u> | <u>P</u> |
|-------------|----------------------------|-----------|----------|
| 2           | 4.51                       | 6         | 0.61     |
| 3           | 2.08                       | 5         | 0.84     |
| Total       | 6.59                       | 11        | 0.83     |

Based on this goodness of fit testing for the control data, we would not reject the assumption of site-specific parameters (i.e., the Jolly-Seber model fits the control data).

#### 2.1.4. Discussion

As a basic strategy, we recommend first computing the goodness of fit tests. If these tests reject the Jolly-Seber assumptions of site-specific parameters, one must consider using more general models than we present here (see the discussion in Section 1.4.4). This type of rejection is frequent in studies in which each release (by occasion or site) contains both new animals and previously marked animals. However, we do not consider such studies herein. When all initial releases are at site 1, there is a high likelihood (in our opinion) that the time-specific assumptions about parameters will be satisfied in a carefully conducted study where the rate of movement between dams is not affected by treatment, and there are no handling effects.

If, based on the results of TESTs 2 and 3, goodness of fit is satisfactory, one then proceeds to find an appropriate model to describe the results of the experiment. The first step in that search should be the computation of TEST 1 and an examination of its components. The set of models to be considered should then be determined by biological considerations. When treatment is "applied" at site 1, as in a fisheries turbine, screen, or bypass study, it is reasonable to consider the sequence of hypotheses presented here. The treatment effect is then expected either to wear off or to manifest itself over time. Thus, we believe that in this experimental setting, the time-ordering of parameters ( $\phi_1, p_2, \phi_3$ , etc.) is relevant in testing for treatment effect. Consequently, we recommend testing to determine if one of the hypotheses of Table 2.2 adequately describes the data. If none do, or if it is logical to investigate alternative hypotheses, one must resort to numerical optimization methods for further testing and estimation. Numerical methods would be required, for example, to analyze the data under a model wherein  $\phi_{c_i} \neq \phi_{n_i}$  (a general effect on survival) but  $p_{c_i} = p_{n_i}$  was assumed (no effects on capture probabilities). Program SURVIV (White 1983) handles this model. Program RELEASE produces output that is easily used as input to program SURVIV for analysis of these alternative scenarios.

## 2.2. First Capture Histories

### 2.2.1. Introduction

Under the first capture history protocol, the easiest of the protocols to understand and analyze, fish released at dam 1 are given a batch mark to distinguish treatment versus control groups. Fish in both groups are sampled at downstream dams 2, 3, ...,  $k$  and, upon first capture, are removed from the population.

The analysis theory for experiments where only one downstream sampling site is used (i.e.,  $k = 2$ ) dates back to Ricker (1945, 1948). His method is often referred to as the *relative recovery rate method* because the estimator of survival rate is the ratio of two "recovery" or recapture rates. Ricker (1958, 1975) extended the method to allow for  $k$  sampling occasions and the estimator was again of a similar form, after some pooling of the data across sampling sites. A more general theory was developed independently by Seber (1970) and Robson and Youngs (unpublished report, 1971) (also see Youngs and Robson 1975). This theory allowed greater generality in that marking could be done at  $n$  time periods (rather than just two), recovery could be done over  $k$  time periods ( $k \geq n$ ), time periods could be unequal, and procedures were free of bias due to truncation. A full discussion of these ML methods can be found in Brownie et al. (1985). The methods of Ricker (1945, 1948), Seber (1970), and Robson and Youngs (unpublished report, 1971) are concerned with the estimation of survival rates based on marking of samples from the population at  $n$  time intervals, often once per year. For example, northern pintail ducks *Anas acuta* might be banded with unique band numbers each October for  $n$  years; therefore, the survival rate is the annual period between banding (e.g., 15 October of year 1 to 14 October of year 2). In the context here, the survival rate of interest relates not to the time between marking periods but rather to a treatment effect. The survival rate is the result of a treatment because the releases of the treatment and control groups are simultaneous, rather than a year apart. Finally, the probability of not being captured must be incorporated into these models, although the estimators of treatment survival remain the same. With this reinterpretation, the theory for the analysis and testing for the first capture history protocol already exists for model  $H_{1\phi}$ . We will use notation and terminology consistent with the rest of this monograph. Interested readers may want to refer to Brownie et al. (1985) for other applications and examples.

### 2.2.2. Model Structure and Expectations

Assuming that fish have independent fates and that all fish in the same treatment group have the same probabilities of being recaptured at downstream dams, the data on first captures are multinomial. If a marked fish is released, it can be captured and removed at dam 2, 3, ...,  $k$ , or "never." The model for this protocol is obtained by specifying the probabilities for

each outcome as a function of the parameters  $\phi_i$  and  $p_i$ . This corresponds to deriving the expected values of the elements in the reduced  $m$ -array,  $E(m_{ij})$ , for the two groups of marked fish. Some examples for the control group will illustrate the concept:

$$E(m_{c12}) = R_{c1}\phi_{c1}p_{c2};$$

$$E(m_{c13}) = R_{c1}\phi_{c1}q_{c2}\phi_{c2}p_{c3};$$

$$E(m_{c14}) = R_{c1}\phi_{c1}q_{c2}\phi_{c2}q_{c3}\phi_{c3}p_{c4}.$$

The first expression is the expected number of recaptures at dam 2 from the  $R_{c1}$  control fish released at dam 1.  $E(m_{c12})$  equals the number of control fish released ( $R_{c1}$ ), times the survival rate from dam 1 to dam 2 ( $\phi_{c1}$ ), times the probability of recapture at dam 2 ( $p_{c2}$ ). The final expectation is read as the expected value of the  $m_{c14}$  equals the number of fish initially released ( $R_{c1}$ ), times the survival probabilities for dams 1 to 2, 2 to 3, and 3 to 4 ( $\phi_{c1}$ ,  $\phi_{c2}$ ,  $\phi_{c3}$ ), times the probability of not being captured at dams 2 and 3 ( $q_{c2}$ ,  $q_{c3}$ ), times the probability of recapture at dam 4 ( $p_{c4}$ ). The treatment fish have similar expectations, although parameters  $\phi$  and  $p$  may differ from those in the control group:

$$E(m_{t12}) = R_{t1}\phi_{t1}p_{t2};$$

$$E(m_{t13}) = R_{t1}\phi_{t1}q_{t2}\phi_{t2}p_{t3};$$

$$E(m_{t14}) = R_{t1}\phi_{t1}q_{t2}\phi_{t2}q_{t3}\phi_{t3}p_{t4}.$$

The observed data are then functions of the dam-to-dam survival probabilities ( $\phi_i$ ), the recapture probabilities ( $p_i$ ), and the probability of not being captured ( $q_i = 1 - p_i$ ). In more complex protocols, the  $\phi_i$  and  $p_i$  parameters can be estimated separately but are not individually estimable with the data collected under the first capture history protocol. Also, only limited tests of assumptions are possible under the first capture history protocol. Products of the other parameters can be estimated, but these are of little interest (e.g.,  $\phi_{v1}p_{v2}$ ,  $\phi_{v1}q_{v2}\phi_{v2}p_{v3}$ , and  $\phi_{v1}q_{v2}\phi_{v2}\cdots\phi_{vk-1}p_{vk}$ ). For this reason, subsequent modeling is simplified if the following notation is used:

$$\pi_{ij} = \phi_{i1}q_{i+1}\phi_{i+1}q_{i+2}\cdots\phi_{ij-1}p_{ij}$$

and

$$\pi_{cij} = \phi_{ci}q_{ci+1}\phi_{ci+1}q_{ci+2}\cdots\phi_{cj-1}p_{cj}.$$

The  $\pi_{ij}$  are called "cell probabilities." Under model  $H_{1\phi}$ ,  $\phi_{t1} = S\phi_{c1}$  and all other parameters ( $\phi_i, p_i$ ) are the same by treatment and control groups. Therefore, under model  $H_{1\phi}$ ,  $\pi_{t1j} = S\pi_{c1j}$ .



Table 2.6 presents a summary of the data from the general numerical example and the corresponding notation, expectations, and summary statistics.

Table 2.6. - Example data, symbolic reduced  $m$ -arrays, expectations of the  $m$ -array, and sufficient statistics for the general numerical data under the first capture history protocol.

| Group | Releases<br>$R_{v1}$ | Number recaptured and removed at dam $j, m_{vj}$ |             |               |             |             | Total                    |
|-------|----------------------|--|-------------|---------------|-------------|-------------|--------------------------|
|       |                      | $j = 2$  | 3           | 4             | 5           | 6           |                          |
| $t$   | 30,000               | 1,029  | 238         | 1,669         | 549         | 590         | 4,075                    |
| $c$   | 29,000               | 1,104  | 247         | 1,832         | 571         | 641         | 4,395                    |
| Total |                      | 2,133  | 485         | 3,501         | 1,120       | 1,231       |                          |
| $t$   | $R_{t1}$             | $m_{t12}$  | $m_{t13}$   | $m_{t14}$     | $m_{t15}$   | $m_{t16}$   | $r_{t1}$                 |
| $c$   | $R_{c1}$             | $m_{c12}$  | $m_{c13}$   | $m_{c14}$     | $m_{c15}$   | $m_{c16}$   | $r_{c1}$                 |
| Total |                      | $m_2$  | $m_3$       | $m_4$         | $m_5$       | $m_6$       |                          |
| $t$   | $R_{t1}$             | $\pi_{t12}$                                      | $\pi_{t13}$ | $\pi_{t14}$   | $\pi_{t15}$ | $\pi_{t16}$ | $\sum_{j=2}^6 \pi_{t1j}$ |
| $c$   | $R_{c1}$             | $\pi_{c12}$                                      | $\pi_{c13}$ | $\pi_{c14}^a$ | $\pi_{c15}$ | $\pi_{c16}$ | $\sum_{j=2}^6 \pi_{c1j}$ |

$$^a \pi_{c14} = \phi_{c1} q_{c2} \phi_{c2} q_{c3} \phi_{c3} p_{c4}$$

### 2.2.3. Likelihood Function

The likelihood function is derived from the joint probability function of the data for both groups,

$$\Pr\{m_{v1j} | S, \underline{\phi}, \underline{p}, \underline{R}\} = \prod_{v=t}^c \left[ \left( m_{v12} m_{v13} \cdots m_{v1k} R_{v1} - r_{v1} \right) \times \prod_{j=2}^k \left( \pi_{v1j} \right)^{m_{v1j}} \left( 1 - \lambda_{v1} \right)^{R_{v1} - r_{v1}} \right],$$

where  $v$  is a subscript to indicate the treatment ( $t$ ) and control ( $c$ ) groups, and  $\lambda_{v1} = \sum_{j=2}^k \pi_{v1j}$ .

Terms such as  $\underline{\phi}$  indicate a vector of the dam-to-dam survival rates ( $\underline{\phi} = \phi_1, \phi_2, \dots, \phi_k$ ). The notation is formidable, but a simple example in which only two downstream dams are used ( $k = 3$ ) is helpful:

|                      | <u>Treatment</u>                             | <u>Control</u>                               |
|----------------------|--|--|
| $v$                  | $t$  | $c$  |
| Releases             | $R_{t1}$                                     | $R_{c1}$                                     |
| Recaptures           | $m_{t12}$ and $m_{t13}$                      | $m_{c12}$ and $m_{c13}$                      |
| Never recaptured     | $R_{t1} - r_{t1}$                            | $R_{c1} - r_{c1}$                            |
| Cell probabilities   | $\pi_{t12} = \phi_{t1}p_{t2}$                | $\pi_{c12} = \phi_{c1}p_{c2}$                |
|                      | $\pi_{t13} = \phi_{t1}q_{t2}\phi_{t2}p_{t3}$ | $\pi_{c13} = \phi_{c1}q_{c2}\phi_{c2}p_{c3}$ |
| Pr{never recaptured} | $\lambda_{t1} = 1 - \sum_{j=2}^3 \pi_{t1j}$  | $\lambda_{c1} = 1 - \sum_{j=2}^3 \pi_{c1j}$  |

An explanation of the probability function may be helpful. The joint probability function of the data for both groups is

$$\Pr\{m_{v1j} \mid S, \underline{\phi}, \underline{p}, \underline{R}\}$$

and is read as “the probability of the reduced  $m$ -array, given the parameters  $S, \phi_1, \phi_2, p_2, p_3$  and the known releases  $R_{t1}$  and  $R_{c1}$ .” This probability function has two components: the first is composed of the product of two multinomial coefficients;

$$\left( \begin{matrix} R_{t1} \\ m_{t12} \ m_{t13} \ R_{t1} - r_{t1} \end{matrix} \right) \left( \begin{matrix} R_{c1} \\ m_{c12} \ m_{c13} \ R_{c1} - r_{c1} \end{matrix} \right).$$

Alternatively, these coefficients can be expressed as ratios of factorial expressions,

$$\left( \frac{R_{t1}!}{m_{t12}! m_{t13}! (R_{t1} - r_{t1})!} \right) \left( \frac{R_{c1}!}{m_{c12}! m_{c13}! (R_{c1} - r_{c1})!} \right).$$

These expressions include no unknown parameters and can, therefore, be ignored for purposes of parameter estimation. These expressions are part of the likelihood and are needed for deriving tests of various assumptions.

The second component of the probability function is important for deriving MLEs of the unknown parameters:

$$\prod_{v=t}^c \left( \prod_{j=2}^3 [\pi_{v1j}]^{m_{v1j}} \right) (1 - \lambda_{v1})^{R_{v1} - r_{v1}}.$$

Letting  $v = t$  for treatment, we can write out the first half of this expression,

$$[\pi_{t12}]^{m_{t12}} \times [\pi_{t13}]^{m_{t13}} \times [1 - \lambda_{t1}]^{R_{t1} - r_{t1}}.$$

Letting  $v = c$  for control, the second half is simply

$$[\pi_{c12}]^{m_{c12}} \times [\pi_{c13}]^{m_{c13}} \times [1 - \lambda_{c1}]^{R_{c1} - r_{c1}}.$$

These expressions can be compared with those developed for the die-tossing study in Section 1.2.1 with two differences. First, the cell probabilities  $\pi_{ij}$  are now functions of several parameters rather than being a simple probability (e.g.,  $p_4$  was the probability of getting a four on a die throw); and second, the final cell deals with the probability and number of fish never being recaptured, which is a possible outcome (but has no direct analogy with the throw of a die except, perhaps, if one did not tally the number of "sixes").

The likelihood function relevant for parameter estimation is

$$L(S, \underline{\phi}, \underline{p} \mid m_{vij}) = \prod_{v=t}^c \left[ \prod_{j=2}^3 (\pi_{v1j})^{m_{v1j}} \right] (1 - \lambda_{v1})^{R_{v1} - r_{v1}}$$

and the log-likelihood function is

$$\ln L(S, \underline{\phi}, \underline{p} \mid m_{vij}) = \sum_{v=t}^c \left[ \left( \sum_{j=2}^3 m_{v1j} [\ln(\pi_{v1j})] \right) + (R_{v1} - r_{v1}) \ln(1 - \lambda_{v1}) \right].$$

2.2.4. Estimable Parameters

As noted earlier, individual  $\phi_{vi}$  and  $p_{vi}$  are not estimable from data collected under the first capture history protocol. However, under certain assumptions concerning the  $\phi_{vi}$  and  $p_{vi}$ , treatment effects are estimable. In particular, if the treatment effect is direct, so that  $\phi_{t1} = S\phi_{c1}$ ,  $\phi_{ti} = \phi_{ci}$ ,  $i = 2, \dots, k - 1$ , and  $p_{ti} = p_{ci}$ ,  $i = 2, \dots, k$ , the treatment survival rate  $S = \phi_{t1}/\phi_{c1}$  is estimable. Referring to the sequence of models introduced in Chapter 2.1, we say that  $S = \phi_{t1}/\phi_{c1}$  is estimable if the assumptions of model  $H_{1\phi}$  are met. If the treatment effect persists to dam 2 (the first recapture site) and beyond, models more general than  $H_{1\phi}$  are required and estimators of treatment effects may not be free of bias. We therefore discuss model  $H_{1\phi}$  in some detail and present tests to be used to determine if the model assumptions are met.

Under model  $H_{1\phi}$ , all parameters  $\phi_{vi}$  and  $p_{vi}$  are the same across treatment and control groups, except for  $\phi_{t1}$  and  $\phi_{c1}$ . Writing  $\phi_{t1} = S\phi_{c1}$  shows that  $\pi_{\alpha j} = S\pi_{\alpha j}$  for  $j = 2, \dots, k$ , and  $\lambda_{t1} = S\lambda_{c1}$ . Making these substitutions simplifies the likelihood in Section 2.2.3 and enables the identification of a minimal sufficient statistic and the derivation of estimators.

2.2.5. Minimal Sufficient Statistics

A minimal sufficient statistic (MSS) is

$$MSS = \{r_{t1}, r_{c1}, m_2, m_3, \dots, m_{k-1}\},$$

which is the two row totals and all the column totals, except the  $k$ th, of the reduced  $m$ -array. These summary statistics contain all the information relevant to optimal estimation of the parameters of the model under  $H_{1\phi}$ . The number of terms in the MSS dictates the maximum number of parameters that can be identified (estimated). In the present example,  $k$  "parameters" can be estimated,

|     |              |                         |                                    |     |  |
|-----|--------------|-------------------------|------------------------------------|-----|--|
| 1   | 2            | 3                       | 4                                  | ... | $k$  |
| $S$ | $\phi_1 p_2$ | $\phi_1 q_2 \phi_2 p_3$ | $\phi_1 q_2 \phi_2 q_3 \phi_3 p_4$ | ... | $\phi_1 q_2 \phi_2 q_3 \dots \phi_{k-1} p_k$ |

The previous "parameters" are the cell probabilities  $\pi_{1j}$ , except that the parameter  $S$  is separated and estimated uniquely.

## 2.2.6. Analysis

The MLE of  $S$ , when all the data from dams 2 through  $k$  are used, is

$$\begin{aligned}\hat{S} &= \frac{r_{t1}/R_{t1}}{r_{c1}/R_{c1}} \\ &= \frac{(m_{t12} + m_{t13} + \cdots + m_{t1k})/R_{t1}}{(m_{c12} + m_{c13} + \cdots + m_{c1k})/R_{c1}},\end{aligned}$$

which is the total recapture rate for treatment fish ( $r_{t1}/R_{t1}$ ) divided by the total recapture rate for control fish ( $r_{c1}/R_{c1}$ ). Using the data on first captures from the general numerical example (Table 2.6),

$$\begin{aligned}\hat{S} &= \frac{4,075/30,000}{4,395/29,000} \\ &= \frac{0.1358333}{0.1515517} \\ &= 0.896,\end{aligned}$$

which, in this example, is close to the parameter value of 0.9.

MLEs of products of other parameters are

$$\phi_1 q_2 \phi_2 q_3 \cdots \phi_{j-1} p_j = \frac{r_{c1} m_j}{R_{c1}(r_{t1} + r_{c1})}.$$

These estimates maximize the likelihood function, given the data observed ( $m_{vij}$ ). Other values are "less likely"; however, if a new sample was taken, then the ML estimates would take different values.

The sampling variance of the MLE of the treatment survival rate  $\hat{S}$  under model  $H_{1\phi}$  is

$$\hat{\text{var}}(\hat{S}) = (\hat{S})^2 \left( \frac{1}{r_{t1}} - \frac{1}{R_{t1}} + \frac{1}{r_{c1}} - \frac{1}{R_{c1}} \right),$$

and the estimated standard error is

$$\hat{se}(\hat{S}) = \sqrt{\hat{\text{var}}(\hat{S})}.$$

The estimated sampling variance for the general numerical example is

$$\begin{aligned}\hat{\text{var}}(\hat{S}) &= (0.896)^2 \left( \frac{1}{4,075} - \frac{1}{30,000} + \frac{1}{4,395} - \frac{1}{29,000} \right) \\ &= (0.8028) (0.000212 + 0.000193) \\ &= 0.000325 ;\end{aligned}$$

$$\hat{se}(\hat{S}) = 0.0180.$$

The estimator  $\hat{S}$  has a high, positive sampling correlation with the estimator of its sampling variance,  $\text{corr}[\hat{S}, \hat{\text{var}}(\hat{S})]$ . This correlation can be seen by noting that the first term in the expression for the sampling variance is  $(\hat{S}^2)$ . Therefore, if  $\hat{S}$  is too large, the estimated sampling variance will be too large, and similarly, if  $\hat{S}$  is too small, the estimated sampling variance will also be too small. We computed estimates of this correlation for a few specific cases (see Monte Carlo studies, Part 5) and found them to be high (e.g., 0.89).

An approximate 95% confidence interval (CI) for  $S$  can be computed in the usual manner, assuming that the sample is reasonably large.

$$\begin{aligned}95\% \text{CI} &= \hat{S} \pm 1.96 \hat{se}(\hat{S}) \\ &= 0.896 \pm 0.0354 \\ &= (0.861, 0.932).\end{aligned}$$

Alternatively, the coefficient of variation (cv) can be computed as a measure of precision,

$$\begin{aligned} \hat{cv}(\hat{S}) &= \frac{\hat{se}(\hat{S})}{\hat{S}} \times 100 \\ &= 2.0\% . \end{aligned}$$

Model  $H_{1\phi}$  assumes the only effect of the treatment is to cause a direct mortality (1 - S). This is a strong assumption (see Chapter 1.5).

2.2.7. Tests of Assumptions

The first capture history protocol allows only limited tests of underlying assumptions. Under model  $H_{1\phi}$ , an overall goodness of fit test is in the form of a  $2 \times k - 1$  contingency table,

|           |           |         |           |           |
|-----------|-----------|---------|-----------|-----------|
| $m_{t12}$ | $m_{t13}$ | $\dots$ | $m_{t1k}$ | $m_{t1.}$ |
| $m_{c12}$ | $m_{c13}$ | $\dots$ | $m_{c1k}$ | $m_{c1.}$ |
| $m_{.12}$ | $m_{.13}$ | $\dots$ | $m_{.1k}$ | $m_{.1}$  |

The test statistic is distributed as chi-square with  $k - 2$  df under the null hypothesis, which states that the treatment and control groups have the same parameters except for  $\phi_{t1}$  and  $\phi_{c1}$ , thus,

$$\phi_{ti} = \phi_{ci} \quad \text{for all } i = 2, \dots, k - 1,$$

and

$$p_{ti} = p_{ci} \quad \text{for all } i = 2, \dots, k .$$

The alternative hypothesis for this general test is that model  $H_{k-1,\phi}$  holds (all parameters  $\phi_{ti}$  and  $p_{ti}$  differ by groups). This test is the sum of TESTS 1.T2, 1.T3, ..., 1.Tk - 1.

The contingency table for the general numerical example is

|       |     |       |       |       |       |
|-------|-----|-------|-------|-------|-------|
| 1,029 | 238 | 1,669 | 549   | 590   | 4,075 |
| 1,104 | 247 | 1,832 | 571   | 641   | 4,395 |
| 2,133 | 485 | 3,501 | 1,120 | 1,231 | 8,470 |

Computing the test statistic from the above table gives  $\chi^2 = 3.2$ , 4 df, with  $P = 0.52$ . Thus, we have no evidence to suspect the validity of the null hypothesis ( $H_{1\phi}$  fits the data). We know that the null hypothesis is true in this case because the data were generated from this set of assumptions (cf. Table 1.1).

The goodness of fit test can be viewed in an alternative way that is often more intuitive. Most biologists think of a goodness of fit test as

$$\sum \frac{(\text{observed} - \text{expected})^2}{\text{expected}}$$

The observed data under the first capture history protocol are the  $m_{t1j}$  and  $m_{c1j}$ . Their expected values, assuming  $H_{1\phi}$  is true, can be estimated as

$$\hat{E}(m_{t1j}) = R_{t1} S \phi_1 q_2 \phi_2 \cdots \phi_{j-1} p_j$$

and

$$\hat{E}(m_{c1j}) = R_{c1} \phi_1 q_2 \phi_2 \cdots \phi_{j-1} p_j$$

Therefore, an alternative, but equivalent test of the null hypothesis that  $H_{1\phi}$  holds is

$$\chi^2 = \sum_{v=t}^c \sum_{j=2}^k \frac{[m_{v1j} - \hat{E}(m_{v1j})]^2}{\hat{E}(m_{v1j})}$$

with  $k - 2$  df. The results are equivalent to the contingency table approach unless some pooling is necessary (in which case the contingency table approach should be used). Pooling is required if  $\hat{E}(m_{v1j}) < 2$ . Program RELEASE performs a thorough analysis of data under the first capture history protocol; example output is shown in Table 2.7.



## PART 2. PROTOCOLS FOR STUDIES

Table 2.7. - The output of program RELEASE based on the example data given in Table 2.6. Note, most printers are unable to print subscripts, italics, or Greek letters; thus, for example,  $m_{ij}$  is shown as  $m(i, j)$  and  $\phi$  is shown as phi.

Observed Recaptures for Group 1  
Treatment Group

| i    | R(i)  | m(i, j) |      |      |     |     | r(i) |
|------|-------|---------|------|------|-----|-----|------|
|      |       | j= 2    | 3    | 4    | 5   | 6   |      |
| 1    | 30000 | 1029    | 238  | 1669 | 549 | 590 | 4075 |
| m(j) |       | 1029    | 238  | 1669 | 549 | 590 |      |
| z(j) |       | 3046    | 2808 | 1139 | 590 | 0   |      |

Observed Recaptures for Group 2  
Control Group

| i    | R(i)  | m(i, j) |      |      |     |     | r(i) |
|------|-------|---------|------|------|-----|-----|------|
|      |       | j= 2    | 3    | 4    | 5   | 6   |      |
| 1    | 29000 | 1104    | 247  | 1832 | 571 | 641 | 4395 |
| m(j) |       | 1104    | 247  | 1832 | 571 | 641 |      |
| z(j) |       | 3291    | 3044 | 1212 | 641 | 0   |      |

Sums for the above Groups

|    |       |      |      |      |      |      |
|----|-------|------|------|------|------|------|
| m. | 0     | 2133 | 485  | 3501 | 1120 | 1231 |
| R. | 59000 | 0    | 0    | 0    | 0    | 0    |
| z. | 0     | 6337 | 5852 | 2351 | 1231 |      |
| r. | 8470  | 0    | 0    | 0    | 0    | 0    |

| Maximum Likelihood Estimates under Model H'5Phi  |          |                |                          |          |
|--|----------|----------------|--------------------------|----------|
| Ratio of Survival between Groups for Occasion 6. |          |                |                          |          |
| Parameter  | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| S(1,2)   | 0.889756 | 0.050231       | 0.791303                 | 0.988209 |

Table 2.7. - Continued.

TEST 1.T5: Test of  $p(5)$  and  $\Phi(4)$  equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O| 549 | 590 |1139
E| 542.6| 596.4|
C|  0.1|  0.1|
+-----+-----+
O| 571 | 641 |1212
E| 577.4| 634.6|
C|  0.1|  0.1|
+-----+-----+
          1120  1231  2351
Chi-square=0.2786 (df=1) P=0.5976
    
```

| Maximum Likelihood Estimates under Model H'4Phi         |          |                |                          |          |
|---|----------|----------------|--------------------------|----------|
| Ratio of Survivals between Groups for Occasions 5 to 6. |          |                |                          |          |
| Parameter   | Estimate | Standard Error | 95% Confidence Intervals |          |
|   |          |                | Lower                    | Upper    |
| S(1,2)  | 0.908443 | 0.036736       | 0.836442                 | 0.980445 |

TEST 1.T4: Test of  $p(4)$  and  $\Phi(3)$  equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O|1669 |1139 |2808
E|1679.9|1128.1|
C|  0.1|  0.1|
+-----+-----+
O|1832 |1212 |3044
E|1821.1|1222.9|
C|  0.1|  0.1|
+-----+-----+
          3501  2351  5852
Chi-square=0.3388 (df=1) P=0.5605
    
```

Table 2.7. - Continued.

| Maximum Likelihood Estimates under Model H'3Phi         |          |                |                          |          |
|---|----------|----------------|--------------------------|----------|
| Ratio of Survivals between Groups for Occasions 4 to 6. |          |                |                          |          |
| Parameter   | Estimate | Standard Error | 95% Confidence Intervals |          |
|   |          |                | Lower                    | Upper    |
| S(1,2)  | 0.891721 | 0.022147       | 0.848314                 | 0.935129 |

TEST 1.T3: Test of p(3) and Phi(2) equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O| 238 |2808 |3046
E| 233.1|2812.9|
C| 0.1| 0.0|
+-----+-----+
O| 247 |3044 |3291
E| 251.9|3039.1|
C| 0.1| 0.0|
+-----+-----+
485 5852 6337

```

Chi-square=0.2126 (df=1) P=0.6447

| Maximum Likelihood Estimates under Model H'2Phi         |          |                |                          |          |
|---|----------|----------------|--------------------------|----------|
| Ratio of Survivals between Groups for Occasions 3 to 6. |          |                |                          |          |
| Parameter   | Estimate | Standard Error | 95% Confidence Intervals |          |
|   |          |                | Lower                    | Upper    |
| S(1,2)  | 0.894703 | 0.021254       | 0.853044                 | 0.936361 |

Table 2.7. - Continued.

TEST 1.T2: Test of  $p(2)$  and  $\Phi(1)$  equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O|1029 |3046 |4075
E|1026.2|3048.8|
C| 0.0| 0.0|
+-----+-----+
O|1104 |3291 |4395
E|1106.8|3288.2|
C| 0.0| 0.0|
+-----+-----+
2133 6337 8470

```

Chi-square=0.0196 (df=1) P=0.8887

| Maximum Likelihood Estimates under Model H1Phi          |          |                |                          |          |
|---|----------|----------------|--------------------------|----------|
| Ratio of Survivals between Groups for Occasions 2 to 6. |          |                |                          |          |
| Parameter   | Estimate | Standard Error | 95% Confidence Intervals |          |
|   |          |                | Lower                    | Upper    |
| S(1,2)  | 0.896284 | 0.018040       | 0.860925                 | 0.931642 |

TEST 1.R1: Test of  $\Phi(1)$  equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O| 4075 |25925 |30000
E| 4307.|25693.|
C| 12.5| 2.1|
+-----+-----+
O| 4395 |24605 |29000
E| 4163.|24837.|
C| 12.9| 2.2|
+-----+-----+
8470 50530 59000

```

Chi-square=29.6316 (df=1) P=0.0000

Table 2.7. - Continued.

TEST 1: Overall test of  $H_0$  vs.  $H'5\Phi$

Chi-square=30.4812 (df=5) P=0.0000

TEST 1 is an omnibus test for a treatment effect(s), i.e., significant differences between groups. For the complete capture history protocol and scheme A partial capture history protocol, TEST 1 is an overall test of equality of all survival and capture probabilities among groups.

A second test examines the null hypothesis that  $S = 1$  (no mortality due to the treatment). This test, termed TEST 1.R1, is based on a simple  $2 \times 2$  contingency table:

|     | Recaptured | Not recaptured    |          |
|-----|------------|-------------------|----------|
| $t$ | $r_{t1}$   | $R_{t1} - r_{t1}$ | $R_{t1}$ |
| $c$ | $r_{c1}$   | $R_{c1} - r_{c1}$ | $R_{c1}$ |
|     | $r_{.1}$   | $R_{.1} - r_{.1}$ | $R_{.1}$ |

Using the data from the general numerical example, we obtain

|     |       |        |        |
|-----|-------|--------|--------|
| $t$ | 4,075 | 25,925 | 30,000 |
| $c$ | 4,395 | 24,605 | 29,000 |
|     | 8,470 | 50,530 | 59,000 |

which yields a  $\chi^2$  value of 29.6 with 1 df. The probability of a value this large, if the null hypothesis is true, is virtually zero. Therefore, we correctly conclude  $S < 1$  as we know that  $S = 0.9$  in this example (Table 1.2).

2.2.8. Extended Sequence of Models  $H'_{2\phi}, H'_{3\phi}, \dots, H'_{k-1,\phi}$

In this section we consider a sequence of hypotheses called models  $H'_{2\phi}, H'_{3\phi}, \dots, H'_{k-1,\phi}$  and tests between these models under the first capture history protocol. Our discussion is brief because these models rest on assumptions about the recapture rates that may often be tenuous and because the estimators of treatment survival rates are special cases of the estimators under model  $H_{1\phi}$ . The estimators given in this section may also be useful as approximations to intractable models in certain cases (see Section 3.9.1). These models are mentioned in Part 5, but no other mention of them is made elsewhere in this work.

The sequence of models allows the treatment to affect survival probabilities beyond  $\phi_{t1}$ . However, these models assume  $p_{ti} = p_{ci}$  for all  $i$ . Thus, the treatment is assumed not to affect the recapture rates. The structure of these models is summarized in Table 2.8.

If model  $H_{1\phi}$  is rejected by TEST 1.T2, the following MLE should be considered corresponding to model  $H'_{2\phi}$ .

$$\hat{S} = \frac{(r_{t1} - m_{t12})/R_{t1}}{(r_{c1} - m_{c12})/R_{c1}}$$

or, equivalently,

$$\hat{S} = \frac{(m_{t13} + m_{t14} + \dots + m_{t1k})/R_{t1}}{(m_{c13} + m_{c14} + \dots + m_{c1k})/R_{c1}}$$

Table 2.8. - Cell probabilities  $\pi_{ij}$  for the models  $H_{1\phi}, H'_{2\phi}$ , and  $H'_{3\phi}$  under the first capture history protocol ( $k = 5$ ). Models under this protocol are based on the assumption  $p_{t1} = p_{c1}$  for all  $i$ .

| Model        | $v$ | $j = 2$         | 3                             | 4   | 5  |
|--------------|-----|-----------------|-------------------------------|---|--|
| $H_{1\phi}$  | $t$ | $\phi_1 p_2$    | $\phi_1 q_2 \phi_2 p_3$       | $\phi_1 q_2 \phi_2 q_3 \phi_3 p_4$          | $\phi_1 q_2 \phi_2 q_3 \phi_3 q_4 \phi_4 p_5$          |
|              | $c$ | $\phi_{c1} p_2$ | $\phi_{c1} q_2 \phi_2 p_3$    | $\phi_{c1} q_2 \phi_2 q_3 \phi_3 p_4$       | $\phi_{c1} q_2 \phi_2 q_3 \phi_3 q_4 \phi_4 p_5$       |
| $H'_{2\phi}$ | $t$ | $\phi_1 p_2$    | $\phi_1 q_2 \phi_2 p_3$       | $\phi_1 q_2 \phi_2 q_3 \phi_3 p_4$          | $\phi_1 q_2 \phi_2 q_3 \phi_3 q_4 \phi_4 p_5$          |
|              | $c$ | $\phi_{c1} p_2$ | $\phi_{c1} q_2 \phi_{c2} p_3$ | $\phi_{c1} q_2 \phi_{c2} q_3 \phi_3 p_4$    | $\phi_{c1} q_2 \phi_{c2} q_3 \phi_3 q_4 \phi_4 p_5$    |
| $H'_{3\phi}$ | $t$ | $\phi_1 p_2$    | $\phi_1 q_2 \phi_2 p_3$       | $\phi_1 q_2 \phi_2 q_3 \phi_3 p_4$          | $\phi_1 q_2 \phi_2 q_3 \phi_3 q_4 \phi_4 p_5$          |
|              | $c$ | $\phi_{c1} p_2$ | $\phi_{c1} q_2 \phi_{c2} p_3$ | $\phi_{c1} q_2 \phi_{c2} q_3 \phi_{c3} p_4$ | $\phi_{c1} q_2 \phi_{c2} q_3 \phi_{c3} q_4 \phi_4 p_5$ |

This estimator is similar to the estimator for model  $H_{1\phi}$ ; however, the numbers in each group recaptured at dam 2 are deleted (i.e., the terms  $m_{t12}$  and  $m_{c12}$ ). With these numbers deleted, the estimators of  $S$ , the sampling variance of  $\hat{S}$ , and the goodness of fit test have the same form as under model  $H_{1\phi}$  (however,  $df = k - 3$ , instead of  $k - 2$ ). The estimator  $\hat{S}$  under model  $H_{2\phi}$  actually estimates the quantity

$$S_1 S_2 q_{t2}/q_{c2},$$

where

$$S_1 = \phi_{t1}/\phi_{c1}$$

and

$$S_2 = \phi_{t2}/\phi_{c2}.$$

Thus, the unbiased assessment of the treatment effect must assume  $q_{t2} = q_{c2}$ . This assumption is often poor, but under the first capture history protocol, the parameters  $p_{wi}$  (or  $q_{wi}$ ) cannot be estimated.

A test of model  $H_{1\phi}$  (the null hypothesis) versus  $H'_{2\phi}$  (the alternative hypothesis) is computed from the  $2 \times 2$  contingency table (TEST 1.72)

|           |                             |
|-----------|-----------------------------|
| $m_{t12}$ | $m_{t13} + \dots + m_{t1k}$ |
| $m_{c12}$ | $m_{c13} + \dots + m_{c1k}$ |

which is distributed as a chi-square variable with 1 df. This  $2 \times 2$  contingency table is obtainable from the  $2 \times k - 1$  table for the overall goodness of fit test of model  $H_{1\phi}$  by pooling, within rows, all of the columns 3 through  $k$ . Using data from the general numerical example, the following table is obtained,

|       |       |
|-------|-------|
| 1,029 | 3,046 |
| 1,104 | 3,291 |

yielding  $\chi^2_1 = 0.0196$ ,  $P = 0.89$ , which supports the null hypothesis that  $\phi_{t2} = \phi_{c2}$ .

Estimators of treatment survival for models  $H'_{3\phi}, \dots, H'_{k-1,\phi}$  are similar in that the recapture data from dams 3, ...,  $k - 1$  are deleted, respectively. Estimators of  $S$  and  $\text{var}(\hat{S})$  are summarized in Table 2.9 for models  $H_{1\phi}, H'_{2\phi}, \dots, H'_{k-1,\phi}$ . The sequence of tests corresponding to the models presented in Table 2.9 is given in Table 2.10. This sequence of models, tests, and estimators may often be useful, at least as an approximation where  $p_{ti} = p_{ci}$ . Note, however, that no test of  $p_{ti} = p_{ci}$  is possible based on data from the first capture history protocol. Program RELEASE provides all the relevant test statistics and estimates for this sequence of models (see Table 2.7); additional theory for these "peeled" models appears in Section 3.9.1.

Table 2.9. - Summary of the sequence of estimators available for data from the first capture history protocol. This sequence is similar to that discussed later for the complete capture history protocol.

| Model           | Data from dams | $\hat{S}$   | $\hat{\text{var}}(\hat{S})$  |
|-----------------|----------------|---|--|
| $H_0$           |                | 1   | 0  |
| $H_{1\phi}$     | 2, ..., $k$    | $\frac{r_{t1}/R_{t1}}{r_{c1}/R_{c1}}$   | $(\hat{S})^2 \left[ \frac{1}{r_{t1}} - \frac{1}{R_{t1}} + \frac{1}{r_{c1}} - \frac{1}{R_{c1}} \right]$   |
| $H'_{2\phi}$    | 3, ..., $k$    | $\frac{(r_{t1} - m_{t12})/R_{t1}}{(r_{c1} - m_{c12})/R_{c1}}$                     | $(\hat{S})^2 \left[ \frac{1}{r_{t1} - m_{t12}} - \frac{1}{R_{t1}} + \frac{1}{r_{c1} - m_{c12}} - \frac{1}{R_{c1}} \right]$                     |
| $H'_{3\phi}$    | 4, ..., $k$    | $\frac{(r_{t1} - m_{t12} - m_{t13})/R_{t1}}{(r_{c1} - m_{c12} - m_{c13})/R_{c1}}$ | $(\hat{S})^2 \left[ \frac{1}{r_{t1} - m_{t12} - m_{t13}} - \frac{1}{R_{t1}} + \frac{1}{r_{c1} - m_{c12} - m_{c13}} - \frac{1}{R_{c1}} \right]$ |
| .               | .              | .   | .  |
| .               | .              | .   | .  |
| .               | .              | .   | .  |
| $H'_{k-1,\phi}$ | $k$            | $\frac{m_{t1k}/R_{t1}}{m_{c1k}/R_{c1}}$   | $(\hat{S})^2 \left[ \frac{1}{m_{t1k}} - \frac{1}{R_{t1}} + \frac{1}{m_{c1k}} - \frac{1}{R_{c1}} \right]$                                       |



Table 2.10. - Summary of between-model tests for the first capture history protocol. All tests are in the form of a  $2 \times 2$  contingency table and are computed by program RELEASE.

| Null hypothesis <sup>a</sup> | Alternative hypothesis      | Test number <sup>b</sup> | Contingency table   |              |                             |              |                             |
|------------------------------|-----------------------------|--------------------------|---|--------------|-----------------------------|--------------|-----------------------------|
| $H_0$                        | $H_{1\phi}$                 | 1.R1                     | <table border="1"> <tr> <td><math>r_{t1}</math></td> <td><math>R_{t1} - r_{t1}</math></td> </tr> <tr> <td><math>r_{c1}</math></td> <td><math>R_{c1} - r_{c1}</math></td> </tr> </table>                       | $r_{t1}$     | $R_{t1} - r_{t1}$           | $r_{c1}$     | $R_{c1} - r_{c1}$           |
| $r_{t1}$                     | $R_{t1} - r_{t1}$           |                          |   |              |                             |              |                             |
| $r_{c1}$                     | $R_{c1} - r_{c1}$           |                          |   |              |                             |              |                             |
| $H_{1\phi}$                  | $H'_{2\phi}$                | 1.T2                     | <table border="1"> <tr> <td><math>m_{t12}</math></td> <td><math>m_{t13} + \dots + m_{t1k}</math></td> </tr> <tr> <td><math>m_{c12}</math></td> <td><math>m_{c13} + \dots + m_{c1k}</math></td> </tr> </table> | $m_{t12}$    | $m_{t13} + \dots + m_{t1k}$ | $m_{c12}$    | $m_{c13} + \dots + m_{c1k}$ |
| $m_{t12}$                    | $m_{t13} + \dots + m_{t1k}$ |                          |   |              |                             |              |                             |
| $m_{c12}$                    | $m_{c13} + \dots + m_{c1k}$ |                          |   |              |                             |              |                             |
| $H'_{2\phi}$                 | $H'_{3\phi}$                | 1.T3                     | <table border="1"> <tr> <td><math>m_{t13}</math></td> <td><math>m_{t14} + \dots + m_{t1k}</math></td> </tr> <tr> <td><math>m_{c13}</math></td> <td><math>m_{c14} + \dots + m_{c1k}</math></td> </tr> </table> | $m_{t13}$    | $m_{t14} + \dots + m_{t1k}$ | $m_{c13}$    | $m_{c14} + \dots + m_{c1k}$ |
| $m_{t13}$                    | $m_{t14} + \dots + m_{t1k}$ |                          |   |              |                             |              |                             |
| $m_{c13}$                    | $m_{c14} + \dots + m_{c1k}$ |                          |   |              |                             |              |                             |
| .                            | .                           | .                        | .   |              |                             |              |                             |
| .                            | .                           | .                        | .   |              |                             |              |                             |
| .                            | .                           | .                        | .   |              |                             |              |                             |
| $H'_{k-2,\phi}$              | $H'_{k-1,\phi}$             | 1.Tk - 1                 | <table border="1"> <tr> <td><math>m_{t1,k-1}</math></td> <td><math>m_{t1k}</math></td> </tr> <tr> <td><math>m_{c1,k-1}</math></td> <td><math>m_{c1k}</math></td> </tr> </table>                               | $m_{t1,k-1}$ | $m_{t1k}$                   | $m_{c1,k-1}$ | $m_{c1k}$                   |
| $m_{t1,k-1}$                 | $m_{t1k}$                   |                          |   |              |                             |              |                             |
| $m_{c1,k-1}$                 | $m_{c1k}$                   |                          |   |              |                             |              |                             |

<sup>a</sup> See Table 2.2.

<sup>b</sup> See Tables 2.1 and 2.3.

The sequence of alternative estimators in Table 2.10 is useful if the treatment affects survival beyond dam 2; however, the methods are only completely justified if there are equal recapture rates between groups. The alternative sequence of models can sometimes reduce bias in  $\hat{S}$  substantially under the first capture history protocol, especially if the  $p_{wi}$  are small (see Chapter 3.9). The variance of  $\hat{S}$  increases as more data are deleted from the analysis. For example, if we rejected model  $H_{1\phi}$  and had to use model  $H'_{2\phi}$  (i.e., deleted recaptures from dam 2 in the analysis), we would have computed  $\hat{S} = 0.895$  (compared to  $\hat{S} = 0.896$ , the estimate based on model  $H_{1\phi}$ ), but the precision would have been poorer ( $\hat{se}(\hat{S}) = 0.0213$ , rather than 0.0180). Other comparisons can be made from Table 2.7.

### 2.2.9. Relative Recovery Rate Method

The *relative recovery rate method* is mentioned because it represents a good analysis method for experiments as they have been conducted commonly in the past. The protocol involves first capture histories of batch-marked fish in two groups, as we have discussed. In this special case, however, fish are recaptured at only a single downstream dam (dam 2). Ricker (1945, 1948) gave the MLE of  $S$  as

$$\hat{S} = \frac{m_{t12} R_{c1}}{R_{t1} m_{c12}}$$

or, in our form,

$$\hat{S} = \frac{m_{t12}/R_{t1}}{m_{c12}/R_{c1}}.$$

The estimator of the sampling variance is also a special case of the theory we have just presented,

$$\hat{\text{var}}(\hat{S}) = (\hat{S})^2 \left[ \frac{1}{m_{t12}} - \frac{1}{R_{t1}} + \frac{1}{m_{c12}} - \frac{1}{R_{c1}} \right].$$

Although this procedure is an optimal estimation method for a given field design and certain (restrictive) assumptions, we do not generally recommend it. The data do not allow even minimal tests of assumptions, the assumption that  $p_{t2} = p_{c2}$  in particular. Moreover, the approximate expected value of this  $\hat{S}$  (under any model) is

$$E(\hat{S}) \doteq S \frac{p_{t2}}{p_{c2}};$$

thus,  $\hat{S}$  is sensitive to the assumption that  $p_{t2} = p_{c2}$ . Additional discussion of absolute and relative recovery rates is found in Manly (1981).

### 2.2.10. Discussion

The first capture history protocol has several advantages. Only simple batch marks are required. Record keeping at dams 2, ...,  $k$  is simple, as recaptured fish are removed and not rereleased. Some tests of assumptions are possible, and estimation methods are developed

and available. Although the various estimates and tests can be computed on a small calculator, we urge the use of program RELEASE for a thorough analysis of data.

A potential problem with the first capture history protocol arises because the theoretical variances (i.e., those derived from the likelihood function) may be underestimated due to a possible lack of independence among fish. Heterogeneity in large river systems yields data having more variability than the multinomial variation embedded in the model. This heterogeneity probably arises from a host of sources, but has almost no effect on the point estimators of treatment survival  $S$ . The solution to these issues relies on some form of replication that will enable computation of a proper empirical variance. This replication can be conducted in several potential ways, two of which we mention briefly here. (This subject is treated in more detail in Part 4.)

True replication represents one of two main approaches. Treatment and control fish would be allocated randomly to, say, 10 replicates. Fish in the various replicates would be handled, marked, held, and released together. The appropriate variance is the component due to variation in  $\hat{S}$  among the 10 replicates.

Alternatively, quasi-replicates termed *lots* can be used. In this situation, the team conducting the experiment might release 10 lots, each consisting of 15,000 treatment and 15,000 control fish. The lots might be released over 10 nights. Here, the variance among the 10 estimates of treatment survival contains an additional component: the day-to-day variation. This component would include any known changes in experimental conditions (e.g., blade angle of turbine, river height behind the dam) as well as changes in unknown conditions (e.g., predation pressure). Lots, then, are not identical in terms of experimental conditions. Often, the lot-to-lot variance gives more useful information than if true replicates had been used. In general, the planning team can view the use of replicates or lots as alternatives, depending on the study objectives.

An estimate of the treatment survival rate could be made from the lots or replicates as a weighted or unweighted average of the individual estimates. In the weighted case,

$$\hat{S} = \frac{\sum_{i=1}^{10} w_i \hat{S}_i}{\sum_{i=1}^{10} w_i},$$

where  $w_i = \left[ \frac{1}{r_{t1}} - \frac{1}{R_{t1}} + \frac{1}{r_{c1}} - \frac{1}{R_{c1}} \right]^{-1}$  or a similar expression taken from Table 2.9. The sampling variance of  $\hat{S}$  could then be computed empirically as

$$\hat{\text{var}}(\hat{S}) = \frac{\sum_{i=1}^{10} w_i (\hat{S}_i - \hat{S})^2}{9 \sum_{i=1}^{10} w_i}.$$

If such replication could be done carefully and with proper attention to all the field practicalities, an excellent experiment could be expected.

An alternative procedure would involve subsampling by time periods of the day at dams 2, ...,  $k$ . Consider releasing 150,000 treatment and 150,000 control fish with batch marks. The number recaptured and removed at each downstream dam would be tabulated by time period of the day (e.g., six 4-hour periods). If this subsampling could be done at each dam, six reduced  $m$ -arrays could be analyzed to provide six estimates of treatment survival. Each estimate would be a nearly independent estimate of  $S$ , and an average of the six estimates could be used to estimate the survival rate and an empirical variance. This procedure has advantages, but may not be feasible in all situations. However, our main point is that proper replication or subsampling should be built into the design of experiments involving the first capture history protocol (see Part 4).

Readers interested in further information on the analysis procedures for this general type of protocol are encouraged to study Seber (1970), Robson and Youngs (unpublished report, 1971), and Brownie et al. (1985:1-55, 170-175). However, an understanding of these studies requires the reinterpretation that  $S$  relates to a treatment survival rate rather than to a time-period survival rate. In addition, the  $q_i$  terms do not appear in the reports because the sampling, sport, or commercial exploitation of the population affects the entire population, not just the released, marked animals.

In many treatment-control survival experiments, it is informative to examine the number of losses on capture ( $d$ ), by group, at each dam (this discussion relates to fish lost accidentally, rather than to deliberate removals). It seems reasonable that the losses on capture at each dam are proportional for treatment and control groups. This assumption can be tested by using a simple chi-square test. If  $d_{tj}$  and  $d_{cj}$  are the number of fish lost on capture at dam  $j$  for the treatment and control groups, respectively, the following  $k - 1$  contingency tables can be formed:

|           |                     |
|-----------|---------------------|
| $d_{t1j}$ | $m_{t1j} - d_{t1j}$ |
| $d_{c1j}$ | $m_{c1j} - d_{c1j}$ |

$$j = 2, \dots, k.$$

The total chi-square statistic has  $k - 1$  df, as each  $2 \times 2$  table has 1 df. A rejection of the null hypothesis as the result of this test may be evidence that the treatment has a delayed effect. Fish may be slightly injured, making them more susceptible to predation or other fates (lowered  $\phi_{tj}$ ) or more susceptible to capture (higher  $p_{tj}$ ). Insight into these issues can be achieved by comparison of the pattern of observed and expected values in the contingency table (also see Part 3).

## 2.3. Unknown Capture Histories

## 2.3.1. Introduction

Under the unknown capture history protocol, fish are given a batch mark to distinguish between treatment and control groups released at dam 1. Fish in both groups are recaptured downstream at dams 2, 3, ...,  $k$ , and all fish are rereleased without further marking and without the investigators knowing their previous capture history. The data from an experiment conducted under this protocol are represented as

$$\begin{array}{cccccc}
 R_{t1} & m_{t2} & m_{t3} & \cdots & m_{tk} \\
 \\
 R_{c1} & m_{c2} & m_{c3} & \cdots & m_{ck} .
 \end{array}$$

Note that  $m_{vj}$  is the total number of fish of treatment group  $v$  captured at dam  $j$ . Referring back to Table 1.15, one sees that

$$m_{vj} = m_{v,j} = \sum_{i=1}^{j-1} m_{vij}.$$

Only the total number of fish captured at dam  $j$  is known for each treatment group because capture histories of marked fish are unknown. For example, it is not known how many of the recaptures at dam 3 were also recaptured at dam 2.

To illustrate data under this protocol, we use the data in Table 1.9 from the general numerical example

|     |                      | Recaptures $m_{tj}$ and $m_{cj}$ by dam |     |       |     |     | Totals |
|-----|----------------------|---|-----|-------|-----|-----|--------|
|     | Released at<br>dam 1 | 2                                       | 3   | 4     | 5   | 6   | $m_v$  |
| $t$ | 30,000               | 1,029                                   | 249 | 1,762 | 616 | 691 | 4,347  |
| $c$ | 29,000               | 1,104                                   | 260 | 1,924 | 644 | 758 | 4,690  |

The previous example shows that an additional statistic is needed:

$$m_v = \sum_{j=2}^k m_{vj}.$$

For example,

$$m_t = 4,347 \quad \text{and} \quad m_c = 4,690.$$

These totals are the basis of the estimate of  $S$  under this protocol.

This protocol has been used in many survival experiments conducted on the Columbia River in recent decades. Data collected under this protocol do not lead to an exact statistical analysis in the sense of the other three protocols, except in the special case where  $k = 2$  (Ricker's *relative recovery rate method*, discussed in Sections 2.2.1 and 2.2.9). Although it has undesirable properties, the unknown capture history protocol may be a reasonable approach when the capture rates  $p_j$  are low and are not affected by treatment, and replicate lots enable estimates of precision.

### 2.3.2. Model Structure

The data under the unknown capture history protocol are not multinomial because a specific fish can be caught at more than one downstream dam. In fact, simple expressions for sampling models for these data cannot be derived. Consequently, exact theoretical methods cannot be developed for this protocol. In addition, losses on capture present further difficulties or require further assumptions. In the following material, we consider the case where the capture rates  $p_i$  are low (i.e.,  $< 0.05$ ), the number of capture sites (or times) is small (say,  $k < 7$ ), and the number of fish released in each group is large.

We start with the special case of  $k = 2$  to aid in understanding of this protocol. Only in this special case of the unknown capture history protocol are the capture histories known. The expectations are

$$E(m_{t2}) = E(m_{t12}) = R_{t1} \phi_{t1} p_{t2}$$

and

$$E(m_{c2}) = E(m_{c12}) = R_{c1} \phi_{c1} p_{c2}.$$

We make the assumption that  $p_{t2} = p_{c2}$  and define the treatment survival rate as  $S = \phi_{t1}/\phi_{c1}$ .

Then the exact MLE of the treatment survival  $S$  is

$$\hat{S} = \frac{m_{t2}/R_{t1}}{m_{c2}/R_{c1}},$$

with estimated theoretical sampling variance

$$\hat{\text{var}}(\hat{S}) = (\hat{S})^2 \left( \frac{1}{m_{t2}} - \frac{1}{R_{t1}} + \frac{1}{m_{c2}} - \frac{1}{R_{c1}} \right).$$

Even with replication, we do not recommend this procedure; tests of the critical assumption that  $p_{t2} = p_{c2}$  are not possible, making this a poor scientific design.

Finally, we note that the case of  $k = 2$  is identical to the first capture history protocol with  $k = 2$ . (In fact, all protocols are the same when  $k = 2$ .) That equivalence does not hold for  $k > 2$ . However, we, of necessity, use some first capture history methods even with unknown capture history data.

In the case where  $k > 2$  and there are no losses on capture, the expectation of the number of recaptures at dam  $j$  can be expressed as

$$E(m_{tj}) = R_{t1} \left( \prod_{i=1}^{j-1} \phi_{ti} \right) p_{tj}$$

and

$$E(m_{cj}) = R_{c1} \left( \prod_{i=1}^{j-1} \phi_{ci} \right) p_{cj}.$$

For example, for  $k = 3$ , the expectations for the control group are  $E(m_{c2}) = R_{c1}\phi_{c1}p_{c2}$  and  $E(m_{c3}) = R_{c1}\phi_{c1}\phi_{c2}p_{c3}$ . In general, as long as there are no losses on capture, the expected number of captures at dam  $j$  is just  $R_{c1}$  times the probability of surviving until dam  $j$  multiplied by the (conditional) capture probability at dam  $j$ . Note that when there are no losses on capture, captures at intermediate dams 2 through  $j - 1$  have no effect on the expected value of  $m_{vj}$  (extensions to the case of losses on capture are given in Section 2.3.5).

Some assumptions must be made in order to estimate a treatment effect. It suffices to assume that all of the  $\phi_i$  and  $p_i$  are equal between treatment and control groups except  $\phi_1$  (i.e.,  $\phi_{t2} = \phi_{c2}, \dots, \phi_{t,k-1} = \phi_{c,k-1}, p_{t2} = p_{c2}, \dots, p_{tk} = p_{ck}$ ). This is model  $H_{1\phi}$ . We then define the treatment effect to be  $S = \phi_{t1}/\phi_{c1}$ . These assumptions mean that

$$\frac{E(m_{tj})}{R_{t1}} = S \frac{E(m_{cj})}{R_{c1}}, \quad j=2, \dots, k,$$

and, by the method of moments, the estimator of  $S$  is

$$\hat{S} = \frac{\sum_{j=2}^k m_{tj}/R_{t1}}{\sum_{j=2}^k m_{cj}/R_{c1}} = \frac{m_t/R_{t1}}{m_c/R_{c1}}.$$

This estimator is similar to the MLE of  $S$  under the first capture history protocol for model  $H_{1\phi}$ .

For the first capture history protocol, the MLE is

$$\hat{S} = \frac{r_{t1}/R_{t1}}{r_{c1}/R_{c1}}.$$

The  $r_{t1}$  and  $r_{c1}$  do not include multiple counts of fish due to (unknown) multiple captures. Thus, one always has  $r_{t1} \leq m_t$  and  $r_{c1} \leq m_c$ ; however, the difference  $m_t - r_{t1}$  is small if capture probabilities are small. Contrary to what one might think, the extra counts reflected in  $m_c$  and  $m_t$  do not improve the precision of  $\hat{S}$ . If the  $p_i$  are low, the probability of a specific fish being captured more than once is small and then unknown capture history data are essentially removal data, just like those data under the first capture history protocol. In this case, the unknown capture history estimator is close to the fully efficient MLE of  $S$  for removal data.

An example will illustrate the effect of low capture probabilities. Assume that 30,000 fish are released;  $k = 4$ ,  $p_2 = 0.01$ ,  $p_3 = 0.04$ , and  $p_4 = 0.02$ , and survival rates are constant at 0.98 (i.e.,  $\phi_1 = \phi_2 = \phi_3 = 0.98$ ). Here we would expect only 39 of the 30,000 initially released fish to be caught twice. The expected number of fish caught at all three downstream dams is 0.2, less than one fish. In such cases, the data are similar to data under the first capture history protocol and the estimator can be considered approximately ML. Furthermore, the sampling variance is closely approximated by the theoretical sampling variance developed under the first capture history protocol, and the goodness of fit tests are similar because few fish are captured more than once.

As capture probabilities increase, the number of fish captured more than once increases, making the approximations noted above progressively poorer. However, provided  $H_{1\phi}$  holds, the estimator



$$\hat{S} = \frac{m_t/R_{t1}}{m_c/R_{c1}}$$

remains appropriate. Although the estimator is not the MLE (because the likelihood is intractable), it appears to be the best estimator possible. The variance formula and goodness of fit tests developed for the first capture history protocol are not strictly justified, as capture probabilities or  $k$ , or both, increase, causing a substantial number of fish to be captured more than once. Alternative theoretical variance formulae are considered below. However, even those formulae are not totally satisfactory. The simple fact is that the first capture history protocol is superior to the unknown capture history protocol; we consider the unknown capture history protocol here only because many data have already been collected in this way.

The data for the general numerical example in Table 1.9, which can be used to illustrate the estimation of  $S$ , are reproduced here.

|             |        | Recaptures $m_{tj}$ and $m_{cj}$ by dam |     |       |     |     |       |
|-------------|--------|---|-----|-------|-----|-----|-------|
| Released at |        | Totals                                  |     |       |     |     | $m_w$ |
|             | dam 1  | 2                                       | 3   | 4     | 5   | 6   |       |
| $t$         | 30,000 | 1,029                                   | 249 | 1,762 | 616 | 691 | 4,347 |
| $c$         | 29,000 | 1,104                                   | 260 | 1,924 | 644 | 758 | 4,690 |

Note that losses on capture are included in these counts and in the totals used to compute  $\hat{S}$ . The estimate of  $S$  is

$$\begin{aligned}\hat{S} &= \frac{4,347/30,000}{4,690/29,000} \\ &= 0.896.\end{aligned}$$

From the first capture history protocol one has  $r_{t1} = 4,075$  and  $r_{c1} = 4,395$ ; thus, about 300 fish in each group (treatment and control) were captured more than once (about 1% of releases). When one conducts a study using the unknown capture history protocol, the rate of multiple captures will, of course, not be known.

If we treat the estimator in this example as if it were based on first capture history data, we have (from Chapter 2.2),

$$\begin{aligned}\hat{\text{var}}(\hat{S}) &= (\hat{S})^2 \left[ \frac{1}{m_t} - \frac{1}{R_{t1}} + \frac{1}{m_c} - \frac{1}{R_{c1}} \right] \\ &= (0.896)^2 \left[ \frac{1}{4,347} - \frac{1}{30,000} + \frac{1}{4,690} - \frac{1}{29,000} \right],\end{aligned}$$

which gives  $\hat{\text{se}}(\hat{S}) = 0.0174$ . However, a slightly better formula for the sampling variance of  $\hat{S}$  under the unknown capture history protocol, developed in Section 2.3.5, is used by RELEASE:

$$\hat{\text{var}}(\hat{S}) = (\hat{S})^2 \left\{ \frac{1}{m_t} - \frac{1}{R_{t1}} \left[ \sum_{j=2}^k \left( \frac{m_{tj}}{m_t} \right)^2 \right] + \frac{1}{m_c} - \frac{1}{R_{c1}} \left[ \sum_{j=2}^k \left( \frac{m_{cj}}{m_c} \right)^2 \right] \right\}.$$

Computed here, we obtain,

$$\hat{\text{var}}(\hat{S}) = (0.896)^2 \left[ \frac{1}{4,347} - \frac{0.269}{30,000} + \frac{1}{4,690} - \frac{0.272}{29,000} \right],$$

or

$$\hat{\text{se}}(\hat{S}) = 0.0185.$$

This standard error is slightly larger than the one produced by treating these data as first capture history data. We expect, theoretically, that the unknown capture history protocol will produce results less precise than those under the first capture history protocol.

We recommend using empirical sampling variances with the unknown capture history protocol. For the estimation of these variances, we recommend a study design with at least five lots. The sampling variances are then computed empirically from the replicate lots. These ideas are developed in Part 4.

One is forced to use the methods appropriate for the first capture history protocol in testing the assumptions for this protocol. We do not repeat those tests here (see Chapter 2.2).

2.3.3. Estimable Parameters

The only estimable parameter of interest under this protocol is  $S$ , the treatment survival rate (we are assuming an acute treatment effect). Estimates of the products  $\phi_{c1}\phi_2 \cdots \phi_{j-1}p_j$ ,  $j = 2, \dots, k$ , can be made, assuming that the treatment and control groups are alike at, and after, dam 2 (hypothesis  $H_{1\phi}$ ). These products are, however, not intrinsically of interest.

If losses on capture occur, the moment estimator of the treatment survival is valid if it is assumed that losses on capture are not affected by the treatment. An examination of the expectations for the  $m_{tj}$  and  $m_{cj}$  (presented in Section 2.3.5) illustrates this point. Also, this assumption can be tested by using the contingency table method given in Section 2.2.10.

The information on losses on capture for treatment and control groups is examined here to illustrate this procedure. Assuming model  $H_{1\phi}$  (i.e., an acute treatment effect), the losses-on-capture data in Table 1.9 are summarized into the following contingency table as a basis for testing equality of loss rates over treatment and control groups.

|   |  | Dam |    |    |    |    |
|---|--|-----|----|----|----|----|
|   |  | 2   | 3  | 4  | 5  | 6  |
| t |  | 33  | 14 | 85 | 26 | 32 |
| c |  | 33  | 10 | 62 | 28 | 39 |

The chi-square value for this table is 4.1 with 4 df,  $P < 0.48$ . This value provides no evidence that the losses on capture have been affected by the treatment. In addition, there is no reason to suspect delayed mortality due to the treatment.

When program RELEASE is used to compute this chi-square test, it prints the observed and expected values along with the chi-square contribution, thus allowing the investigator to look for patterns among the observed and expected values (Table 2.11).

Table 2.11. - Observed and expected losses on capture and chi-square values for testing that losses on capture are not affected by treatment, for the general numerical example under the unknown capture history protocol.

|       |             | Dam  |      |      |      |      |
|-------|-------------|------|------|------|------|------|
| Group |             | 2    | 3    | 4    | 5    | 6    |
| t     | Observed(O) | 33   | 14   | 85   | 26   | 32   |
|       | Expected(E) | 34.6 | 12.6 | 77.2 | 28.3 | 37.3 |
|       | $(O-E)^2/E$ | 0.08 | 0.16 | 0.80 | 0.19 | 0.74 |
| c     | Observed(O) | 33   | 10   | 62   | 28   | 39   |
|       | Expected(E) | 31.4 | 11.4 | 69.8 | 25.7 | 33.7 |
|       | $(O-E)^2/E$ | 0.09 | 0.17 | 0.88 | 0.21 | 0.82 |

Here, no pattern is suggested and the chi-square value is about what is expected when the null hypothesis is true.

This way of examining losses on capture is valid under model  $H_{1\phi}$  for any protocol when only an acute effect exists. In a test of equal loss rates for treatments and controls, which is valid under any hypothesis about the treatment effects, a series of  $2 \times 2$  tables is used, one for each recovery dam. In this example, for dam 2, the table is

|    |       |       |
|----|-------|-------|
| 33 | 996   | 1,029 |
| 33 | 1,071 | 1,104 |

If we let  $d_{vj}$  = losses on capture for treatment group  $v$  at recapture dam  $j$ , then the general table under the unknown capture history protocol is

|          |                   |          |
|----------|-------------------|----------|
| $d_{tj}$ | $m_{tj} - d_{tj}$ | $m_{tj}$ |
| $d_{cj}$ | $m_{cj} - d_{cj}$ | $m_{cj}$ |

For dam 3 in this example, the general table is

|    |     |     |
|----|-----|-----|
| 14 | 235 | 249 |
| 10 | 250 | 260 |

Here,  $\chi^2 = 0.89$  with 1 df.

In this example, there are five such  $2 \times 2$  tables. The total chi-square (5 df) from these tables also provides an overall test of whether the rate of loss on capture is the same for treatments as for controls. That test statistic value is 7.68, and is not significant.

### 2.3.4. Discussion

The unknown capture history protocol has two operational advantages: only batch marks are needed, and fish do not need to be removed when caught. Schoenemon et al. (1961) presented examples where this protocol has been used. However, there are also serious disadvantages, the most serious of which is that nothing is known about the capture history of the marked fish; thus, a proper likelihood cannot be derived. Theoretically, the likelihood can be written, but it contains a large number of inestimable parameters. The estimator of  $S$  is a moment estimator (hence, of uncertain efficiency) whose theoretical sampling variance can only be approximated. Only limited testing of model assumptions is possible.

Ideally, this protocol might be considered after a conclusive study, in which unique marks are used, indicates that model  $H_{1\phi}$  fits the data generated in a particular experimental setting, i.e., capture probabilities are equal for both treatment and control groups, and  $\phi_2, \dots, \phi_{k-2}$  are equal for both groups. One might then consider further experiments using the shortcut unknown capture history protocol with proper replication. The poorest study design for conducting experiments is the use of the unknown capture history protocol without replication and with  $k = 2$ .

### 2.3.5. Theory for the Unknown Capture History Protocol

Material in this section is provided more for the sake of completeness than for its usefulness in most survival experiments.

In principle, one can write the probability model for the complete capture history case and then derive the likelihood for the unknown capture history case. In practice, however, this approach is difficult. The result is a convolution of different multinomial distributions that is difficult to write, let alone maximize.

We use moment techniques to derive an estimator and theoretical formulae. First we develop some theory for the recaptures  $m_2, \dots, m_k$  from just one arbitrary released cohort of size  $R$ . Some notation used here:

$\pi_j$  is the probability of loss on capture; in practice it suffices to treat this probability as the proportion of the  $m_j$  that is lost on capture,

$$f_j = \begin{cases} \phi_1 p_2, & j = 2 \\ \left[ \prod_{i=2}^{j-1} \phi_{i-1} (1 - p_i \pi_i) \right] \phi_{j-1} p_j, & j = 3, \dots, k. \end{cases}$$

Then

$$E(m_j | R) = Rf_j, \quad j=2, \dots, k.$$

If there are no losses on capture, we put all  $\pi_i = 0$ , giving

$$f_j = \phi_1 \cdots \phi_{j-1} p_j.$$

The marginal distribution of  $m_j$  is binomial ( $R, f_j$ ) under the assumptions that each fish represents an independent Bernoulli event. However, pairwise, the  $m_j$  and  $m_h$  are dependent:

$$\text{cov}(m_j, m_h) = R \left[ p_j(1 - \pi_j) - f_j(1 - \pi_j p_j) \right] \frac{f_h}{1 - p_j \pi_j}, \quad j < h.$$

This covariance can be derived by considering a single fish. Define  $x_j = 1$  if the fish is captured on occasion  $j$ ,  $x_j = 0$  otherwise. Then  $E(x_j) = f_j$  and  $\text{cov}(m_j, m_h) = R(E(x_j x_h) - f_j f_h)$ . Next,

$$\begin{aligned} E(x_j x_h) &= \Pr(x_j = 1 \text{ and } x_h = 1) \\ &= \Pr\{x_j = 1\} \Pr\{x_h = 1 | x_j = 1\} \\ &= f_j(1 - \pi_j) \phi_j(1 - p_{j+1} \pi_{j+1}) \cdots \phi_{h-1} p_h \\ &= \frac{p_j(1 - \pi_j)}{1 - p_j \pi_j} f_h, \quad j < h. \end{aligned}$$

These results allow the derivation of  $\text{var}(m.)$ ,  $m. = \sum_{j=2}^k m_j$ :

$$\begin{aligned} \text{var}(m.) &= R \left[ \sum_{j=2}^k f_j(1-f_j) \right] + 2 \sum_{j=2}^{k-1} \sum_{h=j+1}^k \text{cov}(m_j, m_h) \\ &= R \left[ \sum_{j=2}^k f_j(1-f_j) \right] + 2R \left[ \sum_{j=2}^{k-1} \frac{p_j(1-\pi_j)}{1-p_j\pi_j} \left( \sum_{h=j+1}^k f_h \right) \right] \\ &\quad - R \left[ \left( \sum_{j=2}^k f_j \right)^2 - \sum_{j=2}^k (f_j)^2 \right]. \end{aligned}$$

An alternative expression is

$$\text{var}(m.) = Rf.(1-f.) + 2R \left[ \sum_{j=2}^k \frac{p_j(1-\pi_j)}{1-p_j\pi_j} \left( \sum_{h=j+1}^k f_h \right) \right]$$

Here,  $f. = \sum_{j=2}^k f_j$ .

Note that if  $\pi_2 = \dots = \pi_k = 1$ , the results apply to the first capture history case. At the other extreme, even if all  $\pi_j = 0$ , the theoretical variance of  $m.$  is technically not estimable. In practice, this means that a biased theoretical estimator of  $\text{var}(m.)$  must be used.

Consider point estimation of a treatment effect. Now a subscript is added for treatment or control to all parameters and statistics. Under  $H_{1\phi}$ ,  $f_{tj} = S f_{cj}$ , so

$$\frac{E(m_t)}{R_{t1}} = S \frac{E(m_c)}{R_{c1}}.$$

(Note that this requires  $\pi_{tj} = \pi_{cj}$  for all  $j$ .) Under more general models, there are options for "peeling off" (discarding) data from upstream dams to obtain a better estimate of treatment effect not possible with the unknown capture history protocol. This procedure works like the one for first capture history data (see the discussion in Section 2.2.8).

The theoretical sampling variance of  $\hat{S}$  is

$$\text{var}(\hat{S}) = (S)^2 \left[ \frac{\text{var}(m_t)}{[E(m_t)]^2} + \frac{\text{var}(m_c)}{[E(m_c)]^2} \right].$$

One must select an approximation to  $\text{var}(m.)$  to estimate this sampling variance. Both theory and some numerical work suggest to us that for low rates of loss on capture and low capture probabilities (as in typical turbine studies on the Columbia River), the better approximation is

$$\text{var}(m.) \doteq R \left[ \sum_{j=2}^k f_j(1-f_j) \right].$$

The  $f_j$  are estimable,  $\hat{f}_j = m_j/R$ , but the covariances are not estimable. If these covariances are negligible, an estimator of theoretical sampling variance is

$$\hat{\text{var}}(m_v) = \sum_{j=2}^k m_{vj} \left( 1 - \frac{m_{vj}}{R_{v1}} \right), \quad v = t, c.$$

(The alternative is  $m_v [1 - \frac{m_v}{R_{v1}}]$ .) This approach produces

$$\hat{\text{var}}(\hat{S}) = (\hat{S})^2 \left\{ \frac{1}{m_t} - \frac{1}{R_{t1}} \left[ \sum_{j=2}^k \left( \frac{m_{tj}}{m_t} \right)^2 \right] + \frac{1}{m_c} - \frac{1}{R_{c1}} \left[ \sum_{j=2}^k \left( \frac{m_{cj}}{m_c} \right)^2 \right] \right\}.$$

This formula is used in program RELEASE. If there is sufficient empirical replication, we recommend using an empirical estimator of sampling variance.

The critical point is which approximation is the better for  $\text{var}(m.)$ . The following example is informative. Let  $k = 6$ , all  $p_j = 0.03$ , and all  $\phi_j = 0.98$  (and no losses on capture). The exact result is then  $\text{var}(m.) = R(0.16649)$ . Here  $f. = 0.171236$ , so

$$Rf.(1-f.) = R(0.14192),$$

whereas

$$R \sum_{j=2}^6 f_j(1-f_j) = R(0.16311).$$

From the Cauchy-Schwartz inequality,

$$\left( \sum f_j \right)^2 \geq \sum (f_j)^2;$$

therefore, from the first expression for  $\text{var}(m.)$ , the second and third terms tend to cancel (hence the result in the example). In essence, the Cauchy-Schwartz inequality provides theoretical support for our choice of approximation to  $\text{var}(m.)$ .



## 2.4. Complete Capture Histories

### 2.4.1. Introduction

We here consider the experimental protocol whereby the experimenter can obtain the complete capture history of each marked fish, either by using a unique tag for each fish released or different batch marks at each dam. If we consider one group of fish (treatment or control), the basic model used to analyze these data is a special case of the Jolly-Seber model (Jolly 1965; Seber 1965, 1982:196). We follow only the marked animals and estimate survival and capture probabilities (Cormack 1964), whereas the general Jolly-Seber model also uses marked-to-unmarked ratios to estimate population sizes and numbers of new recruits. Literature on the Jolly-Seber model includes papers by Manly (1971a), Cormack (1973), Buckland (1980), Pollock (1981b), and Pollock and Mann (1983). Pollock and Mann (1983) and Hightower and Gilbert (1984) presented applications of the Jolly-Seber model in fisheries management. The Jolly-Seber approach must be extended in the present work because treatment and control fish potentially have different survival and capture probabilities. Many possible models are available, depending on the number of treatment and control parameters that are different or common (e.g., Table 2.2).

First we present the basic model structure for the case where all parameters are different for the two groups. Because this model is the core of our discussion, we present detailed descriptions of point estimators of parameters and their variances and covariances. We next consider the sequence of models obtained with the complete capture history protocol as we allow the number of parameters common to both treatment and control groups to decrease from all to none, briefly describe goodness of fit testing for this protocol, give a detailed hypothetical example using numbers to illustrate our methodology, and finally present some details of the specific theory for this protocol (complete details are in Part 3).

### 2.4.2. Model $H_{k-1, \phi}$

At the first site ( $i = 1$ ), there is an initial release of marked fish of the treatment and control groups. At downstream sites ( $i = 2, \dots, k$ ), marked fish are recaptured. Typically, marked fish are released again, although some fish may be removed because they are wounded by capture or are needed for other research. The basic data are conveniently summarized initially as a capture history matrix (see Section 1.3.2.1).

Most analyses (except for the goodness of fit tests computed as components of TEST 3) can be performed on the reduced  $m$ -array summarization of the data represented in Table 2.12 (see Section 1.3.2.3), illustrated here for the case of  $k = 4$  sampling times.

Table 2.12. - Data summary (as an  $m$ -array) for the complete capture history protocol ( $k = 4$ ).

| Release site           | Releases $R_{v1}$ | Number recaptured at dam $j, m_{dj}$ |           |           | Total    |
|------------------------|-------------------|--------------------------------------|-----------|-----------|----------|
|                        |                   | $j = 2$                              | 3         | 4         |          |
| <b>Treatment group</b> |                   |                                      |           |           |          |
| 1                      | $R_{t1}$          | $m_{t12}$                            | $m_{t13}$ | $m_{t14}$ | $r_{t1}$ |
| 2                      | $R_{t2}$          |                                      | $m_{t23}$ | $m_{t24}$ | $r_{t2}$ |
| 3                      | $R_{t3}$          |                                      |           | $m_{t34}$ | $r_{t3}$ |
| Totals                 |                   | $m_{t2}$                             | $m_{t3}$  | $m_{t4}$  |          |
| <b>Control group</b>   |                   |                                      |           |           |          |
| 1                      | $R_{c1}$          | $m_{c12}$                            | $m_{c13}$ | $m_{c14}$ | $r_{c1}$ |
| 2                      | $R_{c2}$          |                                      | $m_{c23}$ | $m_{c24}$ | $r_{c2}$ |
| 3                      | $R_{c3}$          |                                      |           | $m_{c34}$ | $r_{c3}$ |
| Totals                 |                   | $m_{c2}$                             | $m_{c3}$  | $m_{c4}$  |          |

To illustrate the parameter structure, Table 2.13 shows the expected values of the number of captures - i.e.,  $E(m_{ij} | R_{ij})$  and  $E(m_{cij} | R_{cij})$  - when all parameters may be different for the treatment and control fish.

Table 2.13. - Expected numbers of recaptures,  $E(m_{dj})$  and  $E(m_{c,dj})$ , for the complete capture history protocol ( $k = 4$ ) under the general model  $H_{k-1,\phi}$

| Releases $R_{v1}$      | Number recaptured at dam $j, m_{dj}$ |  |   | Total                |
|------------------------|--------------------------------------|--|---|----------------------|
|                        | $j = 2$                              | 3                                      | 4   |                      |
| <b>Treatment group</b> |                                      |  |   |                      |
| $R_{t1}$               | $R_{t1}\phi_{11}p_{t2}$              | $R_{t1}\phi_{11}q_{t2}\phi_{12}p_{t3}$ | $R_{t1}\phi_{11}q_{t2}\phi_{12}q_{t3}\phi_{13}p_{t4}$ | $R_{t1}\lambda_{t1}$ |
| $R_{t2}$               |                                      | $R_{t2}\phi_{22}p_{t3}$                | $R_{t2}\phi_{22}q_{t3}\phi_{23}p_{t4}$                | $R_{t2}\lambda_{t2}$ |
| $R_{t3}$               |                                      |  | $R_{t3}\phi_{33}p_{t4}$                               | $R_{t3}\lambda_{t3}$ |
| <b>Control group</b>   |                                      |  |   |                      |
| $R_{c1}$               | $R_{c1}\phi_{c1}p_{c2}$              | $R_{c1}\phi_{c1}q_{c2}\phi_{c2}p_{c3}$ | $R_{c1}\phi_{c1}q_{c2}\phi_{c2}q_{c3}\phi_{c3}p_{c4}$ | $R_{c1}\lambda_{c1}$ |
| $R_{c2}$               |                                      | $R_{c2}\phi_{c2}p_{c3}$                | $R_{c2}\phi_{c2}q_{c3}\phi_{c3}p_{c4}$                | $R_{c2}\lambda_{c2}$ |
| $R_{c3}$               |                                      |  | $R_{c3}\phi_{c3}p_{c4}$                               | $R_{c3}\lambda_{c3}$ |

Under the most general model structure  $H_{k-1, \phi}$ , we can apply the Jolly-Seber method to each group of fish (treatment or control) separately because we assume that every parameter is different for the two groups. Therefore, no information on treatment fish is obtained from control data or vice versa. The point estimators and their variances and covariances were given by Seber (1982:199). However, we use a different representation of these parameter estimators that leads to simpler formulae in the more complex models.

All point estimators depend on the minimal sufficient statistic

$$MSS = \{r_{t1}, r_{t2}, \dots, r_{t,k-1}, m_{t2}, m_{t3}, \dots, m_{t,k-1}, r_{c1}, r_{c2}, \dots, r_{c,k-1}, m_{c2}, m_{c3}, \dots, m_{c,k-1}\}.$$

Notice that the minimal sufficient statistic can be partitioned into two components, one for each group of fish, each component corresponding to the minimal sufficient statistic under the Jolly-Seber model for that single data set.

The parameter estimators under this model are

$$\hat{\lambda}_{ti} = \frac{r_{ti}}{R_{ti}} \left[ \frac{m_{t,i+1}}{T_{t,i+1}} + \frac{z_{t,i+1}R_{t,i+1}}{T_{t,i+1}r_{t,i+1}} \right], \quad i = 1, \dots, k - 2;$$

$$\hat{\phi}_{ci} = \frac{r_{ci}}{R_{ci}} \left[ \frac{m_{c,i+1}}{T_{c,i+1}} + \frac{z_{c,i+1}R_{c,i+1}}{T_{c,i+1}r_{c,i+1}} \right], \quad i = 1, \dots, k - 2;$$

$$\hat{\phi}_{t,k-1} P_{tk} = \frac{r_{t,k-1}}{R_{t,k-1}};$$

$$\hat{\phi}_{c,k-1} P_{ck} = \frac{r_{c,k-1}}{R_{c,k-1}};$$

$$\hat{p}_{ti} = \frac{m_{ti}}{m_{ti} + z_{ti} R_{ti}/r_{ti}}, \quad i = 2, \dots, k - 1; \text{ and}$$

$$\hat{p}_{ci} = \frac{m_{ci}}{m_{ci} + z_{ci} R_{ci}/r_{ci}}, \quad i = 2, \dots, k - 1.$$

Recall that  $T_{ti} = m_{ti} + z_{ti}$  and  $T_{ci} = m_{ci} + z_{ci}$ . Definitions of other terms are in both the Glossary and Section 1.4.2.

The theoretical variances for the treatment group are given as:

$$\hat{\text{var}}(\hat{\phi}_i) = (\hat{\phi}_i)^2 \left[ \frac{1}{r_i} - \frac{1}{R_i} + (\hat{q}_{t,i+1})^2 \left( \frac{1}{r_{t,i+1}} - \frac{1}{R_{t,i+1}} \right) + (\hat{q}_{t,i+1})^2 \left( 1 - \frac{r_{t,i+1}}{R_{t,i+1}} \right)^2 \frac{m_{t,i+1}}{z_{t,i+1} T_{t,i+1}} \right], \quad i = 1, \dots, k-2;$$

$$\hat{\text{var}}(\hat{p}_i) = (\hat{p}_i \hat{q}_i)^2 \left( \frac{1}{r_i} - \frac{1}{R_i} + \frac{1}{m_i} + \frac{1}{z_i} \right), \quad i = 2, \dots, k-1.$$

The survival effect  $\hat{S}_i$  between dams  $i$  and  $i+1$  is estimated by

$$\hat{S}_i = \hat{\phi}_i / \hat{\phi}_{ci}.$$

The estimated variance of  $\hat{S}_i$  is

$$\hat{\text{var}}(\hat{S}_i) = (\hat{S}_i)^2 \left[ \frac{\hat{\text{var}}(\hat{\phi}_i)}{\hat{\phi}_i^2} + \frac{\hat{\text{var}}(\hat{\phi}_{ci})}{\hat{\phi}_{ci}^2} \right].$$

Additional theory for variances and covariances of  $\hat{S}_i$ , under different models, is in Chapter 3.3.

Most of the possible covariances between the  $2k-3$  estimators (within a group) are zero; theoretical formulae for the non-zero covariances for the treatment group are:

$$\hat{\text{cov}}(\hat{\phi}_{t,i-1}, \hat{\phi}_i) = -\hat{\phi}_{t,i-1} \hat{\phi}_i \hat{q}_i \left( \frac{1}{r_i} - \frac{1}{R_i} \right), \quad i = 2, \dots, k-2;$$

$$\hat{\text{cov}}(\hat{\phi}_i, \hat{p}_i) = \hat{\phi}_i \hat{p}_i \hat{q}_i \left( \frac{1}{r_i} - \frac{1}{R_i} \right), \quad i = 2, \dots, k-2;$$

$$\hat{\text{cov}}(\hat{\phi}_i, \hat{p}_{t,i+1}) = -\hat{\phi}_i \hat{p}_{t,i+1} (\hat{q}_{t,i+1})^2 \left[ \frac{1}{r_{t,i+1}} - \frac{1}{R_{t,i+1}} + \left( 1 - \frac{r_{t,i+1}}{R_{t,i+1}} \right) \frac{1}{z_{t,i+1}} \right], \quad i = 1, \dots, k-3.$$

The variances and covariances for the control group estimators are of the same form; subscript  $t$  is replaced by subscript  $c$ . Notice that alternate survival estimators within each treatment group have a negative covariance. Because all parameters are distinct for the two groups in

this model and the data are analyzed separately for each group, all treatment estimators are independent of all control estimators.

### 2.4.3. Model Sequence

The most general model  $H_{k-1,\phi}$ , discussed in Section 2.4.2, is often too general because treatment and control fish may differ only in a few of the initial survival and capture probabilities. In Chapter 2.1, we presented a sequence of models ranging from  $H_0$  (no treatment effect on any parameters) to the most general,  $H_{k-1,\phi}$ . We reiterate the meaning of these hypotheses (models) here, ordered from the least general to the most general model.

- $H_0$ :  $\phi_{t1} = \phi_{c1}, p_{t2} = p_{c2}, \phi_{t2} = \phi_{c2}, p_{t3} = p_{c3}, \dots$   
 "all parameters the same for  $t$  and  $c$ "
- $H_{1\phi}$ :  $\phi_{t1} \neq \phi_{c1}, p_{t2} = p_{c2}, \phi_{t2} = \phi_{c2}, p_{t3} = p_{c3}, \dots$   
 "all parameters the same for  $t$  and  $c$ , except for  $\phi_1$ "
- $H_{2\phi}$ :  $\phi_{t1} \neq \phi_{c1}, p_{t2} \neq p_{c2}, \phi_{t2} = \phi_{c2}, p_{t3} = p_{c3}, \dots$   
 "all parameters the same for  $t$  and  $c$ , except for  $\phi_1, p_2$ "
- $H_{2\phi}$ :  $\phi_{t1} \neq \phi_{c1}, p_{t2} \neq p_{c2}, \phi_{t2} \neq \phi_{c2}, p_{t3} = p_{c3}, \dots$   
 "all parameters the same for  $t$  and  $c$ , except  $\phi_1, p_2$ , and  $\phi_2$ "
- $H_{k-1,\phi}$ :  $\phi_{ti} \neq \phi_{ci}, i = 1, \dots, k-1$  and  $p_{ti} \neq p_{ci}, i = 2, \dots, k$   
 "all parameters different for  $t$  and  $c$ "

In the following sections, we present more details on models  $H_0$ ,  $H_{1\phi}$ , and  $H_{2\phi}$  giving, in particular, point estimators and variances and covariances.

### 2.4.4. Model $H_0$

Under model  $H_0$ , all the parameters for treatment and control groups are assumed to be common. Therefore, the minimal sufficient statistic is

$$\text{MSS} = \{r_{.1}, \dots, r_{.k-1}, m_{.2}, \dots, m_{.k-1}\},$$

which is the usual Jolly-Seber case, with all statistics pooled across groups. Recall that  $r_{.i} = r_{ti} + r_{ci}$  and  $m_{.i} = m_{ti} + m_{ci}$ . Also, this results in  $z_{.i} = z_{ti} + z_{ci}$  and  $T_{.i} = T_{ti} + T_{ci}$ .

The parameter estimators under model  $H_0$  are structurally the same as those given for model  $H_{k-1,\phi}$ . We give these estimators below for comparison with results under model  $H_{k-1,\phi}$ :

$$\hat{\phi}_i = \frac{r_i}{R_i} \left[ \frac{m_{.,i+1}}{T_{.,i+1}} + \frac{z_{.,i+1} R_{.,i+1}}{T_{.,i+1} r_{.,i+1}} \right], \quad i = 1, \dots, k-2;$$

$$\hat{\phi}_{k-1} p_k = \frac{r_{.,k-1}}{R_{.,k-1}},$$

$$\hat{p}_i = \frac{m_i}{m_i + z_i R_i / r_i}, \quad i = 2, \dots, k-1.$$

The variances and covariances of the above are structurally identical to those given for the treatment group in Section 2.4.2; one just replaces the subscript  $t$  with a period “.” (i.e., pool over  $t$  and  $c$ ) throughout those variance-covariance formulae. For that reason, and because RELEASE computes these variances and covariances, we do not explicitly give their formulae under model  $H_0$ . (Note: all parameter estimators, variances, and covariances under all models for the complete capture history are given in Section 3.1.3.)

#### 2.4.5. Model $H_{1\phi}$

Model  $H_{1\phi}$  has all parameters common except the first survival rates ( $\phi_{t1} \neq \phi_{c1}$ ). This model is reasonable if the treatment effect wears off completely by the second sampling time (i.e., is an acute effect).

This is an important model, so we present (for  $k = 4$ ) the conditional expectations  $E(m_{ij} | R_{ij})$  and  $E(m_{ci} | R_{ci})$  in Table 2.14. Model  $H_{1\phi}$  is closely related to models considered originally by Robson (1969) and Pollock (1975) for temporary trap response and to the age-dependent version of the Jolly-Seber model described by Pollock (1981b).

The minimal sufficient statistic under  $H_{1\phi}$  is

$$\text{MSS} = \{r_{t1}, r_{c1}, r_{.2}, \dots, r_{.,k-1}, m_{.2}, \dots, m_{.,k-1}\}.$$

Table 2.14. - Expected numbers of recaptures  $E(m_{t1j} | R_{t1})$  and  $E(m_{c1j} | R_{c1})$  for the complete capture history protocol ( $k = 4$ ) model  $H_{1\phi}$

| Releases<br>$R_{\cdot}$ | Number recaptured at dam $j, m_{\cdot j}$ |                               |  | Total                |
|-------------------------|---|-------------------------------|--|----------------------|
|                         | $j = 2$                                   | 3                             | 4                                      |                      |
| <b>Treatment group</b>  |   |                               |  |                      |
| $R_{t1}$                | $R_{t1}\phi_{11}p_2$                      | $R_{t1}\phi_{11}q_2\phi_2p_3$ | $R_{t1}\phi_{11}q_2\phi_2q_3\phi_3p_4$ | $R_{t1}\lambda_{t1}$ |
| $R_{t2}$                |   | $R_{t2}\phi_2p_3$             | $R_{t2}\phi_2q_3\phi_3p_4$             | $R_{t2}\lambda_{t2}$ |
| $R_{t3}$                |   |                               | $R_{t3}\phi_3p_4$                      | $R_{t3}\lambda_{t3}$ |
| <b>Control group</b>    |   |                               |  |                      |
| $R_{c1}$                | $R_{c1}\phi_{c1}p_2$                      | $R_{c1}\phi_{c1}q_2\phi_2p_3$ | $R_{c1}\phi_{c1}q_2\phi_2q_3\phi_3p_4$ | $R_{c1}\lambda_{c1}$ |
| $R_{c2}$                |   | $R_{c2}\phi_2p_3$             | $R_{c2}\phi_2q_3\phi_3p_4$             | $R_{c2}\lambda_{c2}$ |
| $R_{c3}$                |   |                               | $R_{c3}\phi_3p_4$                      | $R_{c3}\lambda_{c3}$ |

The parameter estimators under model  $H_{1\phi}$  are:

$$\hat{\phi}_{t1} = \frac{r_{t1}}{R_{t1}} \left[ \frac{m_{.2}}{T_{.2}} + \frac{z_{.2}R_{.2}}{T_{.2}r_{.2}} \right];$$

$$\hat{\phi}_{c1} = \frac{r_{c1}}{r_{c1}} \left[ \frac{m_{.2}}{T_{.2}} + \frac{z_{.2}R_{.2}}{T_{.2}r_{.2}} \right];$$

$$\hat{\phi}_i = \frac{r_{.i}}{R_{.i}} \left[ \frac{m_{.,i+1}}{T_{.,i+1}} + \frac{z_{.,i+1}R_{.,i+1}}{T_{.,i+1}r_{.,i+1}} \right], \quad i = 2, \dots, k-2;$$

$$\hat{\phi}_{k-1}p_k = \frac{r_{.,k-1}}{R_{.,k-1}}; \text{ and}$$

$$\hat{p}_i = \frac{m_{.i}}{m_{.i} + z_{.i}R_{.i}/r_{.i}}, \quad i = 2, \dots, k-1.$$

Our recommended definition of the treatment effect (see Chapter 1.5) under model  $H_{1\phi}$  is

$$S = \frac{\phi_{t1}}{\phi_{c1}} ;$$

hence,  $\hat{S} = \frac{\hat{\phi}_{t1}}{\hat{\phi}_{c1}}$ , which gives the simple result

$$\hat{S} = \frac{r_{t1}/R_{t1}}{r_{c1}/R_{c1}} .$$

The theoretical variance of  $\hat{S}$  is

$$\hat{\text{var}}(\hat{S}) = (\hat{S})^2 \left[ \frac{1}{r_{t1}} - \frac{1}{R_{t1}} + \frac{1}{r_{c1}} - \frac{1}{R_{c1}} \right] .$$

The variances and covariances of the  $\hat{\phi}$  and  $\hat{p}$  are:

$$\hat{\text{var}}(\hat{\phi}_{t1}) = (\hat{\phi}_{t1})^2 \left[ \frac{1}{r_{t1}} - \frac{1}{R_{t1}} + (\hat{q}_2)^2 \left( \frac{1}{r_2} - \frac{1}{R_2} \right) + (\hat{q}_2)^2 \left( 1 - \frac{r_2}{R_2} \right)^2 \frac{m_2}{z_2 T_2} \right] ;$$

$\hat{\text{var}}(\hat{\phi}_{c1})$  is as above with subscript  $t$  replaced by subscript  $c$ ;

$$\begin{aligned} \hat{\text{var}}(\hat{\phi}_i) = & (\hat{\phi}_i)^2 \left[ \frac{1}{r_i} - \frac{1}{R_i} + (\hat{q}_{i+1})^2 \left( \frac{1}{r_{i+1}} - \frac{1}{R_{i+1}} \right) \right. \\ & \left. + (\hat{q}_{i+1})^2 \left( 1 - \frac{r_{i+1}}{R_{i+1}} \right)^2 \left( \frac{m_{i+1}}{z_{i+1} T_{i+1}} \right) \right] , \quad i = 2, \dots, k-2 ; \end{aligned}$$

$$\hat{\text{var}}(\hat{p}_i) = (\hat{p}_i \hat{q}_i)^2 \left[ \frac{1}{r_i} - \frac{1}{R_i} + \frac{1}{m_i} + \frac{1}{z_i} \right] , \quad i = 2, \dots, k-1 ;$$



$$\hat{\text{cov}}(\hat{\phi}_{t1}, \hat{\phi}_{c1}) = \hat{\phi}_{t1} \hat{\phi}_{c1} (\hat{q}_2)^2 \left[ \frac{1}{r_{.2}} - \frac{1}{R_{.2}} + \left( 1 - \frac{r_{.2}}{R_{.2}} \right)^2 \frac{m_{.2}}{z_{.2} T_{.2}} \right];$$

$$\hat{\text{cov}}(\hat{\phi}_{t1}, \hat{\phi}_2) = -\hat{\phi}_{t1} \hat{\phi}_2 \hat{q}_2 \left( \frac{1}{r_{.2}} - \frac{1}{R_{.2}} \right);$$

$\hat{\text{cov}}(\hat{\phi}_{c1}, \hat{\phi}_2)$  is as above with subscript  $t$  replaced by subscript  $c$ ;

$$\hat{\text{cov}}(\hat{\phi}_i, \hat{\phi}_{i+1}) = -\hat{\phi}_i \hat{\phi}_{i+1} \hat{q}_{i+1} \left( \frac{1}{r_{.,i+1}} - \frac{1}{R_{.,i+1}} \right), \quad i = 2, \dots, k-3;$$

$$\hat{\text{cov}}(\hat{\phi}_{t1}, \hat{p}_2) = -\hat{\phi}_{t1} \hat{p}_2 (\hat{q}_2)^2 \left( \frac{1}{r_{.2}} - \frac{1}{R_{.2}} + \frac{1 - \frac{r_{.2}}{R_{.2}}}{z_{.2}} \right);$$

$\hat{\text{cov}}(\hat{\phi}_{c1}, \hat{p}_2)$  is as above with subscript  $t$  replaced by subscript  $c$ ;

$$\hat{\text{cov}}(\hat{\phi}_i, \hat{p}_i) = \hat{\phi}_i \hat{p}_i \hat{q}_i \left( \frac{1}{r_i} - \frac{1}{R_i} \right), \quad i = 2, \dots, k-2; \text{ and}$$

$$\hat{\text{cov}}(\hat{\phi}_i, \hat{p}_{i+1}) = -\hat{\phi}_i \hat{p}_{i+1} (\hat{q}_{i+1})^2 \left( \frac{1}{r_{.,i+1}} - \frac{1}{R_{.,i+1}} + \frac{1 - \frac{r_{.,i+1}}{R_{.,i+1}}}{z_{.,i+1}} \right), \quad i = 2, \dots, k-2.$$

#### 2.4.6. Model $H_{2p}$

In model  $H_{2p}$ , it is assumed that only  $\phi_1$  and  $p_2$  are affected by the treatment. Hence, this model has all parameters common except the first survival rate ( $\phi_{t1} \neq \phi_{c1}$ ) and the first capture probability ( $p_{t2} \neq p_{c2}$ ). Again, it is informative to present the expected data values  $E(m_{ij} | R_{ti})$  and  $E(m_{ij} | R_{ci})$  as in Table 2.15. Model  $H_{2p}$  is closely related to a temporary trap response model originally presented by Pollock (1975).

Table 2.15. - Expected numbers of recaptures under model  $H_{2p}$  for the complete capture history protocol ( $k = 4$ ).

| Releases<br>$R_i$      | Number recaptured at dam $j, m_{ij}$ |  |   | Total                |
|------------------------|--------------------------------------|--|---|----------------------|
|                        | $j = 2$                              | 3                                      | 4   |                      |
| <b>Treatment group</b> |                                      |  |   |                      |
| $R_{t1}$               | $R_{t1}\phi_{t1}p_{t2}$              | $R_{t1}\phi_{t1}q_{t2}\phi_{t3}p_{t3}$ | $R_{t1}\phi_{t1}q_{t2}\phi_{t3}q_{t3}\phi_{t4}p_{t4}$ | $R_{t1}\lambda_{t1}$ |
| $R_{t2}$               |                                      | $R_{t2}\phi_{t2}p_{t3}$                | $R_{t2}\phi_{t2}q_{t3}\phi_{t4}p_{t4}$                | $R_{t2}\lambda_{t2}$ |
| $R_{t3}$               |                                      |  | $R_{t3}\phi_{t3}p_{t4}$                               | $R_{t3}\lambda_{t3}$ |
| <b>Control group</b>   |                                      |  |   |                      |
| $R_{c1}$               | $R_{c1}\phi_{c1}p_{c2}$              | $R_{c1}\phi_{c1}q_{c2}\phi_{c3}p_{c3}$ | $R_{c1}\phi_{c1}q_{c2}\phi_{c3}q_{c3}\phi_{c4}p_{c4}$ | $R_{c1}\lambda_{c1}$ |
| $R_{c2}$               |                                      | $R_{c2}\phi_{c2}p_{c3}$                | $R_{c2}\phi_{c2}q_{c3}\phi_{c4}p_{c4}$                | $R_{c2}\lambda_{c2}$ |
| $R_{c3}$               |                                      |  | $R_{c3}\phi_{c3}p_{c4}$                               | $R_{c3}\lambda_{c3}$ |

The minimal sufficient statistic under  $H_{2p}$  is given by

$$MSS = \{r_{t1}, r_{c1}, r_{.2}, \dots, r_{.,k-1}, m_{t2}, m_{c2}, m_{.3}, \dots, m_{.,k-1}\}.$$

The parameter estimators under model  $H_{2p}$  are:

$$\hat{\phi}_{t1} = \frac{r_{t1}}{R_{t1}} \left[ \frac{m_{t2}}{T_{t2}} + \frac{z_{t2}R_{.2}}{T_{t2}r_{.2}} \right];$$

$$\hat{\phi}_{c1} = \frac{r_{c1}}{R_{c1}} \left[ \frac{m_{c2}}{T_{c2}} + \frac{z_{c2}R_{.2}}{T_{c2}r_{.2}} \right];$$

$$\hat{\phi}_i = \frac{r_{.2}}{R_{.2}} \left[ \frac{m_{.,i+1}}{T_{.,i+1}} + \frac{z_{.,i+1}R_{.,i+1}}{T_{.,i+1}r_{.,i+1}} \right], \quad i = 2, \dots, k - 2;$$

$$\phi_{k-1} \hat{p}_k = \frac{r_{.,k-1}}{R_{.,k-1}};$$

$$\hat{p}_{t2} = \frac{m_{t2}}{m_{t2} + z_{t2} R_{.2} / r_{.2}};$$

$$\hat{p}_{c2} = \frac{m_{c2}}{m_{c2} + z_{c2} R_{.2} / r_{.2}}; \text{ and}$$

$$\hat{p}_i = \frac{m_i}{m_i + z_i R_i / r_i}, \quad i = 3, \dots, k-1.$$

The effect of treatment on survival from dam 1 to dam 2 is estimated by

$$\hat{S} = \frac{\hat{\phi}_{t1}}{\hat{\phi}_{c1}}$$

(this ratio does not simplify under model  $H_{2p}$ ). The difference between  $\hat{p}_{t2}$  and  $\hat{p}_{c2}$  also represents a treatment effect, but not one of major interest. The estimated variance of  $\hat{S}$  is

$$\begin{aligned} \hat{\text{var}}(\hat{S}) = & (\hat{S})^2 \left\{ \left[ \frac{1}{\hat{r}_{t1}} - \frac{1}{\hat{R}_{t1}} + \frac{1}{\hat{r}_{c1}} - \frac{1}{\hat{R}_{c1}} \right] \right. \\ & + (\hat{p}_{t2} - \hat{p}_{c2})^2 \left[ \frac{1}{\hat{r}_{.2}} - \frac{1}{\hat{R}_{.2}} \right] \\ & \left. + \frac{(1 - \hat{\lambda}_2)^2}{\hat{\lambda}_2} \left[ \frac{\hat{p}_{t2} \hat{q}_{t2}}{\hat{T}_{t2}} + \frac{\hat{p}_{c2} \hat{q}_{c2}}{\hat{T}_{c2}} \right] \right\}, \end{aligned}$$

where the  $\hat{p}_{t2}$  and  $\hat{p}_{c2}$  are given above and  $\hat{\lambda}_2 = r_{.2} / R_{.2}$ . Compare this formula for  $\hat{\text{var}}(\hat{S})$  under model  $H_{2p}$  to the  $\hat{\text{var}}(\hat{S})$  under model  $H_{1\phi}$ . The first large term of the above is the  $\hat{\text{var}}(\hat{S})$  under model  $H_{1\phi}$ . The additional terms in the above reflect loss of precision in  $\hat{S}$  when one uses model  $H_{2p}$  (actually that loss of precision is not great).

The variance formulae do not show us the bias that  $\hat{S}$  will have if model  $H_{2p}$  is true but  $H_{1\phi}$  is used. If model  $H_{1\phi}$  is true,  $\hat{S}$  is essentially unbiased. However, if model  $H_{2p}$  is true and one uses model  $H_{1\phi}$  as the basis of one's estimator of  $S$ , we have, approximately,

$$E(\hat{S}) = S \frac{p_{t2} + q_{t2}\lambda_2}{p_{c2} + q_{c2}\lambda_2}.$$

Using these formulae, one can evaluate bias and precision of  $\hat{S}$  if model  $H_{2p}$  is true but model  $H_{1\phi}$  is used for data analysis.

The variances and covariances of the above estimators of the  $\phi$  and  $p$  are:

$$\hat{\text{var}}(\hat{\phi}_{t1}) = (\hat{\phi}_{t1})^2 \left[ \frac{1}{r_{t1}} - \frac{1}{R_{t1}} + (\hat{q}_{t2})^2 \left( \frac{1}{r_{.2}} - \frac{1}{R_{.2}} \right) + (\hat{q}_{t2})^2 \left( 1 - \frac{r_{.2}}{R_{.2}} \right)^2 \frac{m_{t2}}{z_{t2}T_{t2}} \right];$$

$\hat{\text{var}}(\hat{\phi}_{c1})$  is as above with subscript  $t$  replaced by subscript  $c$ ;

$$\begin{aligned} \hat{\text{var}}(\hat{\phi}_i) &= (\hat{\phi}_i)^2 \left[ \frac{1}{r_i} - \frac{1}{R_i} + (\hat{q}_{i+1})^2 \left( \frac{1}{r_{.,i+1}} - \frac{1}{R_{.,i+1}} \right) \right. \\ &\quad \left. + (\hat{q}_{i+1})^2 \left( 1 - \frac{r_{.,i+1}}{R_{.,i+1}} \right)^2 \frac{m_{.,i+1}}{z_{.,i+1}T_{.,i+1}} \right], \quad i = 2, \dots, k-2; \end{aligned}$$

$$\hat{\text{var}}(\hat{p}_{t2}) = (\hat{\phi}_{t2}\hat{q}_{t2})^2 \left( \frac{1}{r_{.2}} - \frac{1}{R_{.2}} + \frac{1}{m_{t2}} + \frac{1}{z_{t2}} \right);$$

$\hat{\text{var}}(\hat{p}_{c2})$  is as above with subscript  $t$  replaced by subscript  $c$ ;

$$\hat{\text{var}}(\hat{p}_i) = (\hat{p}_i\hat{q}_i)^2 \left( \frac{1}{r_i} - \frac{1}{R_i} + \frac{1}{m_i} + \frac{1}{z_i} \right), \quad i = 3, \dots, k-1;$$

$$\hat{\text{cov}}(\hat{\phi}_{t1}, \hat{\phi}_{c1}) = \hat{\phi}_{t1}\hat{q}_{t2}\hat{\phi}_{c1}\hat{q}_{c2} \left( \frac{1}{r_{.2}} - \frac{1}{R_{.2}} \right);$$

$$\hat{\text{cov}}(\hat{\phi}_{t1}, \hat{\phi}_2) = \hat{\phi}_{t1} \hat{\phi}_2 \hat{q}_{t2} \left( \frac{1}{r_2} - \frac{1}{R_2} \right);$$

$\hat{\text{cov}}(\hat{\phi}_{c1}, \hat{\phi}_2)$  is as above with subscript  $t$  replaced by subscript  $c$ ;

$$\hat{\text{cov}}(\hat{\phi}_i, \hat{\phi}_{i+1}) = \hat{\phi}_i \hat{\phi}_{i+1} \hat{q}_{i+1} \left( \frac{1}{r_{i+1}} - \frac{1}{R_{i+1}} \right), \quad i = 2, \dots, k-3;$$

$$\hat{\text{cov}}(\hat{\phi}_{t1}, \hat{\phi}_{t2}) = \hat{\phi}_{t1} \hat{p}_{t2} (\hat{q}_{t2})^2 \left[ \frac{1}{r_2} - \frac{1}{R_2} + \frac{1 - \frac{r_2}{R_2}}{z_{t2}} \right];$$

$\hat{\text{cov}}(\hat{\phi}_{c1}, \hat{p}_{c2})$  is as above with subscript  $t$  replaced by subscript  $c$ ;

$$\hat{\text{cov}}(\hat{\phi}_{t1}, \hat{p}_{c2}) = \hat{\phi}_{t1} \hat{p}_{c2} \hat{q}_{t2} \hat{q}_{c2} \left( \frac{1}{r_2} - \frac{1}{R_2} \right);$$

$$\hat{\text{cov}}(\hat{\phi}_{c1}, \hat{p}_{t2}) = \hat{\phi}_{c1} \hat{p}_{t2} \hat{q}_{c2} \hat{q}_{t2} \left( \frac{1}{r_2} - \frac{1}{R_2} \right);$$

$$\hat{\text{cov}}(\hat{\phi}_2, \hat{p}_{t2}) = \hat{\phi}_2 \hat{p}_{t2} \hat{q}_{t2} \left( \frac{1}{r_2} - \frac{1}{R_2} \right);$$

$\hat{\text{cov}}(\hat{\phi}_2, \hat{p}_{c2})$  is as above with subscript  $t$  replaced by subscript  $c$ ;

$$\hat{\text{cov}}(\hat{\phi}_i, \hat{p}_i) = \hat{\phi}_i \hat{p}_i \hat{q}_i \left( \frac{1}{r_i} - \frac{1}{R_i} \right), \quad i = 3, \dots, k-2; \text{ and}$$

$$\hat{\text{cov}}(\hat{\phi}_i, \hat{p}_{i+1}) = -\hat{\phi}_i \hat{p}_{i+1} (\hat{q}_{i+1})^2 \left[ \frac{1}{r_{\cdot, i+1}} - \frac{1}{R_{\cdot, i+1}} + \frac{1 - \frac{r_{\cdot, i+1}}{R_{\cdot, i+1}}}{z_{\cdot, i+1}} \right] \quad i = 3, \dots, k-2.$$

#### 2.4.7. Comments on Models $H_{2\phi}$ to $H_{k-1, \phi}$

The remaining models in the sequence, i.e.,  $H_{2\phi}$  through  $H_{k-1, \phi}$ , are not discussed here in detail. For each of these models, explicit estimators of the parameters are given in Section 3.1.3. The estimators of  $\phi_{t1}$  and  $\phi_{c1}$ , hence,  $S = \phi_{t1}/\phi_{c1}$  and  $\text{var}(\hat{S})$  are identical for all models  $H_{2\phi}$  through  $H_{k-1, \phi}$  (general results for  $H_{k-1, \phi}$  are given in Section 2.4.2). In particular, for  $\hat{S} = \hat{\phi}_{t1}/\hat{\phi}_{c1}$  under any of these models,

$$\begin{aligned} \hat{\text{var}}(\hat{S}) = & (\hat{S})^2 \left[ \left( \frac{1}{r_{t1}} - \frac{1}{R_{t1}} + \frac{1}{r_{c1}} - \frac{1}{R_{c1}} \right) \right. \\ & + (\hat{q}_{t2})^2 \left( \frac{1}{r_{t2}} - \frac{1}{R_{t2}} \right) + (\hat{q}_{c2})^2 \left( \frac{1}{r_{c2}} - \frac{1}{R_{c2}} \right) \\ & \left. + \left[ \frac{(1 - \hat{\lambda}_{t2})^2}{\hat{\lambda}_{t2}} \frac{\hat{p}_{t2} \hat{q}_{t2}}{T_{t2}} + \frac{(1 - \hat{\lambda}_{c2})^2}{\hat{\lambda}_{c2}} \frac{\hat{p}_{c2} \hat{q}_{c2}}{T_{c2}} \right] \right], \end{aligned}$$

where  $\hat{\lambda}_{t2} = r_{t2}/R_{t2}$ ,  $\hat{\lambda}_{c2} = r_{c2}/R_{c2}$ . Compare this variance to  $\text{var}(\hat{S})$  under models  $H_{1\phi}$  and  $H_{2\phi}$ .

Program RELEASE computes results for these models and does the between-model tests. In fisheries or other experiments involving a treatment survival effect that is predominantly acute, models  $H_{1\phi}$  and  $H_{2\phi}$  are by far the most useful models. If most new releases of fish (or other test animals) are at occasion 1 and capture probabilities are low, the only parameters estimable with good precision are  $\phi_{t1}$ ,  $\phi_{c1}$ ,  $p_{t2}$ , and  $p_{c2}$ , because the releases  $R_{ti}$  and  $R_{ci}$  at occasions  $i = 2, \dots, k-1$  are so small relative to  $R_{t1}$  and  $R_{c1}$ . If these releases at occasion 2, ...,  $k-1$  are increased, other models in the sequence allow efficient parameter estimation.

With an acute treatment effect, the design having no new animals introduced after occasion 1 is effective. If the treatment effect is chronic and capture rates are not too high, this design is poor. With chronic effects, one needs efficient estimators of all the  $\phi_{ti}$ ,  $\phi_{ci}$ ,  $i = 1, 2, \dots, k-2$ ; it is then important to have the full sequence of models. Alternative model sequences may then also be important. For example, one may want to have  $p_{ti} = p_{ci}$ ,  $i = 2, \dots, k$  with only the  $\phi_{ti}$  and  $\phi_{ci}$  showing a possible effect. Such models do not have closed-form estimators;

rather, their analysis requires numerical methods (which can be done by using program SURVIV in conjunction with RELEASE).

#### 2.4.8. On Alternative Forms of the Estimators

Much of the literature on the Jolly-Seber model presents the estimators of  $\phi_i$  and  $p_i$  in a different form than we have used here (see, however, Brownie and Robson 1983). For example, one would usually see

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - m_i + R_i}$$

and

$$\hat{p}_i = \frac{m_i}{\hat{M}_i},$$

where

$$\hat{M}_i = m_i + \frac{z_i R_i}{r_i}.$$

This manner of presentation is tied to the heuristics of early capture-recapture developments wherein the emphasis was (initially) on estimating population size. That emphasis motivated concentration on the number of marked (and unmarked) animals still alive in the population at occasion  $i$ : the  $M_i$ . We could have followed this practice; however, theoretical derivations and expressions of formulae are simpler under the multinomial modeling approach. In particular, variances simplify greatly. Results are (or would be) the same under either approach. To illustrate this, substitute  $\hat{M}_i$  and  $\hat{M}_{i+1}$  into the above formula for  $\hat{\phi}_i$  (the subtle part is knowing that  $T_{i+1} = r_i + z_i$ ):

$$\begin{aligned} \hat{M}_i - m_i &= \frac{z_i R_i}{r_i} \\ M_i - m_i + R_i &= R_i + \frac{z_i R_i}{r_i} \\ &= R_i \left( \frac{r_i + z_i}{r_i} \right) \end{aligned}$$

$$= R_i \frac{T_{i+1}}{r_i};$$

hence,

$$\hat{\phi}_i = \frac{m_{i+1} + \frac{z_{i+1}R_{i+1}}{r_{i+1}}}{R_i \frac{T_{i+1}}{r_i}}$$

$$= \frac{r_i}{R_i} \left[ \frac{m_{i+1}}{T_{i+1}} + \frac{z_{i+1}R_{i+1}}{T_{i+1}r_{i+1}} \right].$$

Compare the form of the  $\hat{\phi}_i$  above with that in any of the formulae for  $\hat{\phi}$  presented earlier in this chapter: it is the same.

#### 2.4.9. Tests of Assumptions

We distinguish two types of assumption tests: (1) goodness of fit, separately by treatment group, to the Jolly-Seber model, and (2) tests among treatment groups to determine the extent and nature of the treatment effect. The latter tests may be thought of as tests made between models in an attempt to select the most appropriate model. We presented this testing material in detail in Chapter 2.1. Program RELEASE computes all the tests discussed in that chapter.

Each type of test involves a series of contingency tables. The goodness of fit testing, as we develop it here, involves only the subcohorts (based on capture history) at each release occasion. Under the complete capture history protocol, there is maximal information for goodness of fit testing. TESTS 2 and 3, taken together, constitute the goodness of fit testing under the complete capture history protocol. Details of these tests are given in Chapter 2.1.

TEST 1 and its subcomponents provide the test between models. Given that the goodness of fit testing confirms the Jolly-Seber assumptions (time-specific parameters, i.e., no behavioral effects), it is reasonable to use TEST 1 to select a best model. "Best" means the model with the fewest parameters that fits the data and is biologically reasonable (one can get good-fitting models that are not biologically reasonable). TEST 1 is not unique to the complete capture history protocol, and we have presented it in Chapter 2.1. The first few tests in the TEST 1 sequence are especially important in the context of the hydroelectric fisheries experiments.



2.4.9.1. *TEST 1.R1.* – The test of whether  $\phi_{t1} = \phi_{c1}$ , given all the other parameters are equal, is computed from the  $2 \times 2$  table

|          |                   |
|----------|-------------------|
| $r_{t1}$ | $R_{t1} - r_{t1}$ |
| $r_{c1}$ | $R_{c1} - r_{c1}$ |

The test computed from this table is the usual chi-square contingency table test. The alternative hypothesis is that  $\phi_{t1} \neq \phi_{c1}$ . TEST 1.R1 is equivalently testing that  $S = 1$  versus  $S \neq 1$  ( $S = \phi_{t1}/\phi_{c1}$ ). Provided that the treatment effect is mostly a direct, acute effect, and that model  $H_{1\phi}$  holds, TEST 1.R1 is one's best test for a significant treatment effect.

2.4.9.2. *TEST 1.T2.* – The next test in the sequence tests that model  $H_{1\phi}$  holds versus the alternative model  $H_{2\phi}$ . TEST 1.T2 can also be considered as a determination of whether  $p_{t2} = p_{c2}$ , given  $\phi_{t1} \neq \phi_{c1}$  but all other parameters are equal. The test is based on the  $2 \times 2$  contingency table

|          |          |
|----------|----------|
| $m_{t2}$ | $z_{t2}$ |
| $m_{c2}$ | $z_{c2}$ |

It is labeled TEST 1.T2 because  $m_{v2} + z_{v2} = T_{v2}$ . If this test fails to reject and the composite results of TESTS 1.R2, 1.T3, ..., 1.Rk - 1 (the rest of the TEST 1 components) fail to reject, one is justified in concluding that model  $H_{1\phi}$  is the appropriate model. If, however, TEST 1.T2 rejects model  $H_{1\phi}$ , one proceeds to a closer examination of the next model in the sequence,  $H_{2\phi}$ .

2.4.9.3. *TEST 1.R2.* – The test of whether  $\phi_{t2} = \phi_{c2}$ , given  $\phi_{t1} \neq \phi_{c1}$  and  $p_{t2} \neq p_{c2}$  but every other set of parameters is equal, is computed from the table

|          |                   |
|----------|-------------------|
| $r_{t2}$ | $R_{t2} - r_{t2}$ |
| $r_{c2}$ | $R_{c2} - r_{c2}$ |

If this test does not reject (and the remaining components of TEST 1 do not reject), we conclude that model  $H_{2p}$  adequately describes the data. Thus, in this case, one has shown a treatment effect on both  $\phi_1$  and on  $p_2$ . This result is conceivable in fisheries experiments, although it has never been tested. Even if  $H_{2p}$  is the model selected, the best estimator of the treatment effect on survival is still  $\hat{S} = \hat{\phi}_{t1}/\hat{\phi}_{c1}$ ; but now the estimators of  $\phi_{t1}$  and  $\phi_{c1}$  are those computed under model  $H_{2p}$ , not those from model  $H_{1\phi}$ .

#### 2.4.10. Comprehensive Example

In Chapter 1.3 we introduced our general numerical (simulated) example data set. That example has  $k = 6$  and the true model is  $H_{1\phi}$ ; Table 1.2 gives the values of the parameters. For the complete capture history protocol, the data one will start from, for data analysis, will be either the capture history matrix (such as that shown in Table 1.1) or the set of full  $m$ -arrays (see Tables 1.3 and 1.4). For the analysis of these example data when RELEASE is used, the input form is the capture history matrix, as shown in Table 1.1; 22 pages of output are then generated. The first page of output (see Table 2.16) gives various data summaries. TEST 3 is then computed and summarized (Tables 2.17 and 2.18), followed by TEST 2 (Tables 2.19 and 2.20). The rest of the output consists of an analysis under each possible model and the corresponding between-model test components of TEST 1 (Tables 2.21-2.23). The first model presented is  $H_{k-1,\phi}$ , followed sequentially by models where more of the parameters have common values. Thus, model  $H_0$  is the last model considered.

Not all 22 pages of output are presented here. The interested reader is encouraged to obtain RELEASE (which comes with these example data) and to run these data and other analyses as an integral part of learning the methods discussed in this monograph. The summary page (Table 2.16) gives the data as  $m$ -arrays, by group, and the summary statistics  $R$ ,  $r$ ,  $m$ , and  $z$ . Note also that RELEASE recognizes that all capture histories start with a one (1), i.e., no new fish were released after dam 1. Accordingly, adjustments to TEST 3 are made automatically. RELEASE will also handle Jolly-Seber data involving new releases as well as releases of previously marked animals at each occasion.

Table 2.17 shows all the components computable here for TEST 3 for the treatment group (group 1). This same set of tests is repeated for controls (group 2). The format is to print the test name, the corresponding table, and the test result. As part of the (usually)  $2 \times 2$  tables, the data are shown as well as the expected cell values (under the null hypothesis) and, for each cell, the value of  $(O - E)^2/E$ , which is labeled as "C." This pattern is used by RELEASE for all chi-square contingency table tests.

All components of TEST 3 are summarized in Table 2.18. For example, the three separate chi-squares for TESTs 3.SR3, 3.SR4, and 3.SR5 for group 1 sum to 0.7845; this summation constitutes TEST 3.SR. None of the test components here lead to rejection of the (general) null hypothesis that recapture probabilities are independent of capture history at time of release. The overall result for TEST 3 is a chi-square value of 3.9387 with 10 df; this result is not statistically significant. Thus, based on the goodness of fit information for TEST 3, the Jolly-Seber model would not be rejected for these data.

## PART 2. PROTOCOLS FOR STUDIES

Table 2.16. - Summary output from RELEASE for the general numerical example under the complete capture history protocol.

---

| Observed Recaptures for Group 1 |       |        |      |      |     |     |      |
|---------------------------------|-------|--------|------|------|-----|-----|------|
| Treatment group                 |       |        |      |      |     |     |      |
| i                               | R(i)  | m(i,j) |      |      |     |     | r(i) |
|                                 |       | j = 2  | 3    | 4    | 5   | 6   |      |
| 1                               | 30000 | 1029   | 238  | 1669 | 549 | 590 | 4075 |
| 2                               | 1000  |        | 11   | 73   | 17  | 27  | 128  |
| 3                               | 235   |        |      | 20   | 7   | 5   | 32   |
| 4                               | 1677  |        |      |      | 43  | 50  | 93   |
| 5                               | 590   |        |      |      |     | 19  | 19   |
| m(j)                            |       | 1029   | 249  | 1762 | 616 | 691 |      |
| z(j)                            |       | 3046   | 2925 | 1195 | 672 | 0   |      |

  

| Observed Recaptures for Group 2 |       |        |      |      |     |     |      |
|---------------------------------|-------|--------|------|------|-----|-----|------|
| Control group                   |       |        |      |      |     |     |      |
| i                               | R(i)  | m(i,j) |      |      |     |     | r(i) |
|                                 |       | j = 2  | 3    | 4    | 5   | 6   |      |
| 1                               | 29000 | 1104   | 247  | 1832 | 571 | 641 | 4395 |
| 2                               | 1071  |        | 13   | 75   | 19  | 29  | 136  |
| 3                               | 250   |        |      | 17   | 4   | 10  | 31   |
| 4                               | 1862  |        |      |      | 50  | 52  | 102  |
| 5                               | 616   |        |      |      |     | 26  | 26   |
| m(j)                            |       | 1104   | 260  | 1924 | 644 | 758 |      |
| z(j)                            |       | 3291   | 3167 | 1274 | 732 | 0   |      |

  

| Sums for the above Groups |       |      |      |      |      |      |  |
|---------------------------|-------|------|------|------|------|------|--|
| m.                        | 0     | 2133 | 509  | 3686 | 1260 | 1449 |  |
| z.                        | 0     | 6337 | 6092 | 2469 | 1404 |      |  |
| R.                        | 59000 | 2071 | 485  | 3539 | 1206 |      |  |
| r.                        | 8470  | 264  | 63   | 195  | 45   |      |  |

---

Data type is Complete Capture Histories.

All capture histories have a 1 for occasion 1, so tests will ignore this initial release.

---

TEST 2 contributes additional, independent goodness of fit (to Jolly-Seber) information. These tests are based on the cohort data summarized in the *m*-array representation of the data.

Table 2.17. - Results of TEST 3 (goodness of fit) applied to group 1 (treatment) data for the complete capture history protocol data of the general numerical example.

Goodness of fit test of seen before vs. not seen before  
against seen again vs. not seen again by capture occasions.

Test for Group 1  
Treatment Group

TEST 3.SR3: Animals captured on occasion 3

|   |     |     |    |
|---|-----|-----|----|
| O | 1   | 10  | 11 |
| E | 1.4 | 9.6 |    |
| C | 0.1 | 0.0 |    |

  

|   |      |       |     |
|---|------|-------|-----|
| O | 31   | 193   | 224 |
| E | 30.6 | 193.5 |     |
| C | 0.0  | 0.0   |     |

  

|  |    |     |     |
|--|----|-----|-----|
|  | 32 | 205 | 235 |
|--|----|-----|-----|

Chi-square=0.2010 (df=1) P=0.6539  
Fisher's Exact Test P=1.0000

\*\* WARNING \*\* One or more expected values were < 2.0.

TEST 3.SR4: Animals captured on occasion 4

|   |     |      |    |
|---|-----|------|----|
| O | 5   | 84   | 89 |
| E | 4.9 | 84.1 |    |
| C | 0.0 | 0.0  |    |

  

|   |      |        |      |
|---|------|--------|------|
| O | 88   | 1500   | 1588 |
| E | 88.1 | 1580.9 |      |
| C | 0.0  | 0.0    |      |

  

|  |    |      |      |
|--|----|------|------|
|  | 93 | 1584 | 1677 |
|--|----|------|------|

Chi-square=0.0009 (df=1) P=0.9755  
Fisher's Exact Test P=1.0000

Table 2.17. - Continued.

TEST 3.SR5: Animals captured on occasion 5

```

+-----+-----+
O|  1 | 63 | 64
E| 2.1| 61.9|
C| 0.5|  0.0|
+-----+-----+
O| 18 | 508 | 526
E| 16.9| 509.1|
C|  0.1|  0.0|
+-----+-----+
          19   571   590
    
```

Chi-square=0.6331 (df=1) P=0.4262

Fisher's Exact Test P=0.5098

Cumulative result of TEST 3.SR over occasions for group 1

Chi-square= 0.8350 (df=3) P= 0.8411

Goodness of Fit Test of seen before versus not seen before  
against when next seen again by capture occasions.

Test for Group 1  
Treatment Group

TEST 3.Sm3: Animals captured on occasion 3

```

+-----+-----+
O| 19 | 12 | 31
E| 19.4| 11.6|
C|  0.0|  0.0|
+-----+-----+
O|  1 |  0 |  1
E|  0.6|  0.4|
C|  0.2|  0.4|
+-----+-----+
          20   12   32
    
```

Chi-square=0.6194 (df=1) P=0.4313

Fisher's Exact Test P=0.1000

\*\* WARNING \*\* One or more expected values were < 2.0.

Table 2.17. - Continued.

---

TEST 3.Sm4: Animals captured on occasion 4

|               |      |      |    |
|---------------|------|------|----|
| +-----+-----+ |      |      |    |
| O             | 40   | 48   | 88 |
| E             | 40.7 | 47.3 |    |
| C             | 0.0  | 0.0  |    |
| +-----+-----+ |      |      |    |
| O             | 3    | 2    | 5  |
| E             | 2.3  | 2.7  |    |
| C             | 0.2  | 0.2  |    |
| +-----+-----+ |      |      |    |
|               | 43   | 50   | 93 |

Chi-square=0.4027 (df=1) P=0.5257  
Fisher's Exact Test P=0.6595

Cumulative result of TEST 3.Sm over occasions for group 1  
Chi-square=1.0220 (df=2) P=0.5999

---

Table 2.18. - Summary of TEST 3 (goodness of fit) results for the complete capture history example data.

---

| Summary of TEST 3 (Goodness of fit) Results |           |            |    |         |                 |
|---|-----------|------------|----|---------|-----------------|
| Group 1                                     | Component | Chi-square | df | P-level | Sufficient Data |
| -----                                       |           |            |    |         |                 |
| 1   | 3.SR3     | 0.2010     | 1  | 0.6539  | No              |
| 1   | 3.SR4     | 0.0009     | 1  | 0.9755  | Yes             |
| 1   | 3.SR5     | 0.6331     | 1  | 0.4262  | Yes             |
| Group 1                                     | 3.SR      | 0.8350     | 3  | 0.8411  |                 |
| 1   | 3.Sm3     | 0.6194     | 1  | 0.4313  | No              |
| 1   | 3.Sm4     | 0.4027     | 1  | 0.5257  | Yes             |
| Group 1                                     | 3.Sm      | 1.0220     | 2  | 0.5999  |                 |
| Group 1                                     | TEST 3    | 1.8570     | 5  | 0.8686  |                 |
| 2   | 3.SR3     | 0.2798     | 1  | 0.5968  | No              |
| 2   | 3.SR4     | 0.0128     | 1  | 0.9100  | Yes             |
| 2   | 3.SR5     | 0.3633     | 1  | 0.5467  | Yes             |

Table 2.18. - Continued.

|            |        |        |    |        |     |
|------------|--------|--------|----|--------|-----|
| Group 2    | 3.SR   | 0.6558 | 3  | 0.8835 |     |
| 2          | 3.Sm3  | 1.2548 | 1  | 0.2626 | No  |
| 2          | 3.Sm4  | 0.1712 | 1  | 0.6791 | Yes |
| Group 2    | 3.Sm   | 1.4259 | 2  | 0.4902 |     |
| Group 2    | TEST 3 | 2.0817 | 5  | 0.8377 |     |
| All Groups | TEST 3 | 3.9387 | 10 | 0.9501 |     |

Table 2.19 presents results of TEST 2 for group 1. Each component of the overall test is presented (by group), followed by a summary table of results (see Table 2.20). The overall goodness of fit test statistic (to the Jolly-Seber model) is shown in Table 2.20:  $\chi^2 = 11.10$  with 22 df; it is not significant. This nonsignificance provides the evidence that our general assumption about parameters being only time-specific is plausible; thus we can confidently proceed to select a model (i.e., evaluate the treatment effect).

Table 2.19. - Results of TEST 2 (goodness of fit) applied to group 1 (treatment) data for the complete capture history protocol data of the general numerical example.

Goodness of fit test of recaptures partitioned by rows.

Test for Group 1  
Treatment Group

TEST 2.C2: Test of row 1 vs. row 2

|   |       |        |       |       |      |
|---|-------|--------|-------|-------|------|
| O | 238   | 1669   | 549   | 590   | 3046 |
| E | 239.0 | 1671.7 | 543.2 | 592.1 |      |
| C | 0.0   | 0.0    | 0.1   | 0.0   |      |
| O | 11    | 73     | 17    | 27    | 128  |
| E | 10.0  | 70.3   | 22.8  | 24.9  |      |
| C | 0.1   | 0.1    | 1.5   | 0.2   |      |
|   | 249   | 1742   | 566   | 617   | 3174 |

Chi-square=1.9445 (df=3) P= 0.5840

Table 2.19. - Continued.

TEST 2.C3: Test of rows 1-2 vs. row 3

```

+-----+-----+-----+
O|1742 | 566 | 617 |2925
E|1742.9| 566.8| 615.3|
C| 0.0| 0.0| 0.0|
+-----+-----+-----+
O| 20 | 7 | 5 | 32
E| 19.1| 6.2| 6.7|
C| 0.0| 0.1| 0.4|
+-----+-----+-----+

```

1762 573 622 2957

Chi-square= 0.6003 (df=2) P= 0.7407

TEST 2.C4: Test of rows 1-3 vs. row 4

```

+-----+-----+
O| 573 | 622 |1195
E| 571.5| 623.5|
C| 0.0| 0.0|
+-----+-----+
O| 43 | 50 | 93
E| 44.5| 48.5|
C| 0.0| 0.0|
+-----+-----+

```

616 672 1288

Chi-square= 0.1015 (df=1) P= 0.7500



Table 2.20. - Summary of TEST 2 and overall goodness of fit results for the complete capture history example data.

| Summary of TEST 2 (Goodness of fit) Results |           |            |    |         |                 |
|---|-----------|------------|----|---------|-----------------|
| Group                                       | Component | Chi-square | df | P-level | Sufficient Data |
| 1   | 2.C2      | 1.9445     | 3  | 0.5840  | Yes             |
| 1   | 2.C3      | 0.6003     | 2  | 0.7407  | Yes             |
| 1   | 2.C4      | 0.1015     | 1  | 0.7500  | Yes             |
| Group 1 TEST 2                              |           | 2.6463     | 6  | 0.8518  |                 |
| 2   | 2.C2      | 1.8265     | 3  | 0.6092  | Yes             |
| 2   | 2.C3      | 2.4691     | 2  | 0.2910  | Yes             |
| 2   | 2.C4      | 0.2175     | 1  | 0.6409  | Yes             |
| Group 2 TEST 2                              |           | 4.5131     | 6  | 0.6076  |                 |
| All Groups TEST 2                           |           | 7.1594     | 12 | 0.8469  |                 |

## Goodness of Fit Results (TEST 2 + TEST 3) by Group

| Group | Chi-square | df | P-level |
|-------|------------|----|---------|
| 1     | 4.5033     | 11 | 0.9528  |
| 2     | 6.5949     | 11 | 0.8309  |
| Total | 11.0981    | 22 | 0.9733  |

Results for model  $H_{5\phi}$  are shown in Table 2.21. In general, for any model, RELEASE presents the parameter estimates that differ by group, and then estimates of parameters that are the same for all groups. There are no parameters common to both groups for model  $H_{k-1,\phi}$  ( $H_{5\phi}$  in this case). In addition to the  $\hat{\phi}$  and  $\hat{p}$ , the ratios  $\hat{S}_j = \hat{\phi}_{tj}/\hat{\phi}_{cj}$  are shown along with these standard errors. For example, from Table 2.21,  $\hat{S}_4$  is denoted as  $S(1,2,PHI(4))$ ; thus, this  $\hat{S}_4$  is the ratio  $\hat{\phi}_{14}/\hat{\phi}_{24}$ . From other places in the output we know that  $v = 1$  corresponds to treatment and  $v = 2$  corresponds to control. Note how the standard errors of  $\hat{S}_2$  to  $\hat{S}_4$  increase substantially over  $\hat{se}(\hat{S}_1)$ . The true  $S (= S_1)$  is 0.9; however, if separate Jolly-Seber models were used as the basis of the inference, one would conclude that there was no treatment effect on survival (e.g., the 95% CI on  $S$  under model  $H_{5\phi}$  is 0.69 to 1.08).

RELEASE also prints out some of the sampling correlations between estimates. Within a treatment group, for example,  $\text{Corr}(\text{Phi}(1), \text{Phi}(2))$  denotes the estimated sampling correlation of  $\hat{\phi}_{v1}$  and  $\hat{\phi}_{v2}$ . From Table 2.21, this correlation is -0.443444 for the treatment group. Correlations are also given between pairs of values for  $\hat{\phi}_i$  and  $\hat{\phi}_{ci}$ ; these correlations are relevant in obtaining variances and correlations of  $\hat{S}_i$ .  $\text{Corr}(1,2, \text{Phi}(1))$  denotes the sampling correlation of  $\hat{\phi}_{1i}$  and  $\hat{\phi}_{2i}$ ; again we will know from the output which one (i.e., 1 or 2) is treatment and which is control. Under model  $H_{k-1,\phi}$  all these correlations are zero.

Table 2.21. - Estimates of parameters under model  $H_{\phi}$  for the complete capture history protocol data of the general numerical example.

| Maximum Likelihood Estimates under Model H5Phi |          |                |                          |          |
|--|----------|----------------|--------------------------|----------|
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| -----  |          |                |                          |          |
| Estimates for Group 1                          |          |                |                          |          |
| Treatment Group                                |          |                |                          |          |
| Phi(1)   | 0.827529 | 0.066869       | 0.696467                 | 0.958591 |
| Phi(2)   | 0.876299 | 0.159697       | 0.563292                 | 1.189305 |
| Phi(3)   | 1.073454 | 0.203826       | 0.673955                 | 1.472952 |
| Phi(4)   | 0.924989 | 0.224379       | 0.485205                 | 1.364772 |
| p(2)   | 0.041449 | 0.003579       | 0.034435                 | 0.048463 |
| p(3)   | 0.011459 | 0.002006       | 0.007528                 | 0.015390 |
| p(4)   | 0.075588 | 0.007513       | 0.060863                 | 0.090314 |
| p(5)   | 0.028673 | 0.006475       | 0.015983                 | 0.041364 |
| Phi(5)p(6)                                     | 0.032203 | 0.007268       | 0.017958                 | 0.046449 |
| Corr(Phi(1),Phi(2))                            |          | -0.443444      |                          |          |
| Corr(Phi(2),Phi(3))                            |          | -0.771173      |                          |          |
| Corr(Phi(3),Phi(4))                            |          | -0.203837      |                          |          |
| Estimates for Group 2                          |          |                |                          |          |
| Control Group                                  |          |                |                          |          |
| Phi(1)   | 0.931746 | 0.073081       | 0.788507                 | 1.074984 |
| Phi(2)   | 0.956006 | 0.176612       | 0.609846                 | 1.302165 |
| Phi(3)   | 0.976364 | 0.186592       | 0.610643                 | 1.342085 |
| Phi(4)   | 0.716070 | 0.150306       | 0.421470                 | 1.010669 |
| p(2)   | 0.040858 | 0.003423       | 0.034149                 | 0.047566 |
| p(3)   | 0.010077 | 0.001796       | 0.006557                 | 0.013598 |
| p(4)   | 0.076408 | 0.007256       | 0.062186                 | 0.090629 |
| p(5)   | 0.035804 | 0.006883       | 0.022313                 | 0.049296 |
| Phi(5)p(6)                                     | 0.042208 | 0.008101       | 0.026330                 | 0.058086 |
| Corr(Phi(1),Phi(2))                            |          | -0.424913      |                          |          |
| Corr(Phi(2),Phi(3))                            |          | -0.792323      |                          |          |
| Corr(Phi(3),Phi(4))                            |          | -0.213359      |                          |          |
| Ratio of Survivals between Groups              |          |                |                          |          |
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| -----  |          |                |                          |          |
| S(1,2,Phi(1))                                  | 0.888149 | 0.100016       | 0.692118                 | 1.084181 |
| Corr(1,2,Phi(1))                               |          | 0.000000       |                          |          |
| S(1,2,Phi(2))                                  | 0.916625 | 0.237864       | 0.450411                 | 1.382839 |

Table 2.21. - Continued.

|  |  |          |          |          |          |
|--|--|----------|----------|----------|----------|
|  | Corr(1,2,Phi(2))                                       | 0.000000 |          |          |          |
|  | S(1,2,Phi(3))  | 1.099440 | 0.296190 | 0.518908 | 1.679972 |
|  | Corr(1,2,Phi(3))                                       | 0.000000 |          |          |          |
|  | S(1,2,Phi(4))  | 1.291758 | 0.414375 | 0.479582 | 2.103934 |
|  | Corr(1,2,Phi(4))                                       | 0.000000 |          |          |          |
|  | S(i,j,Phi(I)) equals treatment effect estimated as     |          |          |          |          |
|  | Phi(I) for group i / Phi(I) for group j.               |          |          |          |          |
|  | Corr(i,j,Phi(I)) equals estimated sampling correlation |          |          |          |          |
|  | between Phi(I) for group i and Phi(I) for group j.     |          |          |          |          |

Table 2.22 shows the results for models  $H_{2p}$ ,  $H_{1\phi}$ , and  $H_0$  along with TEST 1 components 1.R2, 1.T2, and 1.R1. The same pattern of presenting models separated by the TEST 1 component that tests between them is used for the other models not illustrated here. At the end of the output regarding models, RELEASE gives a summary of TEST 1 (Table 2.23). The strategy for examining this output should be to confirm goodness of fit, then scan the summary of TEST 1 to see if one of the models in the sequence is acceptable (the most appropriate model might not be). From Table 2.23, only TEST 1.R1 leads to rejection. The null hypothesis rejected is that model  $H_0$  fits the data. None of the other TEST 1 components (nor the sum of 1.T2 through 1.R5) reject. Consequently, the appropriate model for these data is judged to be  $H_{1\phi}$ . Given that decision, one can proceed to the results for model  $H_{1\phi}$  (in Table 2.22).

Table 2.22. - Estimates of parameters for model  $H_{2p}$ ,  $H_{1\phi}$ , and  $H_0$  and some test components for the complete capture history protocol data of the general numerical example.

TEST 1.R2: Test of Phi(2) equal across groups,  
 assuming higher order parameters are equal across groups.

```

+-----+-----+
O| 128 | 872 |1000
E| 127.5| 872.5|
C|  0.0|  0.0|
+-----+-----+
O| 136 | 935 |1071
E| 136.5| 934.5|
C|  0.0|  0.0|
+-----+-----+
264  1807  2071
    
```

Chi-square=0.0048 (df=1) P=0.9448

Table 2.22. - Continued.

| Maximum Likelihood Estimates under Model H2p |          |                |                          |          |
|--|----------|----------------|--------------------------|----------|
| Parameter                                    | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| Estimates for Group 1                        |          |                |                          |          |
| Treatment Group                              |          |                |                          |          |
| Phi(1)                                       | 0.830798 | 0.047782       | 0.737145                 | 0.924452 |
| p(2)   | 0.041286 | 0.002686       | 0.036021                 | 0.046550 |
| Corr(Phi(1),Phi(2))                          |          | -0.424661      |                          |          |
| Estimates for Group 2                        |          |                |                          |          |
| Control Group                                |          |                |                          |          |
| Phi(1)                                       | 0.928307 | 0.053214       | 0.824008                 | 1.032606 |
| p(2)   | 0.041009 | 0.002642       | 0.035830                 | 0.046188 |
| Corr(Phi(1),Phi(2))                          |          | -0.426192      |                          |          |
| Estimates for Pooled Groups                  |          |                |                          |          |
| Phi(2)                                       | 0.915510 | 0.118772       | 0.682718                 | 1.148303 |
| Phi(3)                                       | 1.023456 | 0.137818       | 0.753334                 | 1.293579 |
| Phi(4)                                       | 0.804316 | 0.127598       | 0.554224                 | 1.054407 |
| p(3)   | 0.010737 | 0.001341       | 0.008108                 | 0.013365 |
| p(4)   | 0.076008 | 0.005219       | 0.065779                 | 0.086236 |
| p(5)   | 0.032401 | 0.004744       | 0.023103                 | 0.041700 |
| Phi(5)p(6)                                   | 0.037313 | 0.005458       | 0.026617                 | 0.048010 |
| Corr(Phi(2),Phi(3))                          |          | -0.782090      |                          |          |
| Corr(Phi(3),Phi(4))                          |          | -0.209588      |                          |          |
| Ratio of Survivals between Groups            |          |                |                          |          |
| Parameter                                    | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| S(1,2,Phi(1))                                | 0.894961 | 0.020341       | 0.855093                 | 0.934829 |
| Corr(1,2,Phi(1))                             |          | 0.921665       |                          |          |

Table 2.22. - Continued.

TEST 1.T2: Test of p(2) equal across groups,  
 assuming higher order parameters are equal across groups.

```

+-----+-----+
O|1029 |3046 |4075
E|1026.2|3048.8|
C| 0.0| 0.0|
+-----+-----+
O|1104 |3291 |4395
E|1106.8|3288.2|
C| 0.0| 0.0|
+-----+-----+
2133 6337 8470
    
```

Chi-square=0.0196 (df=1) P=0.8887

| Maximum Likelihood Estimates under Model H1Phi |          |                |                          |          |
|--|----------|----------------|--------------------------|----------|
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| Estimates for Group 1                          |          |                |                          |          |
| Treatment Group                                |          |                |                          |          |
| Phi(1)   | 0.831435 | 0.047607       | 0.738126                 | 0.924745 |
| Corr(Phi(1),Phi(2))                            |          | -0.426617      |                          |          |
| Estimates for Group 2                          |          |                |                          |          |
| Control Group                                  |          |                |                          |          |
| Phi(1)   | 0.927648 | 0.052962       | 0.823843                 | 1.031452 |
| Corr(Phi(1),Phi(2))                            |          | -0.427860      |                          |          |
| Estimates for Pooled Groups                    |          |                |                          |          |
| Phi(2)   | 0.915510 | 0.118772       | 0.682718                 | 1.148303 |
| Phi(3)   | 1.023456 | 0.137818       | 0.753334                 | 1.293579 |
| Phi(4)   | 0.804316 | 0.127598       | 0.554224                 | 1.054407 |
| p(2)   | 0.041142 | 0.002474       | 0.036294                 | 0.045990 |
| p(3)   | 0.010737 | 0.001341       | 0.008108                 | 0.013365 |
| p(4)   | 0.076008 | 0.005219       | 0.065779                 | 0.086236 |
| p(5)   | 0.032401 | 0.004744       | 0.023103                 | 0.041700 |
| Phi(5)p(6)                                     | 0.037313 | 0.005458       | 0.026617                 | 0.048010 |
| Corr(Phi(2),Phi(3))                            |          | -0.782090      |                          |          |
| Corr(Phi(3),Phi(4))                            |          | -0.209588      |                          |          |

Table 2.22. - Continued.

| Ratio of Survivals between Groups |          |                |                          |          |
|-----------------------------------|----------|----------------|--------------------------|----------|
| Parameter                         | Estimate | Standard Error | 95% Confidence Intervals |          |
|                                   |          |                | Lower                    | Upper    |
| S(1,2,Phi(1))                     | 0.896284 | 0.018040       | 0.860925                 | 0.931642 |
| Corr(1,2,Phi(1))                  |          | 0.938042       |                          |          |

TEST 1.R1: Test of Phi(1) equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O| 4075 |25925 |30000
E| 4307. |25693. |
C| 12.5| 2.1|
+-----+-----+
O| 4395 |24605 |29000
E| 4163. |24837. |
C| 12.9| 2.2|
+-----+-----+

```

8470 50530 59000  
Chi-square=29.6316 (df=1) P=0.0000

| Maximum Likelihood Estimates under Model H0 |          |                |                          |          |
|---|----------|----------------|--------------------------|----------|
| Parameter                                   | Estimate | Standard Error | 95% Confidence Intervals |          |
|   |          |                | Lower                    | Upper    |
| Estimates for Pooled Groups                 |          |                |                          |          |
| Phi(1)                                      | 0.878726 | 0.049456       | 0.781793                 | 0.975660 |
| Phi(2)                                      | 0.915510 | 0.118772       | 0.682718                 | 1.148303 |
| Phi(3)                                      | 1.023456 | 0.137818       | 0.753334                 | 1.293579 |
| Phi(4)                                      | 0.804316 | 0.127598       | 0.554224                 | 1.054407 |
| p(2)  | 0.041142 | 0.002474       | 0.036294                 | 0.045990 |
| p(3)  | 0.010737 | 0.001341       | 0.008108                 | 0.013365 |
| p(4)  | 0.076008 | 0.005219       | 0.065779                 | 0.086236 |
| p(5)  | 0.032401 | 0.004744       | 0.023103                 | 0.041700 |
| Phi(5)p(6)                                  | 0.037313 | 0.005458       | 0.026617                 | 0.048010 |
| Corr(Phi(1),Phi(2))                         |          | -0.434024      |                          |          |
| Corr(Phi(2),Phi(3))                         |          | -0.782090      |                          |          |
| Corr(Phi(3),Phi(4))                         |          | -0.209588      |                          |          |

Table 2.22. - Continued.

---

TEST 1: Overall test of  $H_0$  vs.  $H_{5\Phi}$   
 Chi-square=31.3078 (df=9)  $P=0.0003$   
 TEST 1 is an omnibus test for a treatment effect(s),  
 i.e., significant differences between groups. For the  
 complete capture history protocol and scheme A partial  
 capture history protocol, TEST 1 is an overall test of  
 equality of all survival and capture probabilities  
 among groups.

---

Table 2.23. - Summary of TEST 1 (model selection) results for the data from the complete capture history example.

| TEST   | Chi-square | df | P     |
|--------|------------|----|-------|
| 1.R5   | 0.84       | 1  | 0.360 |
| 1.75   | 0.28       | 1  | 0.607 |
| 1.R4   | 0.01       | 1  | 0.930 |
| 1.74   | 0.21       | 1  | 0.646 |
| 1.R3   | 0.16       | 1  | 0.690 |
| 1.73   | 0.15       | 1  | 0.694 |
| 1.R2   | 0.01       | 1  | 0.945 |
| 1.72   | 0.02       | 1  | 0.889 |
| 1.R1   | 29.63      | 1  | 0.001 |
| TEST 1 | 31.3078    | 9  | 0.001 |

Because the data were simulated under model  $H_{1\phi}$ , we consider the model  $H_{1\phi}$  output in Table 2.22 in some detail. The output for the other models is similar. Notice that treatment and control survival estimates for the first period are  $\hat{\phi}_{t1} = 0.8314$  and  $\hat{\phi}_{c1} = 0.9276$ , which are the only estimates allowed to differ for the treatment and control groups under this model. The standard errors and confidence limits are also given for these estimates. The coefficients of variation are  $0.0476/0.8314 = 0.06$  and  $0.0530/0.9276 = 0.06$  for treatment and control groups, respectively. These coefficients of variation indicate that the estimates are relatively precise. The other survival estimates ( $\hat{\phi}_{v2}$ ,  $\hat{\phi}_{v3}$ ,  $\hat{\phi}_{v4}$ ) are relatively less precise (coefficients of variation are about 0.12 to 0.14). The capture probability estimates are also presented; for example,  $\hat{p}_2 = 0.0411$  ( $\hat{se} = 0.00247$ ).

Perhaps the most important estimate presented is the treatment survival rate,

$$\hat{S} = \frac{\hat{\phi}_{t1}}{\hat{\phi}_{c1}} = \frac{0.8314}{0.9276}$$

$$= 0.896$$

(denoted  $S(1,2,Phi(1))$ , with  $\hat{se}(\hat{S}) = 0.01804$ . The 95% CI on  $S$  is 0.861 to 0.932. Recall that when model  $H_{5\phi}$  is used, the standard error of the corresponding  $\hat{S}$  is 0.10. The use of a parsimonious model has allowed us to say definitely that there is a treatment effect (either from TEST 1.R1 or the CI on  $\hat{S}$ ).

Note again the meaning of some of the output:  $Corr(Phi(1),Phi(2))$  is the sampling correlation of  $\hat{\phi}_{v1}$  with either  $\hat{\phi}_{v2}$ , e.g., under model  $H_{5\phi}$ , or with  $\hat{\phi}_2$ , e.g., under models  $H_{2p}$  and  $H_{1\phi}$  where  $\phi_{v1}$  varies by group, but  $\phi_2$  is the same for both groups. For example, under model  $H_{2p}$  the sampling correlation of  $\hat{\phi}_{t1}$  and  $\hat{\phi}_2$  is -0.4247. Under  $H_{2p}$  the sampling correlation of  $\hat{\phi}_3$  and  $\hat{\phi}_4$  is -0.2096, this quantity being denoted by  $Corr(Phi(3),Phi(4))$ . Also of interest are the correlations of  $\hat{\phi}_i$  and  $\hat{\phi}_{ci}$  for any  $i$  where these survivals are allowed to differ. In Table 2.22,  $t$  and  $c$  are indexed as 1 and 2, respectively. Under model  $H_{2p}$ , the correlation of  $\hat{\phi}_{t1}$  and  $\hat{\phi}_{c1}$  is denoted as  $Corr(1,2,Phi(1))$  and equals 0.9217. Under model  $H_{1\phi}$  the same correlation is 0.9380. It is largely this strong, positive correlation that makes  $\hat{S} = \hat{\phi}_{t1}/\hat{\phi}_{c1}$  so precise under these two models (a standard error of around 0.02 as compared to  $se(S) = 0.1$  when model  $H_{5\phi}$  is used).

#### 2.4.11. Likelihood Function for Models $H_{k-1,\phi}$ , $H_{2p}$ , $H_{1\phi}$

Our philosophy in writing this monograph is to present the theory along with the applied results. Moreover, it is important that all users have a basic understanding of the nature of the underlying theory. First, a sound theory must exist for survival experiments based on animal release-recapture, and second, the theory must be based on specific assumptions and subsequent probability models for the experimental data. Although the full mathematical details may extend beyond the training of some biologists, advanced training in quantitative methods is becoming increasingly common. Consequently, we include a section that gives the probability model formulae (likelihoods) for several models discussed in Chapter 2.4.

For a one-group Jolly-Seber study, the probability distribution of the number of fish recaptured,  $r_i$ , from those released,  $R_i$ , at occasion  $i$  is the binomial distribution



$$\Pr\{r_i | R_i\} = \binom{R_i}{r_i} (\lambda_i)^{r_i} (1 - \lambda_i)^{R_i - r_i}, \quad i = 1, \dots, k - 1,$$

$$\lambda_i = E(r_i | R_i)/R_i \text{ [or } \lambda_i = \phi_i(p_{i+1} + q_{i+1}\lambda_{i+1})].$$

Similarly, one can consider the (marginal) probability distribution of  $m_i$  given  $T_i = m_i + z_i$ ; it also is binomial:

$$\Pr\{m_i | T_i\} = \binom{T_i}{m_i} (\tau_i)^{m_i} (1 - \tau_i)^{T_i - m_i}, \quad i = 2, \dots, k - 1,$$

where  $\tau_i = E(m_i | T_i)/T_i$ , or  $\tau_i = p_i/(p_i + q_i\lambda_i)$ .

It has been proved (e.g., Brownie and Robson 1983) that the MSS (for estimating the  $\phi$  and  $p$ ) is representable as  $r_i$  given  $R_i$ ,  $i = 1, \dots, k - 1$  and  $m_i$  given  $T_i$ ,  $i = 2, \dots, k - 1$ , and that this conditioning on  $R_i$  and  $T_i$  renders these binomial distributions conditionally independent. This means that for a one-group Jolly-Seber release-recapture study the probability distribution of the MSS is given as the products of  $2k - 3$  independent binomial distributions:

$$\Pr\{\text{MSS}\} = \left[ \prod_{i=1}^{k-1} \binom{R_i}{r_i} (\lambda_i)^{r_i} (1 - \lambda_i)^{R_i - r_i} \right] \left[ \prod_{i=2}^{k-1} \binom{T_i}{m_i} (\tau_i)^{m_i} (1 - \tau_i)^{T_i - m_i} \right].$$

The above formula is the likelihood function for such a study; this probability distribution is the basis for ML inferences about survival rates from Jolly-Seber data.

For model  $H_{k-1, \phi}$ , no parameters are in common across the two experimental groups. As a consequence, it follows that the likelihood function for model  $H_{k-1, \phi}$  can be written as

$$\Pr\{\text{MSS} | \text{model } H_{k-1, \phi}\} = \left[ \prod_{i=1}^{k-1} \binom{R_{t i}}{r_{t i}} (\lambda_{t i})^{r_{t i}} (1 - \lambda_{t i})^{R_{t i} - r_{t i}} \right] \left[ \prod_{i=2}^{k-1} \binom{T_{t i}}{m_{t i}} (\tau_{t i})^{m_{t i}} (1 - \tau_{t i})^{T_{t i} - m_{t i}} \right] \\ \times \left[ \prod_{i=1}^{k-1} \binom{R_{c i}}{r_{c i}} (\lambda_{c i})^{r_{c i}} (1 - \lambda_{c i})^{R_{c i} - r_{c i}} \right] \left[ \prod_{i=2}^{k-1} \binom{T_{c i}}{m_{c i}} (\tau_{c i})^{m_{c i}} (1 - \tau_{c i})^{T_{c i} - m_{c i}} \right].$$

As we proceed to more specialized models in the sequence considered here, terms in the above products collapse into single terms as we pool over various statistics.

The likelihood (i.e., probability distribution) for the MSS under model  $H_{2p}$  is

$$\begin{aligned} \Pr\{\text{MSS} \mid \text{model } H_{2p}\} &= \left[ \binom{R_{t1}}{r_{t1}} (\lambda_{t1})^{r_{t1}} (1 - \lambda_{t1})^{R_{t1} - r_{t1}} \right] \left[ \binom{T_{t2}}{m_{t2}} (\tau_{t2})^{m_{t2}} (1 - \tau_{t2})^{T_{t2} - m_{t2}} \right] \\ &\times \left[ \binom{R_{c1}}{r_{c1}} (\lambda_{c1})^{r_{c1}} (1 - \lambda_{c1})^{R_{c1} - r_{c1}} \right] \left[ \binom{T_{c2}}{m_{c2}} (\tau_{c2})^{m_{c2}} (1 - \tau_{c2})^{T_{c2} - m_{c2}} \right] \\ &\times \left[ \prod_{i=2}^{k-1} \binom{R_i}{r_i} (\lambda_i)^{r_i} (1 - \lambda_i)^{R_i - r_i} \right] \left[ \prod_{i=3}^{k-1} \binom{T_i}{m_i} (\tau_i)^{m_i} (1 - \tau_i)^{T_i - m_i} \right]. \end{aligned}$$

Bear in mind that the identifiable parameters here are  $\phi_{t1}, p_{t2}, \phi_{c1}, p_{c2}$ , and  $\phi_2, \dots, \phi_{k-2}, (\phi_{k-1}p_k), p_3, \dots, p_{k-1}$ . There are  $2k - 1$  identifiable parameters and  $2k - 1$  terms in the MSS. Basically, that is the reason one gets closed form estimators for this model. Finally, one must also know that  $\lambda_{k-1} = (\phi_{k-1}p_k)$  and

$$\lambda_i = \phi_i(p_{i+1} + q_{i+1}\lambda_{i+1}), \quad i = 2, \dots, k - 2,$$

$$\tau_i = \frac{p_i}{p_i + q_i\lambda_i}, \quad i = 3, \dots, k - 1,$$

$$\tau_{v2} = \frac{p_{v2}}{p_{v2} + q_{v2}\lambda_2}, \quad v = t, c,$$

and

$$\lambda_{v1} = \phi_{v1}(p_{v2} + q_{v2}\lambda_2), \quad v = t, c.$$

Model  $H_{1\phi}$  is developed from  $H_{2p}$  by making the added assumption that  $p_{t2} = p_{c2}$ . This results in  $\tau_{t2} = \tau_{c2}$  so that the two binomials involving  $\tau_{t2}$  and  $\tau_{c2}$  collapse to a single binomial:

$$\begin{aligned} \Pr\{\text{MSS} \mid \text{model } H_{1\phi}\} &= \left[ \binom{R_{t1}}{r_{t1}} (\lambda_{t1})^{r_{t1}} (1 - \lambda_{t1})^{R_{t1} - r_{t1}} \right] \left[ \binom{R_{c1}}{r_{c1}} (\lambda_{c1})^{r_{c1}} (1 - \lambda_{c1})^{R_{c1} - r_{c1}} \right] \\ &\times \left[ \prod_{i=2}^{k-1} \binom{R_i}{r_i} (\lambda_i)^{r_i} (1 - \lambda_i)^{R_i - r_i} \right] \left[ \prod_{i=2}^{k-1} \binom{T_i}{m_i} (\tau_i)^{m_i} (1 - \tau_i)^{T_i - m_i} \right]. \end{aligned}$$

Note that now  $\lambda_{t1} = \phi_{t1}(p_2 + q_2\lambda_2)$ ,  $\lambda_{c1} = \phi_{c1}(p_2 + q_2\lambda_2)$ .

Finally, assuming also that  $\phi_{t1} = \phi_{e1}$  (hence, assuming model  $H_0$ ), then  $\lambda_{t1} = \lambda_{e1}$  and the two terms in  $\lambda_{t1}, \lambda_{e1}$  above reduce to the single term

$$\binom{R_1}{r_1} (\lambda_1)^{r_1} (1 - \lambda_1)^{R_1 - r_1}$$

in  $\Pr\{\text{MSS} \mid \text{model } H_0\}$  (the terms in  $\lambda_2, \dots, \lambda_{k-1}$  and  $\tau_2, \dots, \tau_{k-1}$  from model  $H_{1\phi}$  remain unchanged).

## 2.5. Partial Capture Histories

### 2.5.1. Introduction

The preceding chapters describe the analysis for data arising from two different marking strategies. The most easily implemented strategy (Chapters 2.2 and 2.3) involves use of a distinguishing batch mark at the initial release site. The second strategy (Chapter 2.4) involves use of distinct marks (or of a different batch mark at each recapture site) so that individual capture histories can be followed for each animal. We have shown that this second method provides more data and information but is not a feasible strategy in many situations. In order to present a compromise between these two extremes in terms of feasibility and information loss, we here describe two other experimental protocols, called schemes A and B, and the analysis for resulting data. Both of these protocols provide information concerning second, but not third or later recaptures; thus we refer to them as providing "partial capture histories."

In both schemes A and B, an initial release is assumed in which batch marks distinguish treatment and control groups. Both involve a second batch mark and removal. They differ in that under scheme A a second batch mark, specific to the recovery site, is applied to all first recaptures, whereas under scheme B only recaptures at dam 2 receive a second mark. Also, all fish recaptured for the second time are removed under scheme A, whereas all recaptures below dam 2 are removed under scheme B.

Before describing analyses for data generated by schemes A and B, we note that there are other ways to generate partial capture history information. For example, adding a third mark would provide information about third recaptures. Schemes A and B were chosen because, provided there is no effect on survival due to handling and marking, they appear to be the most practical ways to obtain information in addition to first recaptures. Also, in studies where capture probabilities are low, they result in little loss of information relative to unique marking. Neither scheme A nor scheme B should be used if the associated handling and marking are likely to affect survival.

Notation used in this chapter is the same as in Chapter 2.4, and the assumptions and parameters on which model structure is based are the same here as in Chapter 1.4.

### 2.5.2. Scheme A

**2.5.2.1. Introduction and presentation of data.** – Upon first recapture, a fish is given a second mark specific to the site of recapture. Upon second recapture, the fish is recorded and then removed from the study population. Thus, for each fish recaptured, the occasion of its last capture (release) is known, and the quantities  $m_{ij}$  and  $m_{ci}$ ,  $i = 1$ , recapture data for scheme A is in Table 2.12.

This representation is illustrated by using data for the hypothetical example displayed in Table 2.24. Note that the first two rows of the data arrays for treatment and control groups are the same for scheme A as with unique marks (see Tables 1.5, 1.6, and 2.16). However, because fish are removed after the second recapture, releases and recoveries at dam 3 and below are fewer under scheme A. However, for this example where recapture rates are low, the differences are small.

Table 2.24. – Release-recapture data summarized as reduced  $m$ -array for the hypothetical example under scheme A protocol.

| Release site           | Releases $R_{r1}$ | Number recaptured at dam $j$ , $m_{wj}$ |     |       |     |     | Totals, $r_{t1}$ or $r_{c1}$ |
|------------------------|-------------------|---|-----|-------|-----|-----|------------------------------|
|                        |                   | $j = 2$                                 | 3   | 4     | 5   | 6   |                              |
| <b>Treatment group</b> |                   |   |     |       |     |     |                              |
| 1                      | 30,000            | 1,029                                   | 238 | 1,669 | 549 | 590 | 4,075                        |
| 2                      | 1,000             |   | 11  | 73    | 17  | 27  | 128                          |
| 3                      | 224               |   |     | 19    | 7   | 5   | 31                           |
| 4                      | 1,588             |   |     |       | 40  | 48  | 88                           |
| 5                      | 526               |   |     |       |     | 18  | 18                           |
| Totals $m_{wj}$        |                   | 1,029                                   | 249 | 1,761 | 613 | 688 |                              |
| <b>Control group</b>   |                   |   |     |       |     |     |                              |
| 1                      | 29,000            | 1,104                                   | 247 | 1,832 | 571 | 641 | 4,395                        |
| 2                      | 1,071             |   | 13  | 75    | 19  | 29  | 136                          |
| 3                      | 237               |   |     | 17    | 4   | 9   | 30                           |
| 4                      | 1,775             |   |     |       | 48  | 49  | 97                           |
| 5                      | 546               |   |     |       |     | 24  | 24                           |
| Totals $m_{cj}$        |                   | 1,104                                   | 260 | 1,924 | 642 | 752 |                              |

2.5.2.2. *Models*  $H_0, H_{1\phi}, H_{2\phi}, H_{2\phi}, \dots, H_{k-1,\phi}$  - As in the case of complete capture histories (Chapter 2.4), we consider a series of increasingly general models,  $H_0, H_{1\phi}, H_{2\phi}, H_{2\phi}, \dots, H_{k-1,\phi}$  corresponding to increasingly general assumptions regarding the equality of survival and capture probabilities for treatment and control groups. The structure of each model is represented in terms of matrices of expected values corresponding to the release-recapture data matrices. For scheme A, model structures under  $H_0, H_{1\phi}, H_{2\phi}, H_{2\phi}, \dots, H_{k-1,\phi}$  are exactly as for the complete capture history data in Table 2.2. Statistical theory underlying estimation and testing is, therefore, the same.

Estimable parameters of interest are as in Chapter 2.4 for the series of models  $H_0, H_{1\phi}, H_{2\phi}, H_{2\phi}, \dots, H_{k-1,\phi}$ . Formulae for estimators, variances, and covariances are also as in Chapter 2.4.

2.5.2.3. *Testing between models.* - To determine which model and estimators are appropriate for a given data set, we compare models in the sequence  $H_0, H_{1\phi}, H_{2\phi}, H_{2\phi}, \dots, H_{k-1,\phi}$ . This comparison is done in a certain order, starting with the most general models and progressing to tests involving simpler models, as described in Chapter 2.4 for the unique mark or complete capture history data. Theory and formulae for contingency table chi-squares are exactly as in Chapter 2.4, but actual numbers of recaptures for cohorts released at dam 3 and below are generally smaller for data collected under scheme A.

2.5.2.4. *Goodness of fit tests.* - Under scheme A, removal of all second recaptures means that each  $m_{ij}$  or  $m_{c ij}$  in a data matrix corresponds to a unique capture history. Thus, a finer partitioning of the data into subcohorts, as described in Chapter 2.1, is not possible under scheme A. Goodness of fit tests for the models in the sequence  $H_0, H_{1\phi}, H_{2\phi}, H_{2\phi}, \dots, H_{k-1,\phi}$  are therefore based on TEST 2, computed from the  $m_{ij}$ - and  $m_{c ij}$ -arrays as described in Chapter 2.1. TEST 3 does not exist.

2.5.2.5. *Comparing survival for treatment and control groups.* - Of particular concern in these studies is the comparison of survival rates, for treatment and control groups, between the release and first recovery sites. The most appropriate test for making this comparison will depend on the true underlying model, which is not known. However, the tests between models and goodness of fit tests can be used to choose the model that seems most appropriate for a given data set. The estimates  $\hat{\phi}_{t1}$  and  $\hat{\phi}_{e1}$  and variances and covariances produced when this model is used are then the basis for making inferences about either the ratio  $\phi_{t1}/\phi_{e1}$  or the difference  $\phi_{e1} - \phi_{t1}$ .

As described in Chapter 1.5, if the treatment effect is direct,  $1 - S = 1 - \phi_{t1}/\phi_{e1}$  measures treatment-related mortality, and tests or confidence intervals on  $S$  become of interest. If there is a strong, indirect treatment effect, then differences  $\phi_{ci} - \phi_{ti}$  may also be of interest as measures of that treatment effect. With replicate lots (see Part 4), empirical variances for  $\hat{S}$  or

$\hat{\phi}_{c1} - \hat{\phi}_{t1}$  can be obtained and used in constructing tests or confidence intervals for the corresponding parameters. When there is little or no replication, variances based on theoretical formulae must be used. Program RELEASE prints  $\hat{S}_i = \hat{\phi}_{ti} / \hat{\phi}_{ci}$  and the corresponding standard error and 95% CI for each model and each period for which  $\phi_{ti}$  and  $\phi_{ci}$  are estimated separately. Validity of these confidence intervals for  $S$  produced by RELEASE depends on model assumptions being correct (so that theoretical variances are appropriate) and on sample sizes being large enough to ensure that the distribution of  $\hat{S}$  is approximately normal.

Confidence intervals for the difference  $\phi_{ci} - \phi_{ti}$  are not printed by RELEASE but can be constructed as

$$(\hat{\phi}_{ci} - \hat{\phi}_{ti}) \pm z_\alpha \text{se}(\hat{\phi}_{ci} - \hat{\phi}_{ti}),$$

where

$$\text{se}(\hat{\phi}_{ci} - \hat{\phi}_{ti}) = \sqrt{\text{var}(\hat{\phi}_{ci}) + \text{var}(\hat{\phi}_{ti}) - 2\text{cov}(\hat{\phi}_{ci}, \hat{\phi}_{ti})}$$

and  $z_\alpha$  is the standard normal deviate chosen to give confidence level  $(1 - \alpha)100\%$ . The  $\text{cov}(\hat{\phi}_{ci}, \hat{\phi}_{ti}) = \hat{\text{corr}}(\hat{\phi}_{ci}, \hat{\phi}_{ti})\hat{\text{se}}(\hat{\phi}_{ci})\hat{\text{se}}(\hat{\phi}_{ti})$ , where the correlation between these two estimators is printed by RELEASE, and labeled as  $\text{Corr}(1,2,\text{Phi}(i))$ . Again, if variances and covariances produced by RELEASE are used to obtain  $\text{se}(\hat{\phi}_{ci} - \hat{\phi}_{ti})$ , the validity of the interval will depend on model assumptions being correct.

Sample output in Table 2.25 is used to illustrate construction and interpretation of these confidence intervals in Section 2.5.2.6.

**2.5.2.6. Example.** — Table 2.25 contains part of the computer printout for analysis of the data arising under scheme A for the hypothetical example. Comparison of Tables 2.25 and 2.21 shows the similarity between results for the scheme A and complete capture history protocols. As indicated before, this similarity is a result of little information being lost by failure to return second recaptures to the study population if recapture probabilities are low.

Table 2.25. - Some test summary and example output for the hypothetical sample collected under scheme A.

| Maximum Likelihood Estimates under Model H5Phi |          |                |                          |          |
|--|----------|----------------|--------------------------|----------|
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| -----  |          |                |                          |          |
| Estimates for Group 1                          |          |                |                          |          |
| Treatment Group                                |          |                |                          |          |
| Phi(1)   | 0.827529 | 0.066869       | 0.696467                 | 0.958591 |
| Phi(2)   | 0.862386 | 0.158975       | 0.550796                 | 1.173977 |
| Phi(3)   | 1.092036 | 0.211044       | 0.678390                 | 1.505681 |
| Phi(4)   | 0.872132 | 0.216818       | 0.447169                 | 1.297096 |
| p(2)   | 0.041449 | 0.003579       | 0.034435                 | 0.048463 |
| p(3)   | 0.011644 | 0.002064       | 0.007599                 | 0.015689 |
| p(4)   | 0.075497 | 0.007690       | 0.060425                 | 0.090570 |
| p(5)   | 0.030359 | 0.007014       | 0.016611                 | 0.044107 |
| Phi(5)p(6)                                     | 0.034221 | 0.007927       | 0.018684                 | 0.049757 |
| Corr(Phi(1),Phi(2))                            |          | -0.438387      |                          |          |
| Corr(Phi(2),Phi(3))                            |          | -0.771080      |                          |          |
| Corr(Phi(3),Phi(4))                            |          | -0.206546      |                          |          |
| Estimates for Group 2                          |          |                |                          |          |
| Control Group                                  |          |                |                          |          |
| Phi(1)   | 0.931746 | 0.073081       | 0.788507                 | 1.074984 |
| Phi(2)   | 0.936700 | 0.175128       | 0.593448                 | 1.279951 |
| Phi(3)   | 0.998507 | 0.194106       | 0.618059                 | 1.378955 |
| Phi(4)   | 0.686250 | 0.149105       | 0.394003                 | 0.978496 |
| p(2)   | 0.040858 | 0.003423       | 0.034149                 | 0.047566 |
| p(3)   | 0.010285 | 0.001857       | 0.006646                 | 0.013924 |
| p(4)   | 0.076293 | 0.007408       | 0.061773                 | 0.090813 |
| p(5)   | 0.037317 | 0.007429       | 0.022756                 | 0.051878 |
| Phi(5)p(6)                                     | 0.043956 | 0.008773       | 0.026761                 | 0.061151 |
| Corr(Phi(1),Phi(2))                            |          | -0.419859      |                          |          |
| Corr(Phi(2),Phi(3))                            |          | -0.792805      |                          |          |
| Corr(Phi(3),Phi(4))                            |          | -0.213136      |                          |          |
| Ratio of Survivals between Groups              |          |                |                          |          |
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| -----  |          |                |                          |          |
| S(1,2,Phi(1))                                  | 0.888149 | 0.100016       | 0.692118                 | 1.084181 |
| Corr(1,2,Phi(1))                               |          | 0.000000       |                          |          |
| S(1,2,Phi(2))                                  | 0.920665 | 0.241729       | 0.446875                 | 1.394454 |

Table 2.25. - Continued.

|  |           |                |           |          |
|--|-----------|----------------|-----------|----------|
| Corr(1,2,Phi(2))   | 0.000000  |                |           |          |
| S(1,2,Phi(3))  | 1.093669  | 0.299789       | 0.506081  | 1.681256 |
| Corr(1,2,Phi(3))   | 0.000000  |                |           |          |
| S(1,2,Phi(4))  | 1.270867  | 0.419606       | 0.448440  | 2.093295 |
| Corr(1,2,Phi(4))   | 0.000000  |                |           |          |
| S(i,j,Phi(I)) equals treatment effect estimated as<br>Phi(I) for group i / Phi(I) for group j.               |           |                |           |          |
| Corr(i,j,Phi(I)) equals estimated sampling correlation<br>between Phi(I) for group i and Phi(I) for group j. |           |                |           |          |
| -----  |           |                |           |          |
| Maximum Likelihood Estimates under Model H2p   |           |                |           |          |
| 95% Confidence Intervals   |           |                |           |          |
| Parameter  | Estimate  | Standard Error | Lower     | Upper    |
| -----  |           |                |           |          |
| Estimates for Group 1  |           |                |           |          |
| Treatment Group  |           |                |           |          |
| Phi(1)   | 0.830798  | 0.047782       | 0.737145  | 0.924452 |
| p(2)   | 0.041286  | 0.002686       | 0.036021  | 0.046550 |
| Corr(Phi(1),Phi(2))  | -0.419720 |                |           |          |
| Estimates for Group 2  |           |                |           |          |
| Control Group  |           |                |           |          |
| Phi(1)   | 0.928307  | 0.053214       | 0.824008  | 1.032606 |
| p(2)   | 0.041009  | 0.002642       | 0.035830  | 0.046188 |
| Corr(Phi(1),Phi(2))  | -0.421233 |                |           |          |
| Estimates for Pooled Groups  |           |                |           |          |
| Phi(2)   | 0.898918  | 0.117992       | 0.667654  | 1.130183 |
| Phi(3)   | 1.044057  | 0.143045       | 0.763690  | 1.324425 |
| Phi(4)   | 0.765901  | 0.125252       | 0.520387  | 1.011414 |
| p(3)   | 0.010935  | 0.001383       | 0.008224  | 0.013646 |
| p(4)   | 0.075902  | 0.005335       | 0.065446  | 0.086358 |
| p(5)   | 0.033977  | 0.005926       | 0.023930  | 0.044023 |
| Phi(5)p(6)   | 0.039179  | 0.005926       | 0.027564  | 0.050794 |
| Corr(Phi(2),Phi(3))  | -0.782301 |                |           |          |
| Corr(Phi(3),Phi(4))  | -0.210658 |                |           |          |
| Ratio of Survivals between Groups  |           |                |           |          |
| 95% Confidence Intervals   |           |                |           |          |
| Parameter  | Estimate  | Standard Error | Lower     | Upper    |
| -----  |           |                |           |          |
| S(1,2,Phi(1))  | 0.894961  | 0.020341       | 0.0855093 | 0.934829 |



Table 2.25. - Continued.

|  |           |                |          |          |
|--|-----------|----------------|----------|----------|
| Corr(1,2,Phi(1))                               | 0.921665  |                |          |          |
| Maximum Likelihood Estimates under Model H1Phi |           |                |          |          |
| 95% Confidence Intervals                       |           |                |          |          |
| Parameter                                      | Estimate  | Standard Error | Lower    | Upper    |
| Estimates for Group 1                          |           |                |          |          |
| Treatment Group                                |           |                |          |          |
| Phi(1)   | 0.831435  | 0.047607       | 0.738126 | 0.924745 |
| Corr(Phi(1),Phi(2))                            | -0.421653 |                |          |          |
| Estimates for Group 2                          |           |                |          |          |
| Control Group                                  |           |                |          |          |
| Phi(1)   | 0.927648  | 0.052962       | 0.823843 | 1.031452 |
| Corr(Phi(1),Phi(2))                            | -0.422881 |                |          |          |
| Estimates for Pooled Groups                    |           |                |          |          |
| Phi(2)   | 0.898918  | 0.117992       | 0.667654 | 1.130183 |
| Phi(3)   | 1.044057  | 0.143045       | 0.763690 | 1.324425 |
| Phi(4)   | 0.765901  | 0.125262       | 0.520387 | 1.011414 |
| p(2)   | 0.041142  | 0.002474       | 0.036294 | 0.045990 |
| p(3)   | 0.010935  | 0.001383       | 0.008224 | 0.013646 |
| p(4)   | 0.075902  | 0.005335       | 0.065446 | 0.086358 |
| p(5)   | 0.033977  | 0.005126       | 0.023930 | 0.044023 |
| Phi(5)p(6)                                     | 0.039179  | 0.005926       | 0.027564 | 0.050794 |
| Corr(Phi(2),Phi(3))                            | -0.782301 |                |          |          |
| Corr(Phi(3),Phi(4))                            | -0.210658 |                |          |          |
| Ratio of Survivals between Groups              |           |                |          |          |
| 95% Confidence Intervals                       |           |                |          |          |
| Parameter                                      | Estimate  | Standard Error | Lower    | Upper    |
| S(1,2,Phi(1))                                  | 0.896284  | 0.018040       | 0.860925 | 0.931642 |
| Corr(1,2,Phi(1))                               | 0.938042  |                |          |          |
| Maximum Likelihood Estimates under Model H0    |           |                |          |          |
| 95% Confidence Intervals                       |           |                |          |          |
| Parameter                                      | Estimate  | Standard Error | Lower    | Upper    |
| Estimates for Pooled Groups                    |           |                |          |          |
| Phi(1)   | 0.878726  | 0.049456       | 0.781793 | 0.975660 |
| Phi(2)   | 0.898918  | 0.117992       | 0.667654 | 1.130183 |

Table 2.25. - Continued.

|                     |          |           |          |          |
|---------------------|----------|-----------|----------|----------|
| Phi(3)              | 1.044057 | 0.143045  | 0.763690 | 1.324425 |
| Phi(4)              | 0.765901 | 0.125262  | 0.520387 | 1.011414 |
| p(2)                | 0.041142 | 0.002474  | 0.036294 | 0.045990 |
| p(3)                | 0.010935 | 0.002383  | 0.008224 | 0.013646 |
| p(4)                | 0.075902 | 0.005335  | 0.065446 | 0.086358 |
| p(5)                | 0.033977 | 0.005126  | 0.023930 | 0.044023 |
| Phi(5)p(6)          | 0.039179 | 0.005926  | 0.027564 | 0.050794 |
| Corr(Phi(1),Phi(2)) |          | -0.428974 |          |          |
| Corr(Phi(2),Phi(3)) |          | -0.782301 |          |          |
| Corr(Phi(3),Phi(4)) |          | -0.210658 |          |          |

Summary of TEST 1 (Between Groups Test) Results

| Component | Chi-square | df | P-level | Sufficient Data |
|-----------|------------|----|---------|-----------------|
| 1.R5      | 0.6745     | 1  | 0.4115  | Yes             |
| 1.T5      | 0.2237     | 1  | 0.6363  | Yes             |
| 1.R4      | 0.0095     | 1  | 0.9223  | Yes             |
| 1.T4      | 0.2361     | 1  | 0.6270  | Yes             |
| 1.R3      | 0.1399     | 1  | 0.7084  | Yes             |
| 1.T3      | 0.1543     | 1  | 0.6944  | Yes             |
| 1.R2      | 0.0048     | 1  | 0.9448  | Yes             |
| 1.T2      | 0.0196     | 1  | 0.8887  | Yes             |
| 1.R1      | 29.6316    | 1  | 0.0000  | Yes             |
| TEST 1    | 31.0940    | 9  | 0.0003  |                 |

Summary of TEST 2 (Goodness of fit) Results

| Group      | Component | Chi-square | df | P-level | Sufficient Data |
|------------|-----------|------------|----|---------|-----------------|
| 1          | 2.C2      | 1.9445     | 3  | 0.5840  | Yes             |
| 1          | 2.C3      | 0.5400     | 2  | 0.7634  | Yes             |
| 1          | 2.C4      | 0.2045     | 1  | 0.6511  | Yes             |
| Group 1    | TEST 2    | 2.6890     | 6  | 0.8467  |                 |
| 2          | 2.C2      | 1.8265     | 3  | 0.6092  | Yes             |
| 2          | 2.C3      | 1.6054     | 2  | 0.4481  | Yes             |
| 2          | 2.C4      | 0.2885     | 1  | 0.5912  | Yes             |
| Group 2    | TEST 2    | 3.7203     | 6  | 0.7145  |                 |
| All Groups | TEST 2    | 6.4093     | 12 | 0.8941  |                 |

Table 2.26. - Summary of estimates of various model parameters under model  $H_{1\phi}$  for three protocols. The data from the general numerical example were used.

| Parameters        | Complete capture history protocol |        | Partial capture history protocol |        |               |        |
|-------------------|-----------------------------------|--------|----------------------------------|--------|---------------|--------|
|                   | Estimates                         | se     | Scheme A                         |        | Scheme B      |        |
|                   |                                   |        | Estimates                        | se     | Estimates     | se     |
| $\hat{\phi}_{t1}$ | 0.831                             | 0.0476 | 0.831                            | 0.0476 | 0.831         | 0.0476 |
| $\hat{\phi}_{c1}$ | 0.928                             | 0.0530 | 0.928                            | 0.0530 | 0.928         | 0.0530 |
| $\hat{\phi}_2$    | 0.916                             | 0.1188 | 0.899                            | 0.1180 | Not estimable |        |
| $\hat{\phi}_3$    | 1.023                             | 0.1378 | 1.044                            | 0.1430 | Not estimable |        |

Note that for any specific model, data collected under these two protocols give the same values for  $\hat{\phi}_{t1}$  and  $\hat{\phi}_{c1}$ , as illustrated below for model  $H_{1\phi}$ . Estimates of  $\hat{\phi}_2$ ,  $\hat{\phi}_3$ , etc. are generally less precise with the scheme A data than under the complete capture history protocol. The difference in precision, based on estimated standard errors for model  $H_{1\phi}$ , is shown in Table 2.26 to be small for the hypothetical example.

Estimates under models  $H_{2\phi}$ , ...,  $H_{4\phi}$  are not included in Table 2.25 but are included in the output from RELEASE. For this example, tests between models with scheme A data and with the complete capture history data lead to the same conclusion. The test of  $H_0$  versus  $H_{1\phi}$  rejects  $H_0$  ( $\chi^2 = 29.63$  with 1 df, exactly as in Table 2.23; see TEST 1.R1). Tests comparing  $H_{1\phi}$  with more general models, though not identical to those in Table 2.23, fail to be significant. Thus,  $H_{1\phi}$  is the most appropriate model for these data, suggesting a treatment effect on survival that is negligible beyond dam 2. Examination of this treatment effect is carried out by using model  $H_{1\phi}$  estimates  $\hat{\phi}_{t1}$  and  $\hat{\phi}_{c1}$ . Results given below are the same as those derived from the complete capture history data. In particular, the model  $H_{1\phi}$  estimate  $\hat{S}$ , denoted in RELEASE output as S(1,2,Phi(1)), is 0.896 with estimated  $\hat{se} = 0.0180$ . The 95% CI for  $S$  is  $0.896 \pm (1.96 \times 0.0180)$ , or 0.861 to 0.932.

Using model  $H_{1\phi}$  estimates,  $\hat{\phi}_{c1} - \hat{\phi}_{t1} = 0.9276 - 0.8314 = 0.0962$ . The standard errors and correlation of  $\hat{\phi}_{c1}$ ,  $\hat{\phi}_{t1}$  are given in Table 2.25 under model  $H_{1\phi}$ . In particular, the correlation is 0.9380, hence, the covariance of  $\hat{\phi}_{c1}$  and  $\hat{\phi}_{t1}$  is  $\text{cov}(\hat{\phi}_{c1}, \hat{\phi}_{t1}) = (0.9380)(0.05296)(0.04761) = 0.002365$ . The corresponding standard error of the difference is

$$\hat{se}(\hat{\phi}_{c1} - \hat{\phi}_{t1}) = \sqrt{(0.05296)^2 + (0.04761)^2 - 2(0.002365)}$$

$$= 0.0185.$$

The 95% CI for the difference in treatment and control survival rates is  $0.096 \pm (1.96 \times 0.0185)$ . With 95% confidence, the survival rate in the control group exceeds that in the treatment group by between 0.060 and 0.132.

### 2.5.3. Scheme B

2.5.3.1. *Introduction and presentation of data.* – First recaptures at dam 2 (the first recapture site) are given a second mark and released, and all recaptures at dams 3 to  $k$  are removed from the study population. Thus, there are two releases for treatment and controls:  $R_{t1}$  and  $R_{c1}$  in the initial release, and  $R_{t2}$  and  $R_{c2}$  double-marked releases at dam 2. Hence, at sites 3 to  $k$ , first recaptures ( $m_{t1j}$ ,  $m_{c1j}$ ) can be distinguished from second recaptures ( $m_{t2j}$ ,  $m_{c2j}$ ) because of the double marking and removal. The release-recapture data can be represented symbolically as in Table 2.27.

For the hypothetical example, the data that would result from the use of scheme B are presented in Table 2.28. These data correspond to rows 1 and 2 of the reduced  $m$ -arrays for the complete capture history protocol (see Tables 1.5 and 1.6).

Table 2.27. – Symbolic representation of data for partial capture history, scheme B, protocol for  $k = 5$  dams.

| Release site           | Releases $R_n$ | Numbers recaptured at dam $j$ , $m_{nj}$ |           |           |           | Total    |
|------------------------|----------------|--|-----------|-----------|-----------|----------|
|                        |                | $j = 2$                                  | 3         | 4         | 5         |          |
| <b>Treatment group</b> |                |  |           |           |           |          |
| 1                      | $R_{t1}$       | $m_{t12}$                                | $m_{t13}$ | $m_{t14}$ | $m_{t15}$ | $r_{t1}$ |
| 2                      | $R_{t2}$       |  | $m_{t23}$ | $m_{t24}$ | $m_{t25}$ | $r_{t2}$ |
| Total                  |                | $m_{t2}$                                 | $m_{t3}$  | $m_{t4}$  | $m_{t5}$  |          |
| <b>Control group</b>   |                |  |           |           |           |          |
| 1                      | $R_{c1}$       | $m_{c12}$                                | $m_{c13}$ | $m_{c14}$ | $m_{c15}$ | $r_{c1}$ |
| 2                      | $R_{c2}$       |  | $m_{c23}$ | $m_{c24}$ | $m_{c25}$ | $r_{c2}$ |
| Total                  |                | $m_{c2}$                                 | $m_{c3}$  | $m_{c4}$  | $m_{c5}$  |          |

Table 2.28. - Release-recapture data for the hypothetical example under the scheme B protocol.

| Release site           | Releases $R_{ti}$ | Number recaptured at dam $j, m_{tj}$ |     |       |     |     | Totals, $r_{ti}$ or $r_{ci}$ |
|------------------------|-------------------|--------------------------------------|-----|-------|-----|-----|------------------------------|
|                        |                   | $j = 2$                              | 3   | 4     | 5   | 6   |                              |
| <b>Treatment group</b> |                   |                                      |     |       |     |     |                              |
| 1                      | 30,000            | 1,029                                | 238 | 1,669 | 549 | 590 | 4,075                        |
| 2                      | 1,000             |                                      | 11  | 73    | 17  | 27  | 128                          |
| Totals, $m_{tj}$       |                   | 1,029                                | 249 | 1,742 | 566 | 617 |                              |
| <b>Control group</b>   |                   |                                      |     |       |     |     |                              |
| 1                      | 29,000            | 1,104                                | 247 | 1,832 | 571 | 641 | 4,395                        |
| 2                      | 1,071             |                                      | 13  | 75    | 19  | 29  | 136                          |
| Totals, $m_{cj}$       |                   | 1,104                                | 260 | 1,907 | 590 | 670 |                              |

2.5.3.2. *Models.* - Again, we may conceive of a series of increasingly general models to describe the data resulting from scheme B. However, because these data are more limited than those resulting from scheme A or unique marking (two releases compared to  $k - 1$ ), there are fewer estimable parameters. The underlying statistical theory is presented in Section 2.5.6.

Model  $H_{1\phi}$  assumes that survival may differ for treatment and control groups as far as, but not beyond, dam 2. All recapture probabilities are assumed to be the same for the two groups. The structure of  $H_{1\phi}$  for scheme B data is represented in terms of matrices of expected numbers of recaptures in Table 2.29. Note that the structure of the first two rows in Table 2.14 is identical to those in Table 2.29. Estimable parameters of interest are  $\phi_{t1}$ ,  $\phi_{c1}$ ,

Table 2.29. - Expected numbers of recaptures for model  $H_{1\phi}$  and scheme B data,  $k = 5$  dams.

| Release site                                    | Releases $R_{ti}$ | Number recaptured at dam $j, m_{vij}$ |                               |  |   |  |
|---|-------------------|---------------------------------------|-------------------------------|--|---|--|
|   |                   | $j = 2$                               | 3                             | 4                                      | 5   |  |
| <b>Treatment group, <math>E(m_{t1j})</math></b> |                   |                                       |                               |  |   |  |
| 1   | $R_{t1}$          | $R_{t1}\phi_{t1}p_2$                  | $R_{t1}\phi_{t1}q_2\phi_2p_3$ | $R_{t1}\phi_{t1}q_2\phi_2q_3\phi_2p_4$ | $R_{t1}\phi_{t1}q_2\phi_2q_3\phi_3q_4\phi_4p_5$ |  |
| 2   | $R_{t2}$          |                                       | $R_{t2}\phi_2p_3$             | $R_{t2}\phi_2q_3\phi_2p_4$             | $R_{t2}\phi_2q_3\phi_3q_4\phi_4p_5$             |  |
| <b>Control group, <math>E(m_{c1j})</math></b>   |                   |                                       |                               |  |   |  |
| 1   | $R_{c1}$          | $R_{c1}\phi_{c1}p_2$                  | $R_{c1}\phi_{c1}q_2\phi_2p_3$ | $R_{c1}\phi_{c1}q_2\phi_2q_3\phi_2p_4$ | $R_{c1}\phi_{c1}q_2\phi_2q_3\phi_3q_4\phi_4p_5$ |  |
| 2   | $R_{c2}$          |                                       | $R_{c2}\phi_2p_3$             | $R_{c2}\phi_2q_3\phi_2p_4$             | $R_{c2}\phi_2q_3\phi_3q_4\phi_4p_5$             |  |

and  $p_2$ . From the expectations in Table 2.29, separate estimation of  $\phi_i$  and  $p_{i+1}$  for  $i \geq 2$  appears impossible. Formulae for the estimators  $\hat{\phi}_{t1}$ ,  $\hat{\phi}_{c1}$ , and  $\hat{p}_2$ , and variances and covariances are the same as for model  $H_{1\phi}$  with complete capture history data (see Section 2.4.5.3). Numerical values of estimates  $\hat{\phi}_{t1}$ ,  $\hat{\phi}_{c1}$ , and  $\hat{p}_2$  for the hypothetical example will be the same when data are collected under the complete capture history, scheme A, or scheme B protocols, as noted in Section 2.5.2.6. To illustrate computation of  $\hat{\phi}_{t1}$  for model  $H_{1\phi}$ , we use summary statistics from Tables 2.28 and 2.30 for the hypothetical example. Thus,

$$\begin{aligned}\hat{\phi}_{t1} &= \frac{r_{t1}}{R_{t1}} \left[ \frac{1}{m_{.2} + z_{.2}} \left( m_{.2} + \frac{z_{.2}R_{.2}}{r_{.2}} \right) \right] \\ &= \frac{4,075}{30,000} \left[ \frac{1}{8,470} \left( 2,133 + \frac{6,337(2,071)}{264} \right) \right] \\ &= 0.8314 ,\end{aligned}$$

which agrees with output for model  $H_{1\phi}$  in Table 2.30.

Model  $H_{2p}$  assumes that  $\phi_1$  and  $p_2$  are different for the treatment and control groups, but that other parameters are not. The model structure, represented in terms of expected numbers of recaptures, is determined from the first two rows of each matrix in Table 2.15. Estimable parameters of interest are  $\phi_{t1}$ ,  $\phi_{c1}$ ,  $p_{t2}$ , and  $p_{c2}$ . Formulae for estimators and covariances are as for model  $H_{2p}$  and complete capture history data (see Section 2.4.5.4). Again, numerical values of estimates for the hypothetical data will be the same under the three protocols (complete capture history, scheme A, and scheme B). Similarities can be seen by comparing computer outputs displayed in Tables 2.22, 2.25, and 2.30. Computation of  $\hat{\phi}_{t1}$  and  $\hat{p}_{t2}$  is illustrated below, based on data for the hypothetical example displayed in Tables 2.28 and 2.30.

$$\begin{aligned}\hat{\phi}_{t1} &= \frac{r_{t1}}{R_{t1}} \left[ \frac{1}{m_{t2} + z_{t2}} \left( m_{t2} + \frac{z_{t2}R_{.2}}{r_{.2}} \right) \right] \\ &= \frac{4,075}{30,000} \left[ \frac{1}{4,075} \left( 1,029 + \frac{3,046(2,071)}{264} \right) \right] \\ &= 0.8308 .\end{aligned}$$

$$\begin{aligned}\hat{p}_{t2} &= \frac{m_{t2}r_{.2}}{m_{t2}r_{.2} + z_{t2}R_{.2}} \\ &= \frac{1,029 (264)}{1,029 (264) + 3,046 (2,071)} \\ &= 0.0413.\end{aligned}$$

Models  $H_{2\phi}, \dots, H_{k-1,\phi}$  have assumptions as described in Section 2.4.5, but, for scheme B data, recaptures from only two releases are available. The estimable parameters of interest are  $\phi_{t1}$ ,  $\phi_{c1}$ ,  $p_{t2}$ , and  $p_{c2}$ , with estimators, variances, and covariances as given for model  $H_{k-1,\phi}$  applied to complete capture history data (Section 2.4.4). The estimable parameter sets for models  $H_{2\phi}, \dots, H_{k-1,\phi}$  are all identical under scheme B. Again, computation of  $\hat{\phi}_{t1}$ ,  $\hat{p}_{t2}$  is illustrated by using data in Table 2.30.

$$\begin{aligned}\hat{\phi}_{t1} &= \frac{r_{t1}}{R_{t1}} \left[ \frac{1}{m_{t2} + z_{t2}} \left( m_{t2} + \frac{z_{t2}R_{t2}}{r_{t2}} \right) \right] \\ &= \frac{4,075}{30,000} \left[ \frac{1}{4,075} \left( 1,029 + \frac{3,046 (1,000)}{128} \right) \right] \\ &= 0.8275.\end{aligned}$$

$$\begin{aligned}\hat{p}_{t2} &= \frac{m_{t2}r_{t2}}{m_{t2}r_{t2} + z_{t2}R_{t2}} \\ &= \frac{1,029 (128)}{(1,029) (128) + (3,046) (1,000)} \\ &= 0.0414.\end{aligned}$$

**2.5.3.3. Testing between models.** – In this section, a series of tests is presented to determine which model and estimators to use for a given data set. We cannot distinguish among all models in the series  $H_{2\phi}$  to  $H_{k-1,\phi}$  as only two releases are made for each group under scheme B. On the basis of statistical theory given in Section 2.5.3.7, the following sequence of tests is recommended.

Test (1), model  $H_{2\phi}$  versus  $H_{k-1,\phi}$  is based on a contingency chi-square test with  $k - 3$  df computed from the contingency table

|          |          |         |           |          |
|----------|----------|---------|-----------|----------|
| $m_{t3}$ | $m_{t4}$ | $\dots$ | $m_{t,k}$ | $T_{t3}$ |
| $m_{c3}$ | $m_{c4}$ | $\dots$ | $m_{c,k}$ | $T_{c3}$ |

This test is equivalent to an overall chi-square (with  $k - 3$  df) obtained by summing individual 1-df chi-squares from the  $2 \times 2$  tables

|          |          |
|----------|----------|
| $m_{ti}$ | $z_{ti}$ |
| $m_{ci}$ | $z_{ci}$ |

where  $i = 3, \dots, k - 1$ . These individual chi-squares are printed out by program RELEASE and are labeled TEST 1.T3, TEST 1.T4, ..., TEST1.Tk - 1. Sample values in these tables are generally smaller than in the analogous tables with scheme A or complete capture history data.

Test (2), model  $H_{2p}$  versus  $H_{2\phi}$ , involves a 1 df  $\chi^2$  statistic computed from the contingency table

|          |                   |          |
|----------|-------------------|----------|
| $r_{t2}$ | $R_{t2} - r_{t2}$ | $R_{t2}$ |
| $r_{c2}$ | $R_{c2} - r_{c2}$ | $R_{c2}$ |

It tests equality of  $\phi_{t2}$  and  $\phi_{c2}$ , assuming  $\phi_{ti} = \phi_{ci}, i = 3, \dots, k - 1$ , and  $p_{ti} = p_{ci}, i = 3, \dots, k$ . In output from RELEASE, this test is labeled TEST 1.R2.

Test (3), model  $H_{1\phi}$  versus  $H_{2p}$ , involves a 1 df  $\chi^2$  statistic computed from the contingency table

|          |          |          |
|----------|----------|----------|
| $m_{t2}$ | $z_{t2}$ | $T_{t2}$ |
| $m_{c2}$ | $z_{c2}$ | $T_{c2}$ |

It tests equality of  $p_{t2}$  and  $p_{c2}$ , assuming  $\phi_{ti} = \phi_{ci}, i = 2, \dots, k - 1$ , and  $p_{ti} = p_{ci}, i = 3, \dots, k$ . This test is labeled TEST 1.T2 in RELEASE.



Test (4), model  $H_0$  versus  $H_{1\phi}$ , involves a 1 df  $\chi^2$  computed from the contingency table

|          |                   |          |
|----------|-------------------|----------|
| $r_{t1}$ | $R_{t1} - r_{t1}$ | $R_{t1}$ |
| $r_{c1}$ | $R_{c1} - r_{c1}$ | $R_{c1}$ |

It tests equality of  $\phi_{t1}$  and  $\phi_{c1}$ , assuming  $\phi_{ti} = \phi_{ci}, i = 2, \dots, k - 1$ , and  $p_{ti} = p_{ci}, i = 2, \dots, k$  (see TEST 1.R1 in RELEASE). For the hypothetical example, one sees in Table 2.28 that this table is

|       |        |
|-------|--------|
| 4,075 | 25,925 |
| 4,395 | 24,605 |

yielding a  $\chi^2$  value of 29.63.

2.5.3.4. *Goodness of fit tests.* - Under scheme B, each entry in the data matrices corresponds to a single capture history; thus, there is no finer partitioning of these data (into subcohorts) on which to base tests of fit. Goodness of fit tests, based on the  $m$ -arrays  $m_{ij}$  and  $m_{cij}$ , are carried out as follows.

Test of Fit to  $H_{k-1,\phi}$  involves an overall  $\chi^2$  statistic. To obtain this overall chi-square, one first computes  $\chi^2$  statistics  $\chi^2_t$  and  $\chi^2_c$ , each with  $k - 3$  df from the respective contingency tables

|           |           |         |           |
|-----------|-----------|---------|-----------|
| $m_{t13}$ | $m_{t14}$ | $\dots$ | $m_{t1k}$ |
| $m_{t23}$ | $m_{t24}$ | $\dots$ | $m_{t2k}$ |

|           |           |         |           |
|-----------|-----------|---------|-----------|
| $m_{c13}$ | $m_{c14}$ | $\dots$ | $m_{c1k}$ |
| $m_{c23}$ | $m_{c24}$ | $\dots$ | $m_{c2k}$ |

These tests are labeled TEST 2.C2 in RELEASE. Then " $\chi^2$  for fit to  $H_{k-1,\phi}$ " =  $\chi^2_t + \chi^2_c$  with  $k - 3 + k - 3 = 2(k - 3)$  df. A significantly large, overall  $\chi^2$  indicates that model  $H_{k-1,\phi}$  is not appropriate.

Tests of fit to  $H_{1\phi}$ ,  $H_{2\phi}$ , and  $H_{2\phi}$  are obtained by combining  $\chi^2$  statistics for tests between models and for testing fit to  $H_{k-1,\phi}$ . An outline follows.

(1)  $\chi^2$  for fit to  $H_{2\phi}$  =  $\chi^2$  for  $H_{2\phi}$  versus  $H_{k-1,\phi}$  +  $\chi^2$  for fit to  $H_{k-1,\phi}$ , with  $k - 3 + 2(k - 3) = 3(k - 3)$  df. (This  $\chi^2$  for fit to  $H_{2\phi}$  is the sum of TEST 2.C2 for treatment and control groups plus TESTs 1.T3, 1.T4, ..., 1.Tk - 1).

(2)  $\chi^2$  for fit to  $H_{2\phi}$  =  $\chi^2$  for  $H_{2\phi}$  versus  $H_{2\phi}$  (TEST 1.R2) +  $\chi^2$  for fit to  $H_{2\phi}$ , with  $1 + 3(k - 3) = 3k - 8$  df.

(3)  $\chi^2$  for fit to  $H_{1\phi}$  =  $\chi^2$  for  $H_{1\phi}$  versus  $H_{2\phi}$  (TEST 1.T2) +  $\chi^2$  for fit to  $H_{2\phi}$ , with  $1 + 3k - 8 = 3k - 7$  df.

2.5.3.5. *Comparing survival among treatment and control groups.* – The comments in Section 2.5.2.5 apply here, except that with scheme B data inferences concerning the ratio  $\phi_{i1}/\phi_{ci}$  (or difference  $\phi_{ci} - \phi_{i1}$ ) are only possible for period 1 ( $i = 1$ ).

2.5.3.6. *Example.* – The analysis of scheme B data is illustrated by using output from program RELEASE for the hypothetical example. Part of the printout is displayed in Table 2.30.

Table 2.30. – Selected results for analyses of the hypothetical example, collected under scheme B protocol.

| Observed Recaptures for Group 1 |       |        |      |      |      |      |      |
|---------------------------------|-------|--------|------|------|------|------|------|
| Treatment Group                 |       |        |      |      |      |      |      |
| i                               | R(i)  | m(i,j) |      |      |      |      | r(i) |
|                                 |       | j= 2   | 3    | 4    | 5    | 6    |      |
| 1                               | 30000 | 1029   | 238  | 1669 | 549  | 590  | 4075 |
| 2                               | 1000  |        | 11   | 73   | 17   | 27   | 128  |
| m(j)                            |       | 1029   | 249  | 1742 | 566  | 617  |      |
| z(j)                            |       | 3046   | 2925 | 1183 | 617  | 0    |      |
| Observed Recaptures for Group 2 |       |        |      |      |      |      |      |
| Control Group                   |       |        |      |      |      |      |      |
| i                               | R(i)  | m(i,j) |      |      |      |      | r(i) |
|                                 |       | j= 2   | 3    | 4    | 5    | 6    |      |
| 1                               | 29000 | 1104   | 247  | 1832 | 571  | 641  | 4395 |
| 2                               | 1071  |        | 13   | 75   | 19   | 29   | 136  |
| m(j)                            |       | 1104   | 260  | 1907 | 590  | 670  |      |
| z(j)                            |       | 3291   | 3167 | 1260 | 670  | 0    |      |
| Sums for the above Groups       |       |        |      |      |      |      |      |
| m.                              | 0     | 2133   | 509  | 3649 | 1156 | 1287 |      |
| R.                              | 59000 | 2071   | 0    | 0    | 0    |      |      |
| z.                              | 0     | 6337   | 6092 | 2443 | 1287 |      |      |
| r.                              | 8470  | 264    | 0    | 0    | 0    |      |      |

Data type is scheme B capture histories.

Table 2.30. - Continued.

| Maximum Likelihood Estimates under Model H2Phi |          |                |                          |          |
|--|----------|----------------|--------------------------|----------|
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| Estimates for Group 1                          |          |                |                          |          |
| Treatment Group                                |          |                |                          |          |
| Phi(1)   | 0.827529 | 0.066869       | 0.696467                 | 0.958591 |
| p(2)   | 0.041449 | 0.003579       | 0.034435                 | 0.048463 |
| Estimates for Group 2                          |          |                |                          |          |
| Control Group                                  |          |                |                          |          |
| Phi(1)   | 0.931746 | 0.073081       | 0.788507                 | 1.074984 |
| p(2)   | 0.040858 | 0.003423       | 0.034149                 | 0.047566 |
| Ratio of Survivals between Groups              |          |                |                          |          |
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| S(1,2,Phi(1))                                  | 0.888149 | 0.100016       | 0.692118                 | 1.084181 |
| Corr(1,2,Phi(1))                               |          | 0.000000       |                          |          |
| -----  |          |                |                          |          |
| Maximum Likelihood Estimates under Model H2p   |          |                |                          |          |
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| Estimates for Group 1                          |          |                |                          |          |
| Treatment Group                                |          |                |                          |          |
| Phi(1)   | 0.830798 | 0.047782       | 0.737145                 | 0.924452 |
| p(2)   | 0.041286 | 0.002686       | 0.036021                 | 0.046550 |
| Estimates for Group 2                          |          |                |                          |          |
| Control Group                                  |          |                |                          |          |
| Phi(1)   | 0.928307 | 0.053214       | 0.824008                 | 1.032606 |
| p(2)   | 0.041009 | 0.002642       | 0.035830                 | 0.046188 |
| Ratio of Survivals between Groups              |          |                |                          |          |
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| S(1,2,Phi(1))                                  | 0.894961 | 0.020341       | 0.855093                 | 0.934829 |
| Corr(1,2,Phi(1))                               |          | 0.921665       |                          |          |

Table 2.30. - Continued.

| Maximum Likelihood Estimates under Model H1Phi |          |                |                          |          |
|--|----------|----------------|--------------------------|----------|
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| Estimates for Group 1<br>Treatment Group       |          |                |                          |          |
| Phi(1)   | 0.831435 | 0.047607       | 0.738126                 | 0.924745 |
| Estimates for Group 2<br>Control Group         |          |                |                          |          |
| Phi(1)   | 0.927648 | 0.052962       | 0.823843                 | 1.031452 |
| Estimates for Pooled Groups                    |          |                |                          |          |
| p(2)   | 0.041142 | 0.002474       | 0.036294                 | 0.045990 |
| Ratio of Survivals between Groups              |          |                |                          |          |
| Parameter                                      | Estimate | Standard Error | 95% Confidence Intervals |          |
|  |          |                | Lower                    | Upper    |
| S(1,2,Phi(1))                                  | 0.896284 | 0.018040       | 0.860925                 | 0.931642 |
| Corr(1,2,Phi(1))                               |          | 0.938042       |                          |          |

  

| Estimates under Model H0    |          |                |                          |          |
|-----------------------------|----------|----------------|--------------------------|----------|
| Parameter                   | Estimate | Standard Error | 95% Confidence Intervals |          |
|                             |          |                | Lower                    | Upper    |
| Estimates for Pooled Groups |          |                |                          |          |
| Phi(1)                      | 0.878726 | 0.049456       | 0.781793                 | 0.975660 |
| p(2)                        | 0.041142 | 0.002474       | 0.036294                 | 0.045990 |

Table 2.30. - Continued.

TEST 1.T5: Test of p(5) equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O| 566 | 617 |1183
E| 559.8| 623.2|
C|  0.1|  0.1|

```

```

+-----+-----+
O| 590 | 670 |1260
E| 596.2| 663.8|
C|  0.1|  0.1|

```

```

+-----+-----+
1156  1287  2443

```

Chi-square=0.2542 (df=1) P=0.6141

TEST 1.T4: Test of p(4) equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O|1742 |1183 |2925
E|1752.0|1173.0|
C|  0.1|  0.1|

```

```

+-----+-----+
O|1907 |1260 |3167
E|1897.0|1270.0|
C|  0.1|  0.1|

```

```

+-----+-----+
3649  2443  6092

```

Chi-square=0.2751 (df=1) P=0.6000

TEST 1.T3: Test of p(3) equal across groups,  
assuming higher order parameters are equal across groups.

```

+-----+-----+
O| 249 |2925 |3174
E| 244.7|2929.3|
C|  0.1|  0.0|

```

```

+-----+-----+
O| 260 |3167 |3427
E| 264.3|3162.7|
C|  0.1|  0.0|

```

```

+-----+-----+
509  6092  6601

```

Chi-square=0.1543 (df=1) P=0.6944

Table 2.30. - Continued.

TEST 1.R2: Test of Phi(2) equal across groups,  
assuming higher order parameters are equal across groups.

```
+-----+-----+
O| 128 | 872 |1000
E| 127.5| 872.5|
C|  0.0|  0.0|
```

```
+-----+-----+
O| 136 | 935 |1071
E| 136.5| 934.5|
C|  0.0|  0.0|
```

```
+-----+-----+
                264  1807  2071
```

Chi-square=0.0048 (df=1) P=0.9448

TEST 1.T2: Test of p(2) equal across groups,  
assuming higher order parameters are equal across groups.

```
+-----+-----+
O|1029 |3046 |4075
E|1026.2|3048.8|
C|  0.0|  0.0|
```

```
+-----+-----+
O|1104 |3291 |4395
E|1106.8|3288.2|
C|  0.0|  0.0|
```

```
+-----+-----+
                2133  6337  8470
```

Chi-square=0.0196 (df=1) P=0.8887

TEST 1.R1: Test of Phi(1) equal across groups,  
assuming higher order parameters are equal across groups.

```
+-----+-----+
O| 4075 |25925 |30000
E| 4307.|25693.|
C| 12.5|  2.1|
```

```
+-----+-----+
O| 4395 |24605 |29000
E| 4163.|24837.|
C| 12.9|  2.2|
```

```
+-----+-----+
                8470  50530  59000
```

Chi-square=29.6316 (df=1) P=0.0000

Table 2.30. - Continued.

Goodness of fit test of recaptures partitioned by rows.

Test for Group 1  
Treatment Group

TEST 2.C2: Test of row 1 vs. row 2

|   |       |        |       |       |      |
|---|-------|--------|-------|-------|------|
| O | 238   | 1669   | 549   | 590   | 3046 |
| E | 239.0 | 1671.7 | 543.2 | 592.1 |      |
| C | 0.0   | 0.0    | 0.1   | 0.0   |      |
| O | 11    | 73     | 17    | 27    | 128  |
| E | 10.0  | 70.3   | 22.8  | 24.9  |      |
| C | 0.1   | 0.1    | 1.5   | 0.2   |      |
|   | 249   | 1742   | 566   | 617   | 3174 |

Chi-square=1.9445 (df=3) P=0.5840

Test for Group 2  
Control Group

TEST 2.C2: Test of row 1 vs. row 2

|   |       |        |       |       |      |
|---|-------|--------|-------|-------|------|
| O | 247   | 1832   | 571   | 641   | 3291 |
| E | 249.7 | 1831.3 | 566.6 | 643.4 |      |
| C | 0.0   | 0.0    | 0.0   | 0.0   |      |
| O | 13    | 75     | 19    | 29    | 136  |
| E | 10.3  | 75.7   | 23.4  | 26.6  |      |
| C | 0.7   | 0.0    | 0.8   | 0.2   |      |
|   | 260   | 1907   | 590   | 670   | 3427 |

Chi-square=1.8265 (df=3) P=0.6092

Cumulative result over both cohorts and groups  
Chi-square=3.7710 (df=6) P=0.7076

Under model  $H_{1\phi}$ , estimates of  $\phi_{t1}$ ,  $\phi_{c1}$ , and  $p_2$  are  $\hat{\phi}_{t1} = 0.8314$ ,  $\hat{\phi}_{c1} = 0.9276$ , and  $\hat{p}_2 = 0.0411$ . Note that these values are identical to estimates produced with complete capture history and scheme A data (e.g., see Section 2.5.2.6). Similarly, corresponding standard errors are the same under these three protocols. In contrast,  $\phi_2$  is not estimable with scheme B data but is estimable under the other two protocols.

Estimates under  $H_{2\phi}$  are  $\hat{\phi}_{t1} = 0.8308$ ,  $\hat{\phi}_{c1} = 0.9283$ ,  $\hat{p}_{t2} = 0.0413$ , and  $\hat{p}_{c2} = 0.0410$ . Identical estimates for these same four parameters are obtained for data under scheme A and the complete capture history protocols. This similarity is a result of the estimation of  $\phi_1$  and  $p_2$  depending on information relating to only the first two releases, and the three protocols are the same with respect to releases 1 and 2 and their subsequent recoveries. Thus, for examining a one-period effect on survival, scheme B is equivalent to the more complex scheme A and complete capture history protocols.

Estimates of  $\phi_{t1}$ ,  $\phi_{c1}$ ,  $p_{t2}$ , and  $p_{c2}$  are the same under  $H_{2\phi}$  and other more general models in the sequence. Thus, only results for  $H_{2\phi}$  are shown in Table 2.30. To determine which estimates or model to use for further inferences, we look at results for tests between specific models and goodness of fit tests. Tests involving models more general than  $H_{2\phi}$  produce results under the scheme B protocol different from those for scheme A or the complete capture history data. These tests are labeled TEST 1.75, TEST 1.74, and TEST 1.73 in Table 2.30. Note that not one of these tests yields a significantly large chi-square value, giving no reason to reject any of the models  $H_{2\phi}$ , ...,  $H_{5\phi}$ . Also note that under scheme B, data required for TEST 1.R3, TEST 1.R4, and TEST 1.R5 are not available because there are only two releases for each group (in contrast, see Table 2.25).

The next step is to determine if a model less general than  $H_{2\phi}$  is adequate for these data. In Table 2.30, one sees that TEST 1.R2, which tests  $H_{2\phi}$  against the more general  $H_{2\phi}$ , yields  $\chi^2 = 0.005$  with 1 df ( $P = 0.94$ ), suggesting that  $H_{2\phi}$  is unnecessarily general. Then, TEST 1.72 for  $H_{1\phi}$  against  $H_{2\phi}$  results in  $\chi^2 = 0.02$  with 1 df ( $P = 0.89$ ), suggesting that  $H_{2\phi}$  is also unnecessarily general. Finally, TEST 1.R1 for  $H_0$  versus  $H_{1\phi}$  yields  $\chi^2 = 29.63$  with 1 df ( $P < 0.001$ ), indicating that  $H_0$  is rejected in favor of  $H_{1\phi}$ . Note that tests comparing  $H_0$  versus  $H_{1\phi}$ ,  $H_{1\phi}$  versus  $H_{2\phi}$ , and  $H_{2\phi}$  versus  $H_{2\phi}$  all produce identical results for data under the three protocols. Again, this similarity results from the use in these three tests of information relating to only the first two releases.

Results for goodness of fit tests appear last in Table 2.30. The test of fit to  $H_{5\phi}$  is obtained by summing  $\chi^2$  values (and degrees of freedom) for TEST 2.C2 for treatment and control groups (i.e., groups 1 and 2 in the output). Summing the chi-square values gives a chi-square value of 3.771 with 6 df ( $P = 0.71$ ).

$$\chi^2 \text{ for fit to } H_{4\phi} = \chi^2 \text{ for } H_{4\phi} \text{ versus } H_{5\phi} \text{ (TEST 1.75)} + \chi^2 \text{ for fit to } H_{5\phi} \text{ (TEST 2)} = 0.254 + 3.771 = 4.025 \text{ with 7 df.}$$

$$\chi^2 \text{ for fit to } H_{3\phi} = \chi^2 \text{ for } H_{3\phi} \text{ versus } H_{4\phi} \text{ (TEST 1.74)} + \chi^2 \text{ for fit to } H_{4\phi} = 0.275 + 4.025 = 4.300 \text{ with 8 df.}$$

$$\chi^2 \text{ for fit to } H_{2\phi} = \chi^2 \text{ for } H_{2\phi} \text{ versus } H_{3\phi} \text{ (TEST 1.73)} + \chi^2 \text{ for fit to } H_{3\phi} = 0.154 + 4.300 = 4.454 \text{ with 9 df.}$$



$\chi^2$  for fit to  $H_{2\phi} = \chi^2$  for  $H_{2\phi}$  versus  $H_{2\phi}$  (TEST 1.R2) +  $\chi^2$  for fit to  $H_{2\phi} = .005 + 4.454 = 4.459$  with 10 df.

$\chi^2$  for fit to  $H_{1\phi} = \chi^2$  for  $H_{1\phi}$  versus  $H_{2\phi}$  (TEST 1.T2) +  $\chi^2$  for fit to  $H_{2\phi} = .020 + 4.459 = 4.479$  with 11 df.

$\chi^2$  for fit to  $H_0 = \chi^2$  for  $H_0$  versus  $H_{1\phi}$  (TEST 1.R1) +  $\chi^2$  for fit to  $H_{1\phi} = 29.632 + 4.479 = 34.111$  with 12 df.

Only the test of fit to  $H_0$  produces a significantly large  $\chi^2$  ( $P = <0.001$ ), confirming that model  $H_{1\phi}$  is the appropriate model for these data.

The  $H_{1\phi}$  estimates are used to make inferences about the treatment effect. (As explained previously, these estimates will be identical to inferences based on scheme A or complete capture history data for this particular example.) Thus,  $\hat{S} = \hat{\phi}_{t1}/\hat{\phi}_{c1} = 0.896$ . This result is labeled S(1,2,Phi(1)) in the output in Table 2.30. The 95% CI for  $S$  is seen to be 0.861 to 0.932.

2.5.3.7. *Statistical theory.* – Likelihoods used in deriving scheme B maximum likelihood estimators, tests between models, and goodness of fit tests are presented here for the more useful models in the sequence  $H_0, H_{1\phi}, H_{2\phi}, H_{2\phi}, \dots, H_{k-1,\phi}$ .

A minimal sufficient statistic for model  $H_{1\phi}$  is

$$\text{MSS} = \{r_{t1}, r_{c1}, m_{.2}, r_{.2}, \dots, m_{k-1}\}.$$

For  $k = 5$ , the likelihood under  $H_{1\phi}$  is proportional to

$$\begin{aligned} \Pr\{\text{MSS}\} &= \binom{R_{t1}}{r_{t1}} [\phi_{t1}(p_2 + q_2\lambda_2)]^{r_{t1}} [1 - \phi_{t1}(p_2 + q_2\lambda_2)]^{R_{t1} - r_{t1}} \\ &\times \binom{R_{c1}}{r_{c1}} [\phi_{c1}(p_2 + q_2\lambda_2)]^{r_{c1}} [1 - \phi_{c1}(p_2 + q_2\lambda_2)]^{R_{c1} - r_{c1}} \\ &\times \binom{R_{.2}}{r_{.2}} (\lambda_2)^{r_{.2}} (1 - \lambda_2)^{R_{.2} - r_{.2}} \\ &\times \binom{r_{.1}}{m_{.2}} \left( \frac{p_2}{p_2 + q_2\lambda_2} \right)^{m_{.2}} \left( \frac{q_2\lambda_2}{p_2 + q_2\lambda_2} \right)^{z_{.2}} \\ &\times \binom{r_{.2} + z_{.2}}{m_{.3} m_{.4} m_{.5}} \left( \frac{p_3}{p_3 + q_3\lambda_3} \right)^{m_{.3}} \left( \frac{q_3\phi_3 p_4}{p_3 + q_3\lambda_3} \right)^{m_{.4}} \left( \frac{q_3\phi_3 q_4 \phi_4 p_5}{p_3 + q_3\lambda_3} \right)^{m_{.5}}, \end{aligned}$$

where

$$\lambda_k = 0 \text{ and } \lambda_{i-1} = \phi_{i-1} (p_i + q_i \lambda_i) \quad i = 2, \dots, k.$$

Also note that  $r_{.1} = T_{.1}$  and  $r_{.2} + z_{.2} = T_{.3}$ .

A minimal sufficient statistic for model  $H_{2\phi}$  is

$$\text{MSS} = \{r_{t1}, r_{c1}, m_{t2}, m_{c2}, r_{.2}, m_{.3}, \dots, m_{.k-1}\}.$$

For  $k = 5$ , the likelihood under  $H_{2\phi}$  is proportional to

$$\begin{aligned} \text{Pr}\{\text{MSS}\} &= \binom{R_{t1}}{r_{t1}} [\phi_{t1}(p_{t2} + q_{t2}\lambda_2)]^{r_{t1}} [1 - \phi_{t1}(p_{t2} + q_{t2}\lambda_2)]^{R_{t1} - r_{t1}} \\ &\times \binom{R_{c1}}{r_{c1}} [\phi_{c1}(p_{c2} + q_{c2}\lambda_2)]^{r_{c1}} [1 - \phi_{c1}(p_{c2} + q_{c2}\lambda_2)]^{R_{c1} - r_{c1}} \\ &\times \binom{R_{.2}}{r_{.2}} (\lambda_2)^{r_{.2}} (1 - \lambda_2)^{R_{.2} - r_{.2}} \\ &\times \binom{r_{t1}}{m_{t2}} \left( \frac{p_{t2}}{p_{t2} + q_{t2}\lambda_2} \right)^{m_{t2}} \left( \frac{q_{t2}\lambda_2}{p_{t2} + q_{t2}\lambda_2} \right)^{z_{t2}} \\ &\times \binom{r_{c1}}{m_{c2}} \left( \frac{p_{c2}}{p_{c2} + q_{c2}\lambda_2} \right)^{m_{c2}} \left( \frac{q_{c2}\lambda_2}{p_{c2} + q_{c2}\lambda_2} \right)^{z_{c2}} \\ &\times \binom{r_{.2} + z_{.2}}{m_{.3}, m_{.4}, m_{.5}} \left( \frac{p_3}{p_3 + q_3\lambda_3} \right)^{m_{.3}} \left( \frac{q_3\phi_3 p_4}{p_3 + q_3\lambda_3} \right)^{m_{.4}} \left( \frac{q_3\phi_3 q_4 \phi_4 p_5}{p_3 + q_3\lambda_3} \right)^{m_{.5}} \end{aligned}$$

A minimal sufficient statistic for model  $H_{2\phi}$  is

$$\text{MSS} = \{r_{t1}, r_{c1}, m_{t2}, m_{c2}, r_{.2}, r_{c2}, m_{.3}, \dots, m_{.k-1}\}.$$

For  $k = 5$ , the likelihood is proportional to

$$\begin{aligned} \Pr\{\text{MSS}\} &= \prod_{i=1}^2 \binom{R_{ti}}{r_{ti}} \lambda_{ti}^{r_{ti}} (1 - \lambda_{ti})^{R_{ti} - r_{ti}} \binom{R_{ci}}{r_{ci}} \lambda_{ci}^{r_{ci}} (1 - \lambda_{ci})^{R_{ci} - r_{ci}} \\ &\times \binom{r_{t1}}{m_{t2}} \left( \frac{p_{t2}}{p_{t2} + q_{t2}\lambda_{t2}} \right)^{m_{t2}} \left( \frac{q_{t2}\lambda_{t2}}{p_{t2} + q_{t2}\lambda_{t2}} \right)^{z_2} \\ &\times \binom{r_{c1}}{m_{c2}} \left( \frac{p_{c2}}{p_{c2} + q_{c2}\lambda_{c2}} \right)^{m_{c2}} \left( \frac{q_{c2}\lambda_{c2}}{p_{c2} + q_{c2}\lambda_{c2}} \right)^{z_2} \\ &\times \binom{r_{.2} + z_{.2}}{m_{.3} m_{.4} m_{.5}} \left( \frac{p_3}{p_3 + q_3\lambda_3} \right)^{m_{.3}} \left( \frac{q_3\phi_3 p_4}{p_3 + q_3\lambda_3} \right)^{m_{.4}} \left( \frac{q_3\phi_3 q_4 \phi_4 p_5}{p_3 + q_3\lambda_3} \right)^{m_{.5}}, \end{aligned}$$

where

$$\begin{aligned} \lambda_{t1} &= \phi_{t1}(p_{t2} + q_{t2}\lambda_{t2}), \\ \lambda_{t2} &= \phi_{t2}(p_3 + q_3\lambda_3), \\ \lambda_{c1} &= \phi_{c1}(p_{c2} + q_{c2}\lambda_{c2}), \end{aligned}$$

and

$$\lambda_{c2} = \phi_{c2}(p_3 + q_3\lambda_3).$$

A minimal sufficient statistic for model  $H_{k-1, \phi}$  is

$$\text{MSS} = \{r_{t1}, r_{c1}, r_{t2}, r_{c2}, m_{t2}, m_{c2}, \dots, m_{t,k-1}, m_{c,k-1}\}.$$

For  $k = 5$ , the likelihood is proportional to

$$\begin{aligned} \Pr\{\text{MSS}\} &= \prod_{v=t,c} \prod_{i=1}^2 \binom{R_{vi}}{r_{vi}} \lambda_{vi}^{r_{vi}} (1 - \lambda_{vi})^{R_{vi} - r_{vi}} \\ &\times \prod_{v=t,c} \left\{ \binom{r_{v1}}{m_{v2}} \left( \frac{p_{v2}}{p_{v2} + q_{v2}\lambda_{v2}} \right)^{m_{v2}} \left( \frac{q_{v2}\lambda_{v2}}{p_{v2} + q_{v2}\lambda_{v2}} \right)^{z_{v2}} \right. \\ &\times \left. \binom{r_{v2} + z_{v2}}{m_{v3} m_{v4} m_{v5}} \left( \frac{p_{v3}}{p_{v3} + q_{v3}\lambda_{v3}} \right)^{m_{v3}} \left( \frac{q_{v3}\phi_{v3} p_{v4}}{p_{v3} + q_{v3}\lambda_{v3}} \right)^{m_{v4}} \left( \frac{q_{v3}\phi_{v3} q_{v4} \phi_{v4} p_{v5}}{p_{v3} + q_{v3}\lambda_{v3}} \right)^{m_{v5}} \right\}. \end{aligned}$$

The following examples represent testing between models.

(1)  $H_0$  versus  $H_{1\phi}$  (TEST 1.R1) is based on

$$\Pr_{H_0}\{MSS_{H_{1\phi}} \mid MSS_{H_0}\} = \frac{\begin{pmatrix} R_{t1} \\ r_{t1} \end{pmatrix} \begin{pmatrix} R_{c1} \\ r_{c1} \end{pmatrix}}{\begin{pmatrix} R_{.1} \\ r_{.1} \end{pmatrix}},$$

which tests equality of  $\phi_{t1}(p_{t2} + q_{t2}\lambda_{t2})$  and  $\phi_{c1}(p_{c2} + q_{c2}\lambda_{c2})$ . If all  $p_{vi} = p_i$ ,  $i = 2, \dots, k$  and all  $\phi_{vi} = \phi_i$ ,  $i = 2, \dots, k - 1$ , then the equality of  $\phi_{t1}$  and  $\phi_{c1}$  is being tested. Here  $MSS_{H_0} = \{r_{.1}, r_{.2}, m_{.2}, \dots, m_{.k-1}\}$ , a minimal sufficient statistic under  $H_0$  for scheme B.

(2)  $H_{1\phi}$  versus  $H_{2\phi}$  (TEST 1.T2) is based on

$$\Pr_{H_{1\phi}}\{MSS_{H_{2\phi}} \mid MSS_{H_{1\phi}}\} = \frac{\begin{pmatrix} T_{t2} \\ m_{t2} \end{pmatrix} \begin{pmatrix} T_{c2} \\ m_{c2} \end{pmatrix}}{\begin{pmatrix} T_{.2} \\ m_{.2} \end{pmatrix}},$$

which tests equality of  $\frac{p_{t2}}{p_{t2} + q_{t2}\lambda_{t2}}$  and  $\frac{p_{c2}}{p_{c2} + q_{c2}\lambda_{c2}}$ . If  $p_{vi} = p_i$ ,  $i = 3, \dots, k$  and  $\phi_{vi} = \phi_i$ ,  $i = 2, \dots, k - 1$ , then  $p_{t2} = p_{c2}$  is being tested. Note that  $T_{v2} = r_{v1}$ .

(3)  $H_{2\phi}$  versus  $H_{3\phi}$  (TEST 1.R2) is based on

$$\Pr_{H_{2\phi}}\{MSS_{H_{3\phi}} \mid MSS_{H_{2\phi}}\} = \frac{\begin{pmatrix} R_{t2} \\ r_{t2} \end{pmatrix} \begin{pmatrix} R_{c2} \\ r_{c2} \end{pmatrix}}{\begin{pmatrix} R_{.2} \\ r_{.2} \end{pmatrix}},$$

which tests equality of  $\phi_{t2}(p_{t3} + q_{t3}\lambda_{t3})$  and  $\phi_{c2}(p_{c3} + q_{c3}\lambda_{c3})$ . Again, equality of  $\phi_{t2}$  and  $\phi_{c2}$  is tested if  $p_{vi} = p_i$ ,  $i = 3, \dots, k$  and  $\phi_{vi} = \phi_i$ ,  $i = 3, \dots, k - 1$  is true.

(4)  $H_{2\phi}$  versus  $H_{k-1,\phi}$  (TESTs 1.73 to 1.7k - 1) involves pooling the remaining 1-df  $\chi^2$  tests to give a test based on

$$\Pr_{H_{2\phi}}\{\text{MSS}_{H_{k-1,\phi}} \mid \text{MSS}_{H_{2\phi}}\} = \frac{\begin{pmatrix} r_{t2} + z_{t2} \\ m_{t3} \cdots m_{t,k-1} \end{pmatrix} \begin{pmatrix} r_{c2} + z_{c2} \\ m_{c3} \cdots m_{c,k-1} \end{pmatrix}}{\begin{pmatrix} r_{.2} + z_{.2} \\ m_{.3} \cdots m_{.k-1} \end{pmatrix}}.$$

This multiple hypergeometric can be factored into the following representation:

$$= \prod_{i=3}^{k-1} \frac{\begin{pmatrix} T_{ti} \\ m_{ti} \end{pmatrix} \begin{pmatrix} T_{ci} \\ m_{ci} \end{pmatrix}}{\begin{pmatrix} T_{.i} \\ m_{.i} \end{pmatrix}}.$$

The separate, simple hypergeometric distributions for  $i = 3$  to  $k - 1$  correspond to TEST 1.73 through TEST 1.7k - 1, respectively.

## 2.6. Summary of Models and Protocols

Several models do not exist under certain protocols, just as some tests do not exist, or cannot be computed, under certain protocols. Intensive information on available tests are presented in Tables 2.3 and 2.4. A summary of the model sequence,  $H_0, H_{1\phi}, \dots, H_{k-1,\phi}$  is given in Table 2.2. Finally, a summary of models that exist under each protocol is given for completeness.

| Model           | Protocol |         |          |            |          |
|-----------------|----------|---------|----------|------------|----------|
|                 | First    | Unknown | Complete | Partial CH |          |
|                 | CH       | CH      | CH       | Scheme A   | Scheme B |
| $H_0$           | X        | X       | X        | X          | X        |
| $H_{1\phi}$     | X        | X       | X        | X          | X        |
| $H_{2p}$        |          |         | X        | X          | X        |
| $H_{2\phi}$     |          | X       | X        | X          |          |
| $H_{3p}$        |          |         | X        | X          |          |
| .               |          |         | .        | .          |          |
| .               |          |         | .        | .          |          |
| .               |          |         | .        | .          |          |
| $H_{k-1,\phi}$  |          |         | X        | X          | X        |
| $H'_{2\phi}$    | X        |         |          |            |          |
| $H'_{3\phi}$    | X        |         |          |            |          |
| .               | .        |         |          |            |          |
| .               | .        |         |          |            |          |
| .               | .        |         |          |            |          |
| $H'_{k-1,\phi}$ | X        |         |          |            |          |