Estimating Migration Rates Using Tag-Recovery Data

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SUMMARY

Tag-recovery data are used to estimate migration rates among a set of strata. The model formulation is a simple matrix extension of the formulation of a tag-recovery experiment discussed by Brownie et al. (1985, *Statistical Inference from Band–Recovery Data—A Handbook*, 2nd edition, Washington, D.C.: U.S. Department of the Interior). Estimation is more difficult because of the convolution of parameters between release and recovery and this convolution may cause estimates of the survival/migration parameters to have low precision. Derived parameters of emigration, immigration, harvest derivation, and overall net survival are also estimated. The models are applied to estimate the migration of Pacific herring among spawning grounds off the west coast of Canada. If animals can be re-released after being recaptured, the model corresponds, in its migration/survival components, to that of Arnason (1972, *Researches in Population Ecology* **13,** 97–113). This correspondence is developed, leading to more efficient estimators of these parameters.

1. Introduction

In many species, regular migrations occur and these migration patterns have often been qualitatively outlined through the use of tagging data. Animals are tagged in a number of areas (strata), and the locations of the recoveries of these tags in the future provide an indication of the migration routes and migration intensities. In some cases, the tagging and recovery strata are the same and interest focuses upon the rates of interchange among the strata. For example, birds may be tagged in their wintering areas, recoveries may also occur in the wintering areas, and interest focuses upon the rates of interchange among the wintering areas from year to year (e.g., Hestbeck, Nichols, and Malecki, 1991). Fish may be tagged on the spawning grounds, recoveries may also occur on the spawning grounds, and the rates of interchange among spawning areas from year to year is of interest.

Models for these types of experiments in a capture–recapture context have been considered by previous authors. Chapman and Junge (1956) and Darroch (1961) first considered the general problem of migration from strata determined at the time of release to strata determined at the time of recovery with only two sampling times and without any mortality. In their formulation, animals are captured at the first sampling time and released. Recaptures at the second sampling time are used to estimate the net migration rates (including mortality) from the release- to the recovery-strata. If mortality is present, then restrictions on the mortality rates are imposed to allow identification of the parameters. If the second sample is taken in the same set of strata as the first sample, then their models can be used to estimate the migration rates among strata. Arnason (1972, 1973) and Seber (1982, p. 555) extended these models to the case of more than two sampling times and no restrictions on mortality,

but remained within the capture–recapture setting. They compared the set of animals in years i and $i + 2$ to both those seen in years i and $i + 1$ and those seen in years $i + 1$ and $i + 2$ to estimate the migration rates among the strata between years i and $i + 1$.

In exploited populations, recoveries typically are from dead animals and there is little (if any) chance of recapturing and releasing an animal. An animal is usually seen at most twice, at release and recovery. As well, tag recoveries typically occur over the entire year between tagging times, not just at a point in time as assumed in the previous models.

The model formulations in this paper are matrix extensions to the model formulations of simple tag-recovery experiments developed by Brownie et al. (1985). Estimation is more difficult because of the convolution of parameters between release and recovery and because of the typically low tag-recovery rates. These may cause estimates of the survival/migration parameters to have low precision and the individual survival/migration parameters to be almost nonidentifiable.

Following the definition of our notation, we begin with a discussion of the assumptions that will be made. Next, we develop a stochastic model and discuss model fitting and testing. An example of the migration of herring among spawning areas on the Pacific coast of Canada is presented. Finally, we discuss how inferences in this model can be improved through modifications to the experimental design.

2. Notation

Boldface letters will be used to represent matrices, vectors, and special matrix operators. Elements within a matrix or vector will be identified by superscripts.

Matrix operations and special matrices

$\mathbf{D(X)}$ Transforms the column vector $\mathbf{X}$ into a matrix by placing the elements of $\mathbf{X}$ along the diagonal.

$$\text{If } \mathbf{N} = \begin{bmatrix} 1{,}000 \\ 1{,}000 \end{bmatrix}, \text{ then } \mathbf{D(N)} = \begin{bmatrix} 1{,}000 & 0 \\ 0 & 1{,}000 \end{bmatrix}.$$

$\mathbf{\times}, \div$ Element-by-element multiplication or division.

$$\text{If } \mathbf{A} = \begin{bmatrix} 1 & 2 \\ 3 & 4 \end{bmatrix} \text{ and } \mathbf{B} = \begin{bmatrix} 5 & 6 \\ 7 & 8 \end{bmatrix}, \text{ then } \mathbf{A} \times \mathbf{B} = \begin{bmatrix} 5 & 12 \\ 21 & 32 \end{bmatrix} \text{ and } \mathbf{A} \div \mathbf{B} = \begin{bmatrix} .200 & .333 \\ .429 & .500 \end{bmatrix}.$$

$\mathbf{1}$ A column vector of all ones.

$\mathbf{I}$ The identity matrix.

$\mathbf{J}$ A matrix of all ones.

Fundamental parameters

a The number of strata in which releases and recoveries take place.

k The number of years of releases.

l The number of years of recoveries.

$\mathbf{f}_i$ An $a \times a$ matrix whose (s, t)th element (f_i^{st}) represents the probability that an animal present in stratum s at the time of tagging in year i will be recovered in stratum t between the time of tagging in year i and year $i + 1$ and its tag reported.

$\mathbf{S}_i$ An $a \times a$ matrix whose (s, t)th element (S_i^{st}) represents the probability that an animal alive in stratum s at the time of tagging in year i will survive to and be present in stratum t at the time of tagging in year $i + 1$.

Auxiliary parameters (which must be estimated external to the current experiment)

$\mathbf{N}_i^*$ An $a \times 1$ vector whose sth element (N_i^{s*}) represents the population size in stratum s at the time of tagging in year i.

$\mathbf{\lambda}_i$ An $a \times a$ matrix whose (s, t)th element (λ_i^{st}) represents the tag-reporting rate of animals alive in stratum s at the time of tagging in year i and recovered in stratum t between the time of tagging in year i and year $i + 1$, i.e., the conditional probability that a recovered tag will be detected and reported.

Derived parameters

$\mathbf{\rho}_i$ An $a \times a$ matrix whose (s, t)th element (ρ_i^{st}) represents the total probability that an animal released in year i in stratum s will be recovered at some time during the rest of the experiment in stratum t.

$$\boldsymbol{\rho}_i = \mathbf{f}_i + \mathbf{S}_i \mathbf{f}_{i+1} + \cdots + \mathbf{S}_i \mathbf{S}_{i+1} \cdots \mathbf{S}_{l-1} \mathbf{f}_l$$

$\mathbf{m}_i$ An $a \times a$ matrix whose (s, t)th element (m_i^{st}) represents the emigration rate of animals alive in stratum s at the time of tagging in year i to stratum t at the time of tagging in year $i + 1$ conditional on surviving from year i to year $i + 1$.

$$\mathbf{m}_i = \mathbf{S}_i \div \mathbf{S}_i \mathbf{J}$$

$\mathbf{I}_i$ An $a \times a$ matrix whose (s, t)th element (I_i^{st}) represents the immigration rate of animals into stratum t from stratum s between the time of tagging in year i and the time of tagging in year $i + 1$.

$$\mathbf{I}_i = \mathbf{D}(\mathbf{N}_i^*)\mathbf{S}_i \div \mathbf{J}\mathbf{D}(\mathbf{N}_i^*)\mathbf{S}_i$$

$\mathbf{D}_i$ An $a \times a$ matrix whose (s, t)th element (D_i^{st}) represents the harvest-derivation rate in stratum t from the animals in stratum s between the time of tagging in year i and the time of tagging in year $i + 1$.

$$\mathbf{D}_i = \mathbf{D}(\mathbf{N}_i^*)(\mathbf{f}_i \div \lambda_i) \div \mathbf{J}\mathbf{D}(\mathbf{N}_i^*)(\mathbf{f}_i \div \lambda_i)$$

$\mathbf{S}_i^{\bullet}$ An $a \times 1$ vector whose sth element $(S_i^s{}^{\bullet})$ represents the overall net probability that an animal alive in stratum s at the time of tagging in year i will be alive and present in one of the strata at the time of tagging in year $i + 1$.

$$\mathbf{S}_i^{\bullet} = \mathbf{S}_i \mathbf{1}$$

Statistics

$\mathbf{N}_i$ An $a \times 1$ vector whose sth element (N_i^s) represents the number of animals tagged and released in stratum s in year i.

$\mathbf{R}_{ij}$ An $a \times a$ matrix whose (s, t)th element (R_{ij}^{st}) is the number of animals released in stratum s in year i that are recovered in stratum t in year j.

$\mathbf{R}_{i \cdot}$ An $a \times a$ matrix whose (s, t)th element $(R_{i \cdot}^{st})$ is the total number of animals released in stratum s in year i that are recovered in stratum t at any time at or after year i.

$$\mathbf{R}_{i \cdot} = \sum_{j=1}^{l} \mathbf{R}_{ij}$$

$\mathbf{R}_{\cdot j}$ An $a \times a$ matrix whose (s, t)th element $(R_{\cdot j}^{st})$ is the total number of animals released in stratum s in this or previous years that are recovered in stratum t in year j.

$$\mathbf{R}_{\cdot j} = \sum_{i=1}^{\min(j,k)} \mathbf{R}_{ij}$$

$\mathbf{T}_i$ An $a \times a$ matrix whose (s, t)th element (T_i^{st}) is the total number of animals released in stratum s and recovered in stratum t that were known to be alive in year i.

$$
\begin{aligned}
\mathbf{T}_1 &= \mathbf{R}_{1 \cdot} \\
\mathbf{T}_i &= \mathbf{T}_{i-1} + \mathbf{R}_{i \cdot} - \mathbf{R}_{\cdot i-1} \quad i = 2, \ldots, k \\
\mathbf{T}_i &= \mathbf{T}_{i-1} - \mathbf{R}_{\cdot i-1} \qquad\qquad i = k + 1, \ldots, l
\end{aligned}
$$

$\mathbf{Z}_i$ An $a \times a$ matrix whose (s, t)th element (Z_i^{st}) is the total number of animals released in stratum s and recovered in stratum t that were known to be alive after year i.

$$\mathbf{Z}_i = \mathbf{T}_i - \mathbf{R}_{\cdot i} = \mathbf{T}_{i+1} - \mathbf{R}_{i+1}.$$

3. Assumptions

The usual assumptions for tag-recovery models as outlined by Brownie et al. (1985, §1.3) and discussed by Nichols et al. (1982) and Pollock and Raveling (1982) are applicable: the sample is representative of the population, i.e., the survival and tag-recovery components apply equally to tagged and untagged animals; there is no tag loss; survival rates are not influenced by the tagging process itself; the year and location of the tag-recoveries are correctly tabulated; the fate of each tagged animal is independent of the fate of other tagged animals; and all tagged animals of a stratum have the same survival and tag-recovery rates. As well, it is assumed that releases occur in all strata over a number of years and effort is expended in all strata to recover animals in all years. Strata with no releases or recovery effort in some years will imply that certain parameters are no longer identifiable.

Crissey (1955) outlined the conditions under which tag-recovery data can be used to study migratory populations: the animals tagged must be a representative sample from the population or conclusions

based on the experiment may not be applicable to the population; the absolute or relative population sizes of the strata of release must be known or estimated in order to estimate the immigration and harvest-derivation rates; the tag-reporting rate must be known or estimated in order to estimate the harvest-derivation rates.

It is assumed that: no animals migrate temporarily to a stratum where recoveries and releases do not occur, returning after one or more years of absence (animals may migrate out of the sampled strata permanently; such losses are indistinguishable from mortality); all animals behave independently with respect to migration and recovery (it is assumed that flocking or schooling of animals after release does not occur, or does not influence the migration pattern of the animal); animals behave in a Markovian fashion in each year, i.e., the current migration route does not depend on previous migration choices; independent estimates of the stratum population sizes and the tag-reporting rates are available with estimates of their standard errors. No assumptions are made about the way in which animals move from stratum s in year i to stratum t in year $i + 1$. The animals may move directly between the two strata or may make several intermediate movements to other strata before eventually reaching stratum t in year $i + 1$.

4. Model Development

The number of animals that are released in stratum s in year i and recovered in stratum t in year j can be displayed using matrices as shown in Table 1. Note the resemblance to the display of a simple tag-recovery experiment (Brownie et al., 1985, pp. 13–17), except that now each element of the table is a matrix or a vector.

The probability that an animal is released in stratum s in year i and recovered in stratum t in year j is a function of the fundamental parameters and can be easily computed using matrices as illustrated in Table 2. Again note the similarity of the form of the cell probabilities to those from simple tag-recovery experiments (Brownie et al., 1985, pp. 13–17). The expected number of recoveries can then be computed from the elements of Table 2 and an example of their computation is shown in Table 3.

For example, of the $N_1^2 = 1,000$ animals released in stratum 2 in year 1, the expected number of animals recovered in stratum 1 in year 1 is

$$E(R_{11}^{21}) = N_1^2 \times f_1^{21} = 1,000 \times .03 = 30.0.$$

Similarly, the expected number of these animals recovered in stratum 2 in year 1 is computed as

$$E(R_{11}^{22}) = N_1^2 \times f_1^{22} = 1,000 \times .04 = 40.0.$$

Table 1

Symbolic representation of the number of animals released in stratum s in year i and recovered in stratum t in year j in the case of k = 3 years of releases and l = 4 years of recoveries

Year released	Number released	Number recovered by year			
		1	2	3	4
1	N_1	R_{11}	R_{12}	R_{13}	R_{14}
2	N_2		R_{22}	R_{23}	R_{24}
3	N_3			R_{33}	R_{34}

N_i are $a \times 1$ vectors with elements $[N_i^s]$ and R_{ij} are $a \times a$ matrices with elements $[R_{ij}^{st}]$. The number of animals never seen is not shown, but is easily obtained by subtraction.

Table 2

The probabilities that an animal released in stratum s in year i is recovered in stratum t in year j in the case of k = 3 years of releases and l = 4 years of recoveries

Year released	Number released	Probabilities of recovery by year			
		1	2	3	4
1	N_1	f_1	$S_1 f_2$	$S_1 S_2 f_3$	$S_1 S_2 S_3 f_4$
2	N_2		f_2	$S_2 f_3$	$S_2 S_3 f_4$
3	N_3			f_3	$S_3 f_4$

N_i are $a \times 1$ vectors with elements $[N_i^s]$; f_i are $a \times a$ matrices with elements $[f_i^{st}]$; and S_i are $a \times a$ matrices with elements $[S_i^{st}]$. The probability of never recovering an animal is not shown, but is easily obtained by subtraction.

Table 3

A numerical example of the expected number of recoveries in the case of a = 2 strata, k = 3 years of releases, and l = 4 years of recoveries using the parameter values given at the foot of the table

Year released	Number released	Expected number of recoveries by year			
		1	2	3	4
1	$\mathbf{N}_1 = \begin{bmatrix} 1{,}000 \\ 1{,}000 \end{bmatrix}$	$\begin{bmatrix} 30.0 & 30.0 \\ 30.0 & 40.0 \end{bmatrix}$	$\begin{bmatrix} 24.0 & 27.0 \\ 24.0 & 30.0 \end{bmatrix}$	$\begin{bmatrix} 18.3 & 21.3 \\ 17.4 & 21.0 \end{bmatrix}$	$\begin{bmatrix} 13.7 & 16.2 \\ 12.8 & 15.3 \end{bmatrix}$
2	$\mathbf{N}_2 = \begin{bmatrix} 1{,}000 \\ 1{,}000 \end{bmatrix}$		$\begin{bmatrix} 30.0 & 30.0 \\ 30.0 & 40.0 \end{bmatrix}$	$\begin{bmatrix} 24.0 & 27.0 \\ 21.0 & 26.0 \end{bmatrix}$	$\begin{bmatrix} 18.3 & 21.3 \\ 15.3 & 18.4 \end{bmatrix}$
3	$\mathbf{N}_3 = \begin{bmatrix} 1{,}000 \\ 1{,}000 \end{bmatrix}$			$\begin{bmatrix} 30.0 & 30.0 \\ 30.0 & 40.0 \end{bmatrix}$	$\begin{bmatrix} 24.0 & 27.0 \\ 21.0 & 26.0 \end{bmatrix}$

Here $\mathbf{f}_1 = \mathbf{f}_2 = \mathbf{f}_3 = \mathbf{f}_4 = \begin{bmatrix} .03 & .03 \\ .03 & .04 \end{bmatrix}$, $\mathbf{S}_1 = \begin{bmatrix} .50 & .30 \\ .20 & .60 \end{bmatrix}$, $\mathbf{S}_2 = \mathbf{S}_3 = \begin{bmatrix} .50 & .30 \\ .20 & .50 \end{bmatrix}$.

The row-wise similarities in the expected recoveries are caused by assuming that $\mathbf{S}_2 = \mathbf{S}_3$ and $\mathbf{f}_1 = \mathbf{f}_2 = \mathbf{f}_3 = \mathbf{f}_4$. The parameters $\mathbf{S}_3$ and $\mathbf{f}_4$ are not individually identifiable; only their product may be estimated.

It is also assumed that the auxiliary parameters have the values

$$\mathbf{N}_1^* = \begin{bmatrix} 100{,}000 \\ 200{,}000 \end{bmatrix}, \quad \mathbf{N}_2^* = \begin{bmatrix} 100{,}000 \\ 170{,}000 \end{bmatrix}, \quad \mathbf{N}_3^* = \begin{bmatrix} 100{,}000 \\ 150{,}000 \end{bmatrix}; \quad \lambda_1 = \lambda_2 = \lambda_3 = \begin{bmatrix} .50 & .60 \\ .60 & .40 \end{bmatrix}.$$

The auxiliary parameters are not used in computing the expected recoveries, but are used in the text to compute the derived parameters.

The situation is more complicated for those animals recovered in year 2. The expected number of animals released in stratum 2 in year 1 and recovered in stratum 1 in year 2 is composed of the expected number of animals that returned to stratum 2 in year 1 (but were not recovered) and then migrated to and were recovered in stratum 1 in year 2, plus the expected number of animals that migrated from stratum 2 to stratum 1 in year 1, and then returned to and were recovered in stratum 1 in year 2:

$$E(R_{12}^{21}) = N_1^2 \times S_1^{22} \times f_2^{21} + N_1^2 \times S_1^{21} \times f_2^{11}$$

$$= 1{,}000 \times .6 \times .03 + 1{,}000 \times .2 \times .03 = 18 + 6 = 24.$$

Similarly,

$$E(R_{12}^{22}) = N_1^2 \times S_1^{22} \times f_2^{22} + N_1^2 \times S_1^{21} \times f_2^{12}$$

$$= 1{,}000 \times .6 \times .04 + 1{,}000 \times .2 \times .03 = 24 + 6 = 30.$$

This is easily expressed in terms of matrices:

$$E(\mathbf{R}_{12}) = E\begin{bmatrix} R_{12}^{11} & R_{12}^{12} \\ R_{12}^{21} & R_{12}^{22} \end{bmatrix} = \mathbf{D(N}_1)\mathbf{S}_1\mathbf{f}_2 = \begin{bmatrix} 1{,}000 & 0 \\ 0 & 1{,}000 \end{bmatrix}\begin{bmatrix} .5 & .3 \\ .2 & .6 \end{bmatrix}\begin{bmatrix} .03 & .03 \\ .03 & .04 \end{bmatrix} = \begin{bmatrix} 24.0 & 27.0 \\ 24.0 & 30.0 \end{bmatrix}.$$

The tag-recovery parameters f_i^{st} are interpreted as the probability that an animal alive in stratum s at the time of tagging in year i will be recovered in stratum t between the time of tagging in year i and the time of tagging in year $i + 1$ and the tag reported. This parameter includes a migration component between stratum s and stratum t and the usual harvest, tag-retrieval, and tag-reporting components. These parameters are indexed by both stratum s and stratum t since it is likely that the migration components to stratum t will differ depending on the stratum where the animal was present at the time of tagging in year i even if subsequent harvest, tag-retrieval, and tag-reporting rates in stratum t are homogeneous. These parameters are assumed not to depend on the migration patterns prior to year i.

An important implication is that the tag-recovery rates are assumed to be equal for all animals that leave stratum s in year i and are recovered in stratum t in the next year, regardless of the route they choose. For example, birds that migrate from breeding area 1 to breeding area 2 via different wintering areas are assumed to have equal tag-recovery rates in breeding area 2. If recoveries are obtained by hunting, all animals that migrate between two strata should arrive simultaneously in the hunting

season. If one subset arrives at the beginning of the season and another subset arrives halfway through the season (because of a longer migration route), the tag-recovery rates will not be the same. If the rates are heterogeneous among subsets of animals migrating between strata s and t, then f_i^{st} can be thought of as an average rate. The model will no longer be valid; however, if the degree of heterogeneity is small, the results will still be approximately valid. If there is only one migration route between the two strata, or if the majority of animals choose one route, this assumption is more likely to be (approximately) satisfied.

The survival/migration parameters, S_i^{st}, are interpreted as the probability that an animal alive in stratum s at the time of tagging in year i will be alive and present in stratum t at the time of tagging in year $i + 1$. These parameters include a mortality component and a migration component. All permanent migration to strata where no recoveries or releases occur is indistinguishable from and treated as another form of mortality. It is assumed that these rates do not depend on migration patterns prior to year i.

Again an implication is that the survival/migration rates are applicable to all animals regardless of the route chosen between strata. If there is considerable heterogeneity among subsets, then S_i^{st} can be thought of as an average survival/migration rate.

Formal migration parameters, separate from the survival and tag-recovery parameters, have not been introduced since it is impossible to achieve a meaningful separation of the survival and migration components. Even if it is assumed that animals migrate directly between strata, it is still impossible to separate the migration and mortality rates. The transition rates among strata will consist of an ideal migration component (assuming all animals survived) and a survival component for each group of animals choosing a specific migration route. The net transition rate could be found as the element-by-element product of the absolute migration rates ($\mathbf{M}$) and the survival rates (ϕ), i.e., $\mathbf{S} = \mathbf{M} \times \phi$. Unfortunately, there is an infinite number of pairs of $\mathbf{M}$ and ϕ that lead to the same final net transition matrix ($\mathbf{S}$).

There are several derived parameters of biological interest, which fall into two classes: those estimable from the experiment alone, and those requiring information on auxiliary parameters obtained from independent experiments.

The *emigration rates* are defined as the proportional movement from stratum s to stratum t between the time of tagging in year i and year $i + 1$, conditional on the animal surviving from year i to year $i + 1$. For example, using the parameter values given at the foot of Table 3, the emigration rates in year 1 are computed as

$$\mathbf{m}_1 = \mathbf{S}_1 \div \mathbf{S}_1 \mathbf{J} = \begin{bmatrix} .5 & .3 \\ .2 & .6 \end{bmatrix} \div \begin{bmatrix} .5 & .3 \\ .2 & .6 \end{bmatrix} \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} = \begin{bmatrix} .5 & .3 \\ .2 & .6 \end{bmatrix} \div \begin{bmatrix} .8 & .8 \\ .8 & .8 \end{bmatrix} = \begin{bmatrix} .62 & .38 \\ .25 & .75 \end{bmatrix}.$$

This implies that, of the animals alive in stratum 1 in year 1 that survive to year 2 and remain in stratum 1 or 2, 62% will remain in and be alive in stratum 1 in year 2, and 38% will migrate to and be alive in stratum 2 in year 2.

The *overall net survival rate* is the proportion of animals released in stratum s that survive from the time of tagging in year i to the time of tagging in year $i + 1$ regardless of where they migrate, conditional on the animal migrating to one of strata $1, \ldots, a$. Migration to other strata is treated as another form of mortality. For example, using the parameter values from Table 3,

$$\mathbf{S}_2^* = \mathbf{S}_2 \mathbf{1} = \begin{bmatrix} .5 & .3 \\ .2 & .5 \end{bmatrix} \begin{bmatrix} 1 \\ 1 \end{bmatrix} = \begin{bmatrix} .8 \\ .7 \end{bmatrix}.$$

This implies that, of the animals alive in stratum 1 at the time of tagging in year 2, 80% survive and are present in either stratum 1 or stratum 2 at the time of tagging in year 3.

The *immigration rates* are defined as the proportional movement into stratum t by the time of tagging in year $i + 1$ based on the number of animals alive at the time of tagging in year i. The stratum population sizes in year i are required. For example, using the parameter values given in Table 3, the immigration rates in year 2 are computed as

$$\mathbf{I}_2 = \mathbf{D}(\mathbf{N}_2^*)\mathbf{S}_2 \div \mathbf{J}\mathbf{D}(\mathbf{N}_2^*)\mathbf{S}_2$$

$$= \begin{bmatrix} 100{,}000 & 0 \\ 0 & 170{,}000 \end{bmatrix} \begin{bmatrix} .5 & .3 \\ .2 & .5 \end{bmatrix} \div \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} \begin{bmatrix} 100{,}000 & 0 \\ 0 & 170{,}000 \end{bmatrix} \begin{bmatrix} .5 & .3 \\ .2 & .5 \end{bmatrix}$$

$$= \begin{bmatrix} 50{,}000 & 30{,}000 \\ 34{,}000 & 85{,}000 \end{bmatrix} \div \begin{bmatrix} 84{,}000 & 115{,}000 \\ 84{,}000 & 115{,}000 \end{bmatrix}$$

$$= \begin{bmatrix} .60 & .26 \\ .40 & .74 \end{bmatrix}.$$

This implies that, of the animals alive and present in stratum 2 at the time of tagging in year 3 that came from stratum 1 or 2, 26% came from stratum 1 and 74% came from stratum 2 from the previous year.

The *harvest derivation rates* are defined as the proportion of animals harvested in year i that came from each stratum. They require the stratum population sizes and tag-reporting rates in year i. For example, using the parameter values given in Table 3, the harvest-derivation rates in year 2 are computed as

$$\mathbf{D}_2 = \mathbf{D}(\mathbf{N}_2^*)(\mathbf{f}_2 \div \lambda_2) \div \mathbf{J}\mathbf{D}(\mathbf{N}_2^*)(\mathbf{f}_2 \div \lambda_2)$$

$$= \begin{bmatrix} 100{,}000 & 0 \\ 0 & 170{,}000 \end{bmatrix} \left(\begin{bmatrix} .03 & .03 \\ .03 & .04 \end{bmatrix} \div \begin{bmatrix} .5 & .6 \\ .6 & .4 \end{bmatrix} \right) \div \begin{bmatrix} 1 & 1 \\ 1 & 1 \end{bmatrix} \begin{bmatrix} 100{,}000 & 0 \\ 0 & 170{,}000 \end{bmatrix} \left(\begin{bmatrix} .03 & .03 \\ .03 & .04 \end{bmatrix} \div \begin{bmatrix} .5 & .6 \\ .6 & .4 \end{bmatrix} \right)$$

$$= \begin{bmatrix} 6{,}000 & 5{,}000 \\ 8{,}500 & 17{,}000 \end{bmatrix} \div \begin{bmatrix} 14{,}500 & 22{,}000 \\ 14{,}500 & 22{,}000 \end{bmatrix} = \begin{bmatrix} .41 & .23 \\ .59 & .77 \end{bmatrix}.$$

This implies that, of the animals harvested in stratum 1 in year 2 that came from stratum 1 or 2, 41% came from stratum 1 and 59% came from stratum 2.

5. Model Fitting and Testing

Under the assumptions given earlier, the number of animals released in stratum s in year i and recovered in stratum t in year j ($j = i, \ldots, l; t = 1, \ldots, a$) can be modelled as a multinomial distribution. For example, from Table 1, the elements $\{R_{11}^{11}, R_{11}^{12}, \ldots, R_{11}^{1a}, R_{12}^{11}, R_{12}^{12}, \ldots, R_{12}^{1a}, \ldots, R_{1l}^{1a}\}$ have a multinomial distribution with index N_1^1 and with cell probabilities given by the corresponding elements of Table 2. Animals that are released in different strata in the same year are assumed to be independent of each other, i.e., the elements $\{R_{11}^{21}, R_{11}^{22}, \ldots, R_{11}^{2a}, R_{12}^{21}, R_{12}^{22}, \ldots, R_{12}^{2a}, \ldots, R_{1l}^{2a}\}$ have a multinomial distribution with index N_1^2 independent of the previous set. Releases in successive years are also assumed to be independent.

The likelihood can now be written as a simple product of multinomial distributions (Appendix A); however, the individual cell probabilities are convolutions of the intermediate survival/migration rates and tag-recovery rates.

There are a total of $a^2(k-1)$ survival/migration parameters ($\mathbf{S}_1, \ldots, \mathbf{S}_{k-1}$), $a^2 k$ recovery rate parameters ($\mathbf{f}_1, \ldots, \mathbf{f}_k$), and $a^2(l-k)$ confounded parameters representing the product of survival and recovery in years $k+1, \ldots, l$ ($\mathbf{S}_k\mathbf{f}_{k+1}, \ldots, \mathbf{S}_k\mathbf{S}_{k+1}\mathbf{f}_{k+2}, \ldots, \mathbf{S}_{l-1}\mathbf{f}_l$) for a total of $a^2(l+k-1)$ parameters. Again note the resemblance to simple tag-recovery experiments where there are ($l + k - 1$) parameters. However, the analogy breaks down when the minimal sufficient statistic (MSS) is extracted from the likelihood. Because of the convolutions of the parameters, the MSS is the set of observed counts $\{R_{ij}^{st}, s = 1, \ldots, a; t = 1, \ldots, a; i = 1, \ldots, k; j = i, \ldots, l\}$ with no reduction in dimensionality, i.e., the MSS has dimension $a^2(kl - k(k-1)/2)$.

A closed-form moment estimator of the fundamental parameters in the full model that is analogous to the estimators in simple tag-recovery experiments can be constructed. It is easily shown that:

$$E(\mathbf{R}_{i\cdot}) = \mathbf{D}(\mathbf{N}_i)[\mathbf{f}_i + \mathbf{S}_i\mathbf{f}_{i+1} + \cdots + \mathbf{S}_i\mathbf{S}_{i+1}\cdots\mathbf{S}_{l-1}\mathbf{f}_l] \qquad i = 1, \ldots, k;$$

$$E(\mathbf{T}_i) = [\mathbf{D}(\mathbf{N}_1)\mathbf{S}_1\cdots\mathbf{S}_{i-1} + \mathbf{D}(\mathbf{N}_2)\mathbf{S}_2\cdots\mathbf{S}_{i-1} + \cdots + \mathbf{I}][\mathbf{f}_i + \mathbf{S}_i\mathbf{f}_{i+1} + \cdots + \mathbf{S}_i\mathbf{S}_{i+1}\cdots\mathbf{S}_{l-1}\mathbf{f}_l] \qquad i = 1, \ldots, k;$$

$$E(\mathbf{Z}_i) = [\mathbf{D}(\mathbf{N}_1)\mathbf{S}_1\cdots\mathbf{S}_{i-1} + \mathbf{D}(\mathbf{N}_2)\mathbf{S}_2\cdots\mathbf{S}_{i-1} + \cdots + \mathbf{I}]\mathbf{S}_i[\mathbf{f}_i + \mathbf{S}_i\mathbf{f}_{i+1} + \cdots + \mathbf{S}_i\mathbf{S}_{i+1}\cdots\mathbf{S}_{l-1}\mathbf{f}_l] \qquad i = 1, \ldots, k;$$

$$E(\mathbf{R}_{\cdot i}) = [\mathbf{D}(\mathbf{N}_1)\mathbf{S}_1\cdots\mathbf{S}_{i-1} + \mathbf{D}(\mathbf{N}_2)\mathbf{S}_2\cdots\mathbf{S}_{i-1} + \cdots + \mathbf{I}]\mathbf{f}_i \qquad i = 1, \ldots, k;$$

$$E(\mathbf{R}_{\cdot i}) = [\mathbf{D}(\mathbf{N}_1)\mathbf{S}_1\cdots\mathbf{S}_{k-1} + \mathbf{D}(\mathbf{N}_2)\mathbf{S}_2\cdots\mathbf{S}_{k-1} + \cdots + \mathbf{I}]\mathbf{S}_k\mathbf{S}_{k+1}\cdots\mathbf{S}_{i-1}\mathbf{f}_i \qquad i = k+1, \ldots, l;$$

which leads to the moment estimators (assuming all inverses exist):

$$\tilde{\mathbf{f}}_i = \mathbf{D}(\mathbf{N}_i)^{-1}\mathbf{R}_{i\cdot}\mathbf{T}_i^{-1}\mathbf{R}_{\cdot i} \qquad i = 1, \ldots, k;$$

$$\widetilde{\mathbf{S}}_i = \mathbf{D}(\mathbf{N}_i)^{-1}\mathbf{R}_{i\cdot}\mathbf{T}_i^{-1}\mathbf{Z}_i\mathbf{R}_{i+1\cdot}^{-1}\mathbf{D}(\mathbf{N}_{i+1}) \qquad i = 1, \ldots, k;$$

$$\widetilde{\mathbf{S}_k\cdots\mathbf{S}_{i-1}\mathbf{f}_i} = \mathbf{D}(\mathbf{N}_i)^{-1}\mathbf{R}_{k\cdot}\mathbf{T}_k^{-1}\mathbf{R}_{\cdot i} \qquad i = k+1, \ldots, l.$$

These estimators are simple matrix extensions of the results of Brownie et al. (1985, pp. 13–17) and can be shown to reduce to the estimators of Arnason (1972) when transferred to a capture–recapture context with three sampling times (Appendix B). They estimate the recovery rates reasonably well, but the estimates of the survival/migration parameters can be negative or greater than 1.0.

In general, numerical methods must be used to find the maximum likelihood estimates (MLEs); see Appendix A. Since the variances and covariances are found numerically, it is difficult to give quantitative statements about the precision of the estimates. However, extensive simulations have

shown that the precision of the estimated tag-recovery rates is comparable to that in simple tag-recovery experiments, but the precision of the estimated survival/migration rates may be poor. This loss of precision is caused by the convolution of the intermediate survival/migration terms between release and recovery and the generally low tag-recovery rates in practice. There is a high correlation among the estimated survival/migration rates, which implies that these parameters are nearly nonidentifiable.

The estimates of the derived parameters are found by replacing the fundamental parameters by their MLEs in the definition of the derived parameters, and using the external estimates of the stratum population sizes and tag-reporting rates. Variances and covariances may be estimated using a Taylor-series expansion in conjunction with the estimated variance–covariance matrix of the fundamental parameters and the estimated standard errors of the external estimates. Consequently, the estimated standard errors include sampling error from both the fundamental parameters and the external parameters.

Since the estimates of the survival/migration rates have relatively poor precision and are highly correlated, it is expected that the same will occur with the estimates of the emigration and immigration rates. However, the precision of the overall net survival rates will be good (assuming that the total number of releases in each year is adequate) since it can be estimated approximately by ignoring the strata, and treating the data as an ordinary tag-recovery experiment prestratified at the time of release.

Because the complexity of the full model may give rise to estimates with poor precision and high correlation, model parsimony and procedures for testing among a hierarchy of models are very desirable. There are many types of restrictions that can be placed upon the parameters of the general model to obtain reduced models of biological interest. Some examples are: (i) The migration/survival parameters may be constant over time, i.e., $S_1 = S_2 = \cdots = S_{k-1}$. (ii) The emigration rates may be constant over time but the overall net survival rates may differ among years. For example, the overall survival rates may vary because of environmental conditions but the proportions of surviving animals emigrating to the various strata may be constant over time. (iii) The recovery parameter matrices may be diagonal, i.e., $f_i^{st} = 0$ if $s \neq t$. This model is meaningful if the recovery period is short and occurs prior to any mixing of the populations. In this case, the capture–recapture models of Arnason (1972, 1973) may be more useful. (iv) The tag-recovery parameters may be independent of the stratum where the animal was present at the time of tagging in year i, i.e., $f_i^{st} = f_i^{\cdot t}$ for all s. This would be meaningful if the recovery period occurs after most migration has taken place and the animals are otherwise indistinguishable in terms of harvest, tag-recovery, and tag-reporting—for example, waterfowl harvests occurring on the wintering grounds when all migration is essentially complete. Estimates of the parameters from these reduced models can be obtained numerically using the methods outlined in Aitchison and Silvey (1958), Don (1985), or White (1983).

Closed-form, similar tests as developed by Brownie et al. (1985), Schwarz (unpublished Ph.D. thesis, University of Manitoba, 1988), and Schwarz, Burnham, and Arnason (1988) cannot be derived to distinguish between models since the MSS remains fixed at the entire data array. However, likelihood ratio tests can be used to differentiate between models. A goodness-of-fit test can be constructed using a likelihood ratio test comparing the full model to a saturated model where every cell in the recovery matrices has its own parameter.

6. Example

An extensive tagging and tag-recovery program was carried out on the British Columbia herring (*Clupea harengus pallasi*) from 1937 to 1967. Details of the tagging operations and recovery procedures have been described by Stevenson (unpublished manuscript presented at the International Council for Exploration of the Sea, Special Scientific Meeting on Herring Tagging and Results, 1954), Hourston (1981, 1982a), and the annual reports of the British Columbia Department of Fisheries (1946–1952). Hourston and Haegele (1980) give a general description of this fish species.

Briefly, the migrating stocks of herring of British Columbia form a series of intermixing groups that can be divided into seven "populations" on the basis of mean vertebral count, spawning areas, and feeding areas (Figure 1). Between 1937 and 1967 over 890,000 adult fish were tagged. Most of the tagging took place near the spawning grounds after spawning was complete (March–May) using coded metal tags inserted into the body cavity. Each tagging event consisted of about 2,000 fish and was conducted on discrete schools or larger bodies of fish over several days in a number of subareas with each population (Hourston, 1981). The effect of any nonindependence in behavior caused by sampling a single migrating school is thought to be minimal given the large number of tags released and the admixture of schools on offshore feeding grounds.

Stevenson (unpublished manuscript cited previously) reported a substantial initial tagging mortality but believed that within 13 or 14 weeks, tagging mortality became negligible. This acute mortality
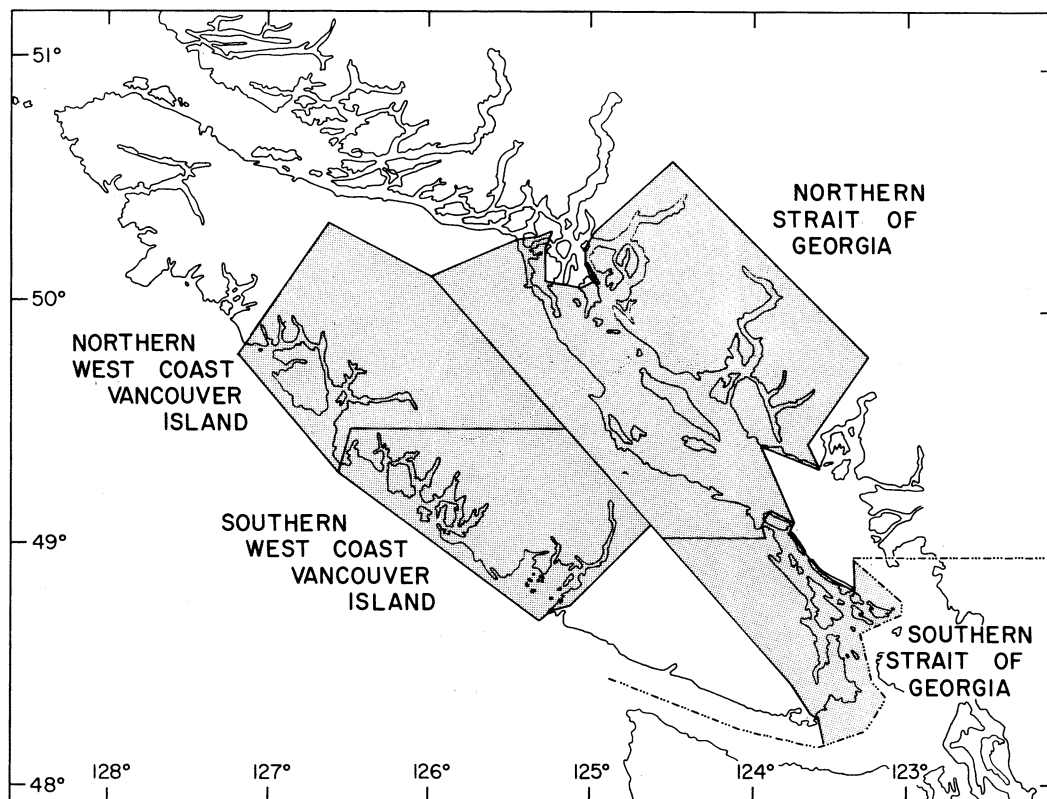
Figure 1. Management divisions of the reduction fishery in British Columbia.

has the effect of reducing the "effective" number of tagged fish released. If the mortality was similar over all releases in all years, then the estimates of the recovery rates will be biased downward, but estimates of the survival/migration components will be unaffected.

After spawning and tagging, the herring migrate to offshore feeding areas (May–September) and then return to and congregate in a few very large schools in inshore waters (October–February) where the reduction fishery occurred prior to 1968. In late February and March, the large schools separate into smaller bodies of fish, which then migrate the short distances to the various spawning grounds utilized by each population. It is not known whether the assumption of Markovian behavior in the fish was reasonable, although Hourston (1981) did not find any increase in the rate of movement of adult fish out of the tagging area with time. Conversely, juveniles tagged near the spawning grounds displayed a greater proclivity to migrate to other areas in the subsequent year.

Following capture, fish were landed at reduction plants where tags were first recovered by electronic detectors on the conveyor belts that brought the fish into the plants. These recoveries could easily be traced back to the vessel that delivered the fish and the location of the capture of the tagged fish could easily be determined. Tags that escaped detection by this means or passed through plants without detectors were recovered during processing by magnets in the meal lines. The location of the capture of the fish carrying the tag could be traced only to the location of all fish captured and processed by the plant at this time. Some plants processed fish from only small areas of capture, and so these magnet-recoveries could be assigned with confidence to an area of capture. The efficiency of detectors and magnets in the various plants in recovering tags was assessed periodically by placing a known number of "test" tags into fish entering the plant. Stevenson reported efficiencies between 60% and 90%.

Two different "types" of data are available from these tagging experiments. The raw data consist of the actual counts of the detector-recoveries and the known magnet-recoveries. Many studies use "adjusted" counts that are obtained by adjusting the raw detector-recoveries by the proportion of the catch at the plant that was searched and then adding the known magnet-recoveries. Both types of data were analyzed with similar results. Only the results from the raw data will be given. Because the effect of the adjustments is to inflate the number of recoveries, estimated standard errors from analyses using the adjusted data will be too precise. Similarly, goodness-of-fit and tests among models

Table 4

Raw data for the number of fish tagged and recovered off the West Coast of Vancouver Island
(N *refers to* N-WCVI; S *refers to* S-WCVI)

Year	Stratum	Number released	1946 S	1946 N	1947 S	1947 N	1948 S	1948 N	1949 S	1949 N	1950 S	1950 N	1951 S	1951 N	Total S	Total N
1946	S	14,921	120	26	69	12	0	4	3	0	1	0	0	0	193	42
	N	13,227	30	128	5	36	1	33	0	2	0	1	0	2	36	202
1947	S	21,763			1,117	106	15	92	53	3	13	0	9	0	1,207	201
	N	8,638			48	126	3	115	2	2	1	1	0	9	54	253
1948	S	14,798					39	96	78	5	33	0	20	0	170	101
	N	17,149					4	588	7	16	0	21	0	42	11	667
1949	S	10,686							197	3	86	0	44	0	327	3
	N	11,170							39	14	0	58	0	80	39	152
1950	S	10,036									230	6	44	0	274	6
	N	16,620									105	157	0	327	105	484
1951	S	12,660											123	0	123	0
	N	8,109											0	263	0	263
Total	S		120	26	1,186	118	54	192	331	11	363	6	240	0		
	N		30	128	53	162	8	736	48	34	106	238	0	723		

Log-likelihood for a model with no structure: −25,513.3 with 84 parameters

will have inflated Type I error rates. As far as can be determined, the inflation factor is on the order of 2 to 4, i.e., the "adjusted" tag-recoveries reported are 2–4 times the actual number of tags reported.

Not every population was tagged in every year. However, between 1945–1946 and 1951–1952, tagging did take place in every year in the North and South portions of the West Coast of Vancouver Island (N-WCVI, S-WCVI, respectively) and the North and South portions of the Gulf of Georgia (N-GULF, S-GULF, respectively). One assumption of the models of this paper is that animals do not temporarily migrate to new areas only to return in later years. Stevenson showed that less than 3% of recoveries of fish tagged in these four areas occurred outside of these four areas with most of the "rogue" recoveries occurring from fish tagged in the N-GULF and caught in a neighboring area. Given the approximate 25% year-to-year survival rate of the herring (Hourston and Haegele, 1980), the number of fish that return to these four areas after an absence of one or more years is small and can be ignored. As well, Hourston (1982b) estimated that combined stocks on the West Coast of Vancouver Island had a 93% homing rate. Consequently, we can focus upon estimating the migration rates between N-WCVI and S-WCVI.

The number of fish tagged and released and the raw recoveries for the North and South portion of WCVI are shown in Table 4. The log-likelihood (excluding constant terms) for a model with no structures is also reported.

The full model allowing for time-specific tag-recovery and survival/migration rates was fit. Estimates and estimated standard errors are presented in Table 5. Note that in some cases, the MLEs occurred on the boundary of the parameter space (e.g., migration/survival estimates of 0 or 1), in which case large-sample theory does not hold and consequently no estimated standard errors are reported. An examination of the difference between the observed and expected recoveries shows the model fit well except for data collected in 1952. Consequently, this model is assumed to be approximately correct.

The tag-recovery rates are not of primary interest and will be only briefly discussed. The estimates would normally reflect the product of the proportion of the catch searched, detector efficiency, and fishing mortality. In this case, they also contain a term for the initial tagging-induced acute mortality. Given that it is estimated that about one-third of the catch was searched, that the detector efficiency was 60%–90%, that the fishery in the 1940s caught about 50% of the available biomass, and that a 60% initial tagging mortality existed, the estimates are reasonable. The standard errors indicate that a good precision was obtained.

The survival/migration parameters estimate the product of both survival and migration between successive tagging times. For example, consider the estimate for 1947–1948:

$$\hat{\mathbf{S}}_{1947-1948} = \begin{bmatrix} .3771 & .0361 \\ .0000 & .3980 \end{bmatrix}.$$

Table 5
Parameter estimates and estimated standard errors from the full model

Year	Stratum of origin	Estimates Destination stratum S	N	Estimated s.e. Destination stratum S	N
Migration/survival rates					
1946–47	S	.0881	.0075	.0109	.0096
	N	.0000	.1702	—	.0212
1947–48	S	.3771	.0361	.0467	.0144
	N	.0000	.3980	—	.0353
1948–49	S	.3010	.0000	.0295	—
	N	.0000	.2820	—	.0346
1949–50	S	.4301	.0000	.0426	—
	N	.0000	.3480	—	.0316
1950–51	S	.7216	.0000	.0984	—
	N	.0000	.6901	—	.0561
Tag-recovery rates					
1946	S	.0080	.0017	.0007	.0003
	N	.0023	.0097	.0004	.0008
1947	S	.0514	.0050	.0015	.0005
	N	.0049	.0149	.0007	.0012
1948	S	.0023	.0068	.0003	.0007
	N	.0004	.0343	.0001	.0014
1949	S	.0184	.0006	.0012	.0002
	N	.0028	.0020	.0004	.0003
1950	S	.0200	.0003	.0013	.0001
	N	.0047	.0105	.0005	.0007
1951	S	.0092	.0000	.0008	—
	N	.0000	.0294	—	.0019

Log-likelihood of fitted model: −25,592.6 with 44 parameters

Table 6
Estimated stock sizes of the herring populations

Year	Stratum	Estimated pop. (tonnes)	Est. s.e. size (tonnes)	Year	Stratum	Estimated pop. (tonnes)	Est. s.e. size (tonnes)
1946	S	33,624	449	1949	S	24,118	325
	N	4,472	341		N	38,999	707
1947	S	39,217	338	1950	S	35,097	327
	N	22,905	392		N	11,226	552
1948	S	27,015	304	1951	S	23,033	365
	N	33,963	758		N	19,027	775

This implies that an estimated 37.71% of the herring migrate from and survive to return to the S-WCVI; an estimated 3.61% migrate and survive from S-WCVI to N-WCVI; no migration is estimated to take place from the N-WCVI to the S-WCVI; and 39.80% migrate from and survive to return to the N-WCVI. The overall net survival rate for the herring tagged in S-WCVI is estimated to be 37.71% + 3.61% = 41.32%; i.e., over 40% of the herring in the S-WCVI are estimated to have survived between spawning in 1947 and spawning in 1948. The biologically unrealistic high estimates of survival in the 1950–1951 season are explainable by looking at the raw data. From Table 4, 263 recoveries from 8,109 releases were made in N-WCVI, corresponding to about a 3% recovery rate. Taking the 327 tags from the 1950 release report recovered in 1951, and assuming a similar recovery rate, implies that $327/.03 \approx 11,000$ tagged fish were alive one year after tagging compared to the 16,000 released! The estimated standard errors indicate that the estimates of return have a coefficient of variation of about 10%, whereas those of migration between strata have coefficients of about 50% because they are so small.

External estimates of the stock sizes and their estimated standard errors are also available for these time periods (Table 6). These can be used to estimate the immigration rates (Table 7). These estimate

Table 7
Estimates and estimated standard errors of the immigration rates

| | | Estimates | | Estimated s.e. | |
| | | Destination stratum | | Destination stratum | |
Year	Stratum of origin	S	N	S	N
		Immigration (tonnes)			
1946–47	S	2,963	251	370	322
	N	0	761	—	111
1947–48	S	14,788	1,414	1,834	566
	N	0	9,116	—	824
1948–49	S	8,130	0	803	—
	N	0	9,576	—	1,193
1949–50	S	10,374	0	1,036	—
	N	0	13,570	—	1,257
1950–51	S	25,325	0	3,463	—
	N	0	7,747	—	736
		Immigration (proportions read in columns)			
1946–47	S	1.000	.248	—	.241
	N	.000	.752	—	.241
1947–48	S	1.000	.134	—	.047
	N	.000	.866	—	.047
1948–49	S	1.000	.000	—	—
	N	.000	1.000	—	—
1949–50	S	1.000	.000	—	—
	N	.000	1.000	—	—
1950–51	S	1.000	.000	—	—
	N	.000	1.000	—	—

the number of tonnes and relative proportions of the fish that were alive in year i that return to the spawning grounds in year $i + 1$. It does not include recruitment. (Standard errors are not computed if an estimate used in the calculation fell on the boundary of a parameter space.)

Estimates of the tag-reporting rate either are not available or in the few cases where data were available, are thought to have poor precision since they must be estimated using the product of the tagging-induced mortality, the detector efficiency, and the proportion of the catch searched. Hence, estimates of harvest-derivation are not reported.

7. Discussion

Ordinary tag-recovery data are theoretically adequate to estimate the fundamental parameters in these models but inference is not completely satisfactory. The parameters of most biological interest, the survival/migration rates (S_i) are not estimated well. They have poor precision and, in many cases, are nearly nonidentifiable. This is caused by the convolution of these parameters between the time of release and recovery in the model formulation and the generally low tag-recovery rates present in practice. As a consequence, the derived parameters of emigration, immigration, and harvest-derivation also have poor precision, and the power to differentiate among models is poor.

Data requirements are stringent; releases must occur in all strata over a number of years along with recoveries in the same period of time. The practice of tagging in different areas in different years is not recommended because it is impossible to estimate most parameters unless very strong assumptions of equality among parameters over time and among areas are made.

The assumptions of the model should be checked carefully. One possible explanation for the anomalous values in the herring example is the nonindependence of the tagged fish. The tagged fish from one part of the release may have remained in a tight school that happened to be harvested together. The recoveries would have been inflated dramatically by the adjustment process. The assumption of equal survival/migration and tag-recovery rates must also be examined carefully. As found in Pollock and Raveling (1982) and Nichols et al. (1982), the effect of heterogeneity in the parameters among animals may introduce bias into the estimates.

Large-scale marking or tagging studies are invariably fraught with logistical difficulties, which results in either minor or serious departures from model assumptions. Nevertheless, as in the example

presented above, the parameter estimates, although crude, provide immensely important information for improved management of the resource under study. Merely knowing that the migration rates between the N-WCVI and S-WCVI herring stocks is low (less than 25%) has important implications for management of the resource and conservation of what appear to be two relatively distinct as opposed to a single panmictic stock. As such, results from what may appear to be poorly conceived or implemented tagging studies should not be dismissed out of hand due to what appear to be failures of model assumptions. The enormous costs associated with these studies warrant at least a cursory investigation of the study results, which may yield significant biological insights into the population behaviour.

The experiment can be improved by obtaining ancillary information as to where the animal has migrated between release and recovery. This can be accomplished by additional sightings (without recovery) between release and ultimate recovery. Mardekian and McDonald (1981) suggested a simple method of combining live recaptures and tag-returns using only final recapture in simple banding studies. However, Brownie and Pollock (1985) pointed out that this may be very inefficient. Schwarz (unpublished Ph.D. thesis cited previously) showed how to combine resighting and recapture data in three other types of migration models. The situation in the models of this paper is much more complex. Currently the likelihood must reflect all possible paths between the stratum of release and stratum of recovery. For example, if there are three strata, then there are nine possible paths between a release in stratum 1 in year 1 and a recovery in stratum 1 between years 3 and 4. If the animal is also sighted in stratum 1 at the time of tagging in year 2, the number of paths is reduced to 3. As can be appreciated, the likelihood incorporating resightings is complex but could be formulated by treating a resighting as another form of tag-release at a later time period in much the same way that Burnham (1991) treated multiple recaptures as a series of releases and subsequent recaptures. Numerical methods will be necessary to obtain parameter estimates.

The time of resightings is important. Since the parameters of most interest are the net movements from tagging time to tagging time, it is preferable to perform the additional sightings at *tagging time*. In this case, the actual stratum of the animal at tagging time in year i is then known and the number of possible migration paths for an animal between release and recovery is reduced. The sighting of an animal in a stratum during the recovery period does not yield as much information since the animal may have migrated after the tagging time but before the time of sighting. The model with these additional sightings at tagging time is now closer in form to that of Arnason (1972, 1973) and Seber (1982, p. 555) since sightings at tagging time may be considered as "captures" and "releases" at a point in time. If the animal can be sighted every year between release and recovery, then the complete migration history of the animal will be known, and the relatively simple method of inference in Markov chains (Basawa and Rao, 1980) can be used. This may be possible if the animals are fitted with a radiotelemetry device. Furthermore, if the "sightings" take place in a small period of time (rather than throughout the year), the methods of Arnason (1972, 1973) can be used since the "sighting" of an animal from its radiotelemetry device will be similar to a recapture and release in his capture–recapture formulation. With modern technology, inexpensive and reliable devices that permit the monitoring of an animal as it migrates among strata between release and recovery may be the most cost-effective method of obtaining good estimates of the survival/migration rates.

8. Computer Software

A computer program that can be used for the analyses described in this paper is available from the first author. This program is written in ANSI FORTRAN-77 and must be linked with IMSL (1987) routines at the user's installation. The documentation available with the program gives detailed explanations on how to format the data and how to write the subroutines required for other reduced models. The program currently runs on an IBM-compatible mainframe system under the MVS-XA operating system, but could be easily adapted to run on a microcomputer.

RÉSUMÉ

Des données de reprises d'individus marqués sont utilisées pour estimer les taux de migration au sein d'un ensemble de strates. La formulation du modèle est une extension matricielle simple de la formulation d'une expérience de reprise d'individus marqués discutée par Brownie et al. (1985,

Statistical Inference from Band-Recovery Data—A Handbook, 2nd edition, Washington, D.C.: U.S. Department of the Interior). L'estimation est rendue plus difficile par la convolution des paramètres entre le lâcher et la reprise, qui peut rendre imprécises les estimations des paramètres de survie et de migration. Des paramètres dérivés concernant l'émigration, l'immigration, les taux de prélèvement, et la survie totale nette sont aussi estimés. Les modèles sont appliqués à l'estimation de migration du Harong du Pacifique entre lieux de frai au large de la côte ouest du Canada. Si les animaux peuvent être relachés après recapture le modèle correspond, pour ses composantes de migration et de survie, à celui de Arnason (1972, *Researches in Population Ecology* **13**, 97–113). Cette correspondence est developpée, et conduit à des estimateurs plus efficaces des paramètres.

REFERENCES

Aitchison, J. and Silvey, S. D. (1958). Maximum likelihood estimation of parameters subject to constraints. *Annals of Mathematical Statistics* **29**, 813–829.

Arnason, A. N. (1972). Parameter estimation from mark–recapture experiments on two populations subject to migration and death. *Researches in Population Ecology* **13**, 97–113.

Arnason, A. N. (1973). The estimation of population size, migration rates, and survival in a stratified population. *Researches in Population Ecology* **15**, 1–8.

Basawa, I. V. and Rao, L. S. P. (1980). *Statistical Inference for Stochastic Processes*. New York: Academic Press.

Brownie, C., Anderson, D. R., Burnham, K. P., and Robson, D. S. (1985). *Statistical Inference from Band-Recovery Data—A Handbook*, 2nd edition. U.S. Fish and Wildlife Service, Resource Publication No. 156. Washington, D.C.: U.S. Department of the Interior.

Brownie, C. and Pollock, K. H. (1985). Analysis of multiple capture–recapture data using band-recovery methods. *Biometrics* **41**, 411–420.

Burnham, K. P. (1991). A unified theory for release–resampling of animal populations. In *Proceedings of the 1990 Taipei Symposium in Statistics*, M.-T. Chao and P. E. Cheng (eds), 11–36. Taipei, Taiwan: Institute of Statistical Science, Academia Sinica.

Chapman, D. G. and Junge, C. O. (1956). The estimation of the size of a stratified animal population. *Annals of Mathematical Statistics* **27**, 375–389.

Conroy, M. J. and Williams, B. K. (1984). A general methodology for maximum likelihood estimation from band-recovery data. *Biometrics* **40**, 739–748.

Crissey, W. F. (1955). The use of banding data in determining waterfowl migration and distribution. *Journal of Wildlife Management* **19**, 75–84.

Darroch, J. N. (1961). The two-sample capture–recapture census when tagging and sampling are stratified. *Biometrika* **48**, 241–260.

Don, F. J. H. (1985). The use of generalized inverses in restricted maximum likelihood estimation. *Linear Algebra and Its Applications* **70**, 225–240.

Graybill, F. A. (1985). *Matrices with Applications in Statistics*. Belmont, California: Wadsworth.

Hestbeck, J. B., Nichols, J. D., and Malecki, R. A. (1991). Estimates of movement and site-fidelity using mark–resight data of wintering Canada geese. *Ecology* **72**, 523–533.

Hourston, A. S. (1981). Tagging and tag recovery data for British Columbia herring, 1937–1967. *Canadian Data Report of Fisheries and Aquatic Sciences* **308**.

Hourston, A. S. (1982a). Effects of the number of years tagged fish were at large on homing to British Columbia herring management units. *Canadian Technical Report of Fisheries and Aquatic Sciences* **1056**.

Hourston, A. S. (1982b). Homing by Canada's West Coast herring to management units and divisions as indicated by tag recoveries. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1414–1422.

Hourston, A. S. and Haegele, C. W. (1980). Herring on Canada's Pacific Coast. *Canadian Special Publication of Fisheries and Aquatic Sciences* **48**.

I.M.S.L. (1987). International Mathematics and Statistics Libraries. Houston: Author.

Mardekian, S. Z. and McDonald, L. (1981). Simultaneous analysis of band-recovery and live-recapture data. *Journal of Wildlife Management* **45**, 789–792.

Nel, D. G. (1980). Matrix differentiation in statistics. *South African Statistical Journal* **14**, 137–193.

Neudecker, H. (1967). On matrix procedures for optimizing differentiable scalar functions of matrices. *Statistica Neerlandica* **21**, 101–107.

Nichols, J. D., Stokes, S. L., Hines, J. E., and Conroy, M. J. (1982). Additional comments on the analysis of homogeneous survival rates in modern bird banding estimation models. *Journal of Wildlife Management* **46**, 953–962.

Pollock, K. H. and Raveling, D. G. (1982). Assumptions of modern band-recovery models with emphasis on heterogeneous survival rates. *Journal of Wildlife Management* **46**, 88–98.

Schwarz, C. J., Burnham, K. P., and Arnason, A. N. (1988). Post-release stratification in band-recovery models. *Biometrics* **44**, 765–785.

Seber, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters*, 2nd edition. London: Griffin.
White, G. C. (1983). Numerical estimation of survival rates from band-recovery and biotelemetry data. *Journal of Wildlife Management* **47**, 716–728.

APPENDIX A

Maximum Likelihood Estimation

The likelihood is constructed as a simple product of multinomial distributions; however, the individual cell probabilities are complex because of the convolution of the intermediate survival/migration and band-recovery rates between release and recovery. The likelihood can be written as

$$L = \prod_{i=1}^{k} \prod_{s=1}^{a} \frac{N_i^s!}{(N_i^s - R_i^s)!} (1 - p_{i:}^2)^{N_i^s - R_{i:}^s} \prod_{j=i}^{l} \prod_{t=1}^{a} \frac{(p_{ij}^{st})^{R_{ij}^{st}}}{R_{ij}^{st}!},$$

where p_{ij}^{st} are the elements of the matrix $\mathbf{p}_{ij} = \mathbf{S}_i \mathbf{S}_{i+1} \mathbf{S}_{i+2} \cdots \mathbf{S}_{j-1} \mathbf{f}_j$, being the probability that an animal released in stratum s in year i is recovered in stratum t in year j as shown in Table 2.

The rules of matrix differentiation (Neudecker, 1967; Nel, 1980; Graybill, 1985) can be used to find explicitly the first-order conditions for the MLEs:

$$\frac{\partial L}{\partial \mathbf{f}_i} = \mathbf{0} = \sum_{r=1}^{i} (\hat{\mathbf{S}}_r \cdots \hat{\mathbf{S}}_{i-1})' (\mathbf{R}_{ri} \div \hat{\mathbf{S}}_r \cdots \hat{\mathbf{S}}_{i-1} \hat{\mathbf{f}}_i - [(\mathbf{N}_r - \mathbf{R}_r.\mathbf{1}) \div (\mathbf{1} - \hat{\rho}_r \mathbf{1})]\mathbf{1}'),$$

$$\frac{\partial L}{\partial \mathbf{S}_k \mathbf{S}_{k+1} \cdots \mathbf{f}_l} = \mathbf{0} = \sum_{r=1}^{k} (\hat{\mathbf{S}}_r \cdots \hat{\mathbf{S}}_{k-1})' (\mathbf{R}_{ri} \div \hat{\mathbf{S}}_r \cdots \hat{\mathbf{S}}_{k-1} \widehat{\mathbf{S}_k \mathbf{S}_{k+1} \cdots \mathbf{f}_l} - [(\mathbf{N}_r - \mathbf{R}_r.\mathbf{1}) \div (\mathbf{1} - \hat{\rho}_r \mathbf{1})]\mathbf{1}'),$$

$$\frac{\partial L}{\partial \mathbf{S}_i} = \mathbf{0} = \sum_{r=1}^{i} \sum_{c=i+1}^{l} (\hat{\mathbf{S}}_r \cdots \hat{\mathbf{S}}_{i-1})' (\mathbf{R}_{rc} \div \hat{\mathbf{S}}_r \cdots \hat{\mathbf{S}}_{c-1} \hat{\mathbf{f}}_c) (\hat{\mathbf{S}}_{i+1} \hat{\mathbf{S}}_{i+2} \cdots \hat{\mathbf{f}}_c)'$$

$$- \sum_{r=1}^{i} (\hat{\mathbf{S}}_r \cdots \hat{\mathbf{S}}_{i-1})' [(\mathbf{N}_r - \mathbf{R}_r.\mathbf{1}) \div (\mathbf{1} - \hat{\rho}_r \mathbf{1})]\mathbf{1}' \hat{\rho}_{i+1},$$

where $\hat{\rho}_i = \hat{\mathbf{f}}_i + \hat{\mathbf{S}}_i \hat{\mathbf{f}}_{i+1} + \hat{\mathbf{S}}_i \hat{\mathbf{S}}_{i+1} \hat{\mathbf{f}}_{i+2} + \cdots + \hat{\mathbf{S}}_i \hat{\mathbf{S}}_{i+1} \cdots \widehat{\mathbf{S}_{k-1} \hat{\mathbf{S}}_k \mathbf{S}_{k+1}} \cdots \hat{\mathbf{f}}_l$ is the estimated probability of recovering an animal during the entire experiment after it is released in year i.

The Hessian is extremely complex to write out explicitly; however, it can be computed using methods similar to those in Conroy and Williams (1984). For example, if θ represents the vector of fundamental parameters, the estimated information matrix can be computed as

$$\sum_{i=1}^{k} \sum_{s=1}^{a} N_i^s \frac{1}{1 - p_{i:}^s} \frac{\partial p_{i:}^s}{\partial \theta} \left(\frac{\partial p_{i:}^s}{\partial \theta'}\right) + \sum_{i=1}^{k} \sum_{s=1}^{a} N_i^s \sum_{j=i}^{l} \sum_{t=1}^{a} \frac{1}{p_{ij}^{st}} \frac{\partial p_{ij}^{st}}{\partial \theta} \left(\frac{\partial p_{ij}^{st}}{\partial \theta'}\right),$$

where $\partial p_{ij}^{st}/\partial \theta$ is easily found using the rules for matrix differentiation.

Given initial starting values, the method of scoring may now be used to obtain the MLEs. The methods of Don (1985) and Aitchison and Silvey (1958) may be used to modify the method of scoring when restrictions are placed upon the parameters. As usual, the estimated information matrix at the last iteration may be used to estimate the asymptotic variances and covariances of the estimates.

APPENDIX B

Extension of Moment Estimator to Capture–Recapture Experiments

The moment estimator for the full model of this paper can be extended to estimating migration rates in capture–recapture studies (Arnason, 1972, 1973; Seber, 1982, p. 555) in much the same way that the estimators from simple tag-recovery experiments can be extended to capture–recapture studies (Brownie et al., 1985, §8.2). We will show that the extension of the moment estimator of this paper to capture–recapture studies uses more information than the one presented in Seber (1982, p. 555) and is, therefore, likely to be more efficient.

In capture–recapture studies, animals are released at a point in time and captured at a point in time, unlike tag-recovery experiments where recoveries take place over a period of time. As well, an animal may be captured more than once in a capture–recapture study, but may be recovered only once in a tag-recovery study. Nevertheless, by a suitable redefinition of the parameters, and a slight

change in data representation, tag-recovery methods may be used to estimate the migration parameters in capture–recapture studies.

Let N_i^s represent the number of animals released at time i in stratum s. This will include those animals that were captured at time i and are being released.

The R_{ij}^{st} now represent the number of animals released in stratum s at time i and *next* captured in stratum t at time j. In capture–recapture studies, $\mathbf{R}_{ii}$ must, by definition, be zero. If an animal is captured at time j, it then becomes a member of N_j and is "removed" from the $\mathbf{N}_i$ cohort (just as a recovery of an animal removes it from the $\mathbf{N}_i$ cohort in tag-recovery studies). Hence only the first recaptures of animals released from $\mathbf{N}_i$ contribute to $\mathbf{R}_{i,i+1}$, $\mathbf{R}_{i,i+2}$, ..., $\mathbf{R}_{i,l}$. But an animal that is captured $v + 1$ times contributes to exactly v of the $\mathbf{R}_{ij}$ and to $v + 1$ of the $\mathbf{N}_i$. The symbolic data representation of the matrices in the case of four sampling times is shown in Table B.1. Note that captures at the first sample time are required only to provide a set of marked animals that will be released back to the population.

Capture–recapture studies require the use of two parameter matrices, ϕ_i and $\mathbf{p}_i$. The elements of ϕ_i (ϕ_i^{st}) represent the probability that an animal alive in stratum s at time i is also alive in stratum t at time $i + 1$. Hence ϕ_i contains both migration and mortality components. Again, it is assumed that if animals migrate to other strata, they do so permanently. The elements of $\mathbf{p}_i$ (p_i^s) represent the probability that an animal alive in stratum s at time i will be captured. All animals in stratum s at time i, regardless of previous migrations or previous captures, are assumed to have the same probability of capture.

The expected number of recoveries in the capture–recapture formulation in the case of four sample times is displayed in Table B.2. The expected number of recoveries involves a convolution of the intermediate survival/migration and capture probabilities between recaptures.

If we compare Table B.2 with Table 2, we note that the diagonal elements of Table B.2 are all zero, but the table has the same general form as Table 2. Table B.3 is a reformulation of Table B.2 using the tag-recovery notation and from it the following equivalences can be made:

$$\mathbf{f}_i = \phi_{i-1}\mathbf{D}(\mathbf{p}_i),$$

$$\mathbf{S}_i = \phi_{i-1}\mathbf{D}(1 - \mathbf{p}_i).$$

By writing out the expected value of the row and column totals, we can develop the following moment estimators:

$$\tilde{\mathbf{f}}_i = \mathbf{D}(\mathbf{N}_{i-1})^{-1}\mathbf{R}_{i-1,\cdot}(\mathbf{T}_i - \mathbf{R}_{i\cdot})^{-1}\mathbf{R}_{\cdot i},$$

$$\tilde{\mathbf{S}}_i = \mathbf{D}(\mathbf{N}_{i-1})^{-1}\mathbf{R}_{i-1,\cdot}(\mathbf{T}_i - \mathbf{R}_{i\cdot})^{-1}(\mathbf{Z}_i - \mathbf{R}_{i\cdot})\mathbf{R}_{i\cdot}^{-1}\mathbf{D}(\mathbf{N}_i).$$

Note that the estimators have a slightly different form from those presented in Section 4.2; this is caused by the empty main diagonal of the data in Table B.1.

Table B.1
Symbolic representation of the number of animals released in stratum s at time i and captured for the next time in stratum t at time j in the case of four sampling times in a capture–recapture context

Time released	Number released	Number captured for the next time at sampling time			
		1	2	3	4
1	$\mathbf{N}_1$	—	$\mathbf{R}_{12}$	$\mathbf{R}_{13}$	$\mathbf{R}_{14}$
2	$\mathbf{N}_2$		—	$\mathbf{R}_{23}$	$\mathbf{R}_{24}$
3	$\mathbf{N}_3$			—	$\mathbf{R}_{34}$

$\mathbf{N}_i$ are $a \times 1$ vectors with elements $[N_i^s]$ and $\mathbf{R}_{ij}$ are $a \times a$ matrices with elements $[R_{ij}^{st}]$. The number of animals never recaptured is not shown, but is easily obtained by subtraction.

Table B.2
The probabilities that an animal released in stratum s at time i is captured for the next time in stratum t at time j in the case of four sampling times in a capture–recapture context

Time released	Number released	Probability of recapture at this sampling time			
		1	2	3	4
1	$\mathbf{N}_1$	—	$\phi_1\mathbf{D}(\mathbf{p}_2)$	$\phi_1\mathbf{D}(1 - \mathbf{p}_2)\phi_2\mathbf{D}(\mathbf{p}_3)$	$\phi_1\mathbf{D}(1 - \mathbf{p}_2)\phi_2\mathbf{D}(1 - \mathbf{p}_3)\phi_3\mathbf{D}(\mathbf{p}_4)$
2	$\mathbf{N}_2$		—	$\phi_2\mathbf{D}(\mathbf{p}_3)$	$\phi_2\mathbf{D}(1 - \mathbf{p}_3)\phi_3\mathbf{D}(\mathbf{p}_4)$
3	$\mathbf{N}_3$			—	$\phi_3\mathbf{D}(\mathbf{p}_4)$

$\mathbf{N}_i$ are $a \times 1$ vectors with elements $[N_{i1}^s]$; $\mathbf{p}_i$ are $a \times 1$ vectors with elements $[p_i^s]$; ϕ_i are $a \times a$ matrices with elements $[\phi_{ij}^{st}]$. The probability of never recapturing an animal is not shown, but is easily obtained by subtraction.

Table B.3
The probabilities that an animal released in stratum s at time i is captured for the next time in stratum t at time j in the case of four sampling times in a capture–recapture context reformulated using tag-recovery notation

Time released	Number released	Probability of recapture at this sampling time			
		1	2	3	4
1	N_1	—	f_2	$S_2 f_3$	$S_2 S_3 f_4$
2	N_2		—	f_3	$S_3 f_4$
3	N_3			—	f_4

N_i are $a \times 1$ vectors with elements $[N_i^s]$; f_i are $a \times a$ matrices with elements $[f_i^{st}]$; S_i are $a \times a$ matrices with elements $[S_{ij}^{st}]$. The probability of never recapturing an animal is not shown, but is easily obtained by subtraction.

Now, using the equivalences above, we obtain the moment estimators:

$$\tilde{\phi}_{i-1} = \tilde{S}_i + \tilde{f}_i, \quad i = 2, \ldots, k,$$
$$\tilde{p}_i = \tilde{\phi}_{i-1}^{-1} \tilde{f}_i \mathbf{1}. \tag{B.1}$$

In the case of sampling on three occasions, the above estimators reduce to those of Arnason (1973, eq. 1.11). Seber (1982, pp. 555–559) suggested that if the experiment has more than three sample times, the estimators of Arnason (1973) be applied to successive groups of three sample times, i.e., use times 1, 2, and 3 to estimate ϕ_1; use times 2, 3, and 4 to estimate ϕ_2; etc. However, that method ignores all information on captures outside of the selected sampling times, whereas these new estimators do not. As a consequence, it is expected that the proposed estimators will be more efficient.

One could obtain MLEs of the capture–recapture parameters by using the computer program developed for the models of this paper by finding $\hat{f}_i$ and $\hat{S}_i$ of Table B.3, and then using the equivalence relations B.1 to obtain the MLEs for ϕ_{i-1} and p_i. However, this procedure is not recommended due to the potential numerical difficulties caused by the high sampling correlations in the estimates. Numerical procedures should be used to obtain the MLEs of the capture–recapture parameters directly.